Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands

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Abstract

Recent, high-resolution palaeoecological records are changing the traditional picture of post-glacial vegetation succession in the Iberian Peninsula. In addition to the influence of Lateglacial and early Holocene climatic changes, other factors are critical in the course of vegetation development and we observe strong regional differences. The floristic composition, location and structure of glacial tree populations and communities may have been primary causes of vegetation development. Refugial populations in the Baetic cordilleras would have been a source, but not the only one, for the early Lateglacial oak expansions. From Mid to Late Holocene, inertial, resilient, and rapid responses of vegetation to climatic change are described, and regional differences in the response are stressed. The role of fire, pastoralism, agriculture, and other anthropogenic disturbances (such as mining), during the Copper, Bronze, Iberian, and Roman times, is analysed. The implications of ecological transitions in cultural changes, especially when they occur as societal collapses, are discussed.

Key words: palaeoecology, palaeogeography, palaeobotany, Iberia, Quaternary, Holocene

INTRODUCTION

Over the last few years, the number of Lateglacial and Holocene records in the Iberian Peninsula has increased considerably. This is particularly true in the case of pollen sequences (Carrión et al. 2007, Fletcher et al. 2007, Muñoz-Sobrino et al. 2007, González-Sampériz et al. 2008) and to a lesser extent in the case of anthracological (Badal et al. 2008) and other macrobotanical records (García-Amorena et al. 2007, Postigo et al. 2008). It was only some decades ago that the publication of palaeoecological sequences without absolute dating was relatively frequent (Dupré 1988, Carrión 1992, Martínez-Atienza 1999). However the chronological control of palaeo-records has improved considerably, probably due to the consolidation of research groups and a better access to research funding programmes.

In this context, the present work aims to understand the vegetation change patterns, and their causes, during the Late Quaternary in the Iberian Peninsula and the Balearic Islands. We examine two different time periods: first, the Lateglacial (14,700-11,500 cal. yr BP) and early Holocene (after 11,500 cal. yr BP), when the deglaciation process was concurrent with global warming (Bradley 2008). In this regard we assess to what extent this multimillennial event was the main controlling factor in the vegetation response, or if instead autoecological processes and high regional topographical variability were more important in regulating the vegetation changes produced (Bennett and Willis 1995). Our second scenario is defined by the appearance of human activity indicators in the palaeoecological record. The emergence of anthropogenic events is detected in some sequences from the Mid-Holocene while it is delayed in others (Carrión et al. 2009).

This paper is the first attempt to review the topic for the whole of the Iberian Peninsula. This is not an easy task, given the physiographical complexity of this area and the information gaps both in time periods and provinces,. We are conscious that the adopted duality (expected *versus* unexpected) may be considered artificial: making a visual inspection of the palaeo-records reveals that there is a continuum in vegetation histories. However, dichotomizing serves a purpose: separating the histories of directional change through time from those that exhibit apparently accidental trajectories, including those that lack significant change. This approach is a test of how to conceptualize the apparently chaotic picture of vegetational developments (Carrión et al. 2000). Often being too busy with the analytical work, we have concentrated on the gaining of new records over the production of theories. But it is our view that observations and theory should be merged and should interact continuously.

METHODOLOGICAL CONSIDERATIONS

We select palaeoecological sequences that exhibit appropriate chronological control of the main vegetation changes at the resolution needed for this paper´s goal. These are only a small fraction of those available, because a number of palaeobotanical records were never dated or are based on fragmentary information. In this regard, a good part of the pollen-analytical effort has been in vain. Carrión et al. (2009) have reported failures with Quaternary pollen analyses in the Iberian Peninsula, that is, case studies where it was not possible to extract palynomorphs for pollen counting. Compiled failures included 204 sites, from which 48.8% were Holocene, and 31.4% Upper Pleistocene. It is therefore worth pondering what the prevailing paradigm of Late Quaternary vegetation of Iberia would have been had these analyses had been successful. As for the study of past fire activity, the lack of continuous, long charcoal sequences prevents any attempt to assess fire regimes and environmental changes at high time resolution. The reconstruction of fire activity is therefore particularly difficult as a consequence of stratigraphical hiatuses in the archaeological sites and the absence of regional information available from charcoal records, in assemblages that are in any case often biased by human selection during harvesting.

An additional problem precluding palaeoenvironmental correlation as well as an adequate regional picture is the absence of open access national databases and repositories as the EPD (European Pollen Database: http://www.europeanpollendatabase.net/) initiative. Some recent proposals such as PALEODIVERSITAS (http://www.paleodiversitas.org/) and LA FLORA EN EL MUNDO IBERICO (http://www.uv.es/floraiberica) intend to cover this lack of information, although these are still in very preliminary phases. As a consequence of all these aspects, quantitative approaches to regional reconstructions are not available yet.

PALAEOECOLOGICAL INDICATORS

In order to elucidate the influences and controls on vegetation change, we have largely followed the interpretation given by authors in their publications, especially for detecting the timing of the first anthropogenically-influenced changes. When possible, we have considered palaeoecological bio-indicators from the same sedimentary record studied by pollen and/or macroremains. In the palaeobotanical literature for the Late Quaternary in the Iberian Peninsula, these mainly include:

- Aridity crises: pollen of xerophytes and halophytes (*Artemisia, Ephedra*, Chenopodiaceae, *Lygeum, Lycium, Periploca, Ziziphus, Withania, Sideritis, Tamarix,* Aizoaceae), and *Pseudoschizaea* cysts (Pantaleón-Cano et al. 1996, Burjachs et al. 1997, Carrión and Navarro 2002, Dorado-Valiño et al. 2002, Carrión et al. 2003, González-Sampériz et al. 2005, 2008, Gil-García et al. 2007, Fletcher et al. 2007, Valero-Garcés et al. 2000a, 2000b, 2004).
- Increased rainfall / reduced summer drought: *Botryococcus, Pediastrum*, mesophyte pollen, aquatic angiosperm pollen (e.g. *Myriophyllum, Potamogeton, Hydrocotyle, Typha, Alisma, Nuphar, Callitriche*, *Hydrocharis*, *Lemna, Sparganium*), aquatic lycophyte (*Isoetes*) and fern (e.g. *Botrychium, Ophioglossum*) spores (López-Sáez et al. 1998, Carrión and van Geel 1999, Carrión et al. 2001a, 2001b, Carrión 2002, González-Sampériz et al. 2008, 2009, Valero-Garcés et al. 2008, Moreno et al. 2009, in press).
- Soil erosion: Glomaceae chlamydospores, *Pseudoschizaea* (Pantaleón et al. 1996, López-Sáez et al. 2000).
- Trophic conditions: Zygnematales, Desmidiales, *Chara* gyrogonites, Cyperaceae and *Juncus* seeds, Protozoa, cyanobacteria (e.g. *Gloeotrichia, Rivularia*), (Mateus 1989, López-Sáez et al. 1998, 2000), and several of the non-pollen palynomorphs described by van Geel et al. (1981, 1986, 1989) and Carrión and van Geel (1999) such as Types 119, 121, and several other types.

- Agriculture / arboriculture: Cerealia*, Polygonum aviculare, Plantago lanceolata-coronopus, Plantago major-media* types, *Rumex, Cannabis, Vitis, Puccinia* teleutospores and *Thecaphora* basidiospores, occasionally *Juglans, Castanea, Fraxinus* and *Olea* (Stevenson 1985, Stevenson and Moore 1988, Tornqvist et al. 1989, Janssen 1994, van der Knaap and van Leeuwen 1995, Franco-Múgica et al. 1997, Conedera et al. 2004, López-García et al. 1997, Carrión et al. 2001b, 2007, Valero-Garcés et al. 2000a, 2000b, 2004, López-Sáez et al. 2003, González-Sampériz 2004, López-Sáez and López-Merino 2005, Moreno et al. 2008.
- Grazing pressure: Sordariaceae (e.g. *Chaetomium, Sordaria, Podospora, Sporormiella*) ascospores, *Riccia* spores, *Trichuris* eggs, Genisteae, *Plantago, Berberis, Urtica dioica* (Montserrat 1992, Carrión 2001b, Carrión and Navarro 2002, López-Sáez and López-Merino 2007).
- Fire events/ increased burning: macro/microcharcoal particles, Cistaceae, *Erica, Ulex* type, *Asphodelus albus, Anagallis arvensis* type*, Pteridium* spores, *Chaetomium* and other carbonicolous fungal spores (Carrión and van Geel 1999, Carrión 2002, Carrión et al. 2003, 2007, López-Sáez et al. 1998, 2000, Stevenson 2000).

IBERIAN VEGETATION COPING WITH THE LATEGLACIAL-EARLY HOLOCENE CLIMATIC CHANGE

The Iberian Peninsula constitutes a territory where climatic, geological, biogeographical and historical conditions converge to produce environmental heterogeneity, large biological diversity, and a remarkable species and ecosystem richness (Rey Benayas and Schneider 2002). The flora of the Iberian Peninsula and Balearic Islands is located in two biogeographical/climatic regions: Eurosiberian and Mediterranean. The first includes the territories located to the north and the northwest of the Peninsula, with wet, cool climate and without marked summer drought, whereas the rest of the peninsular territory, including the Balearic Islands, enters within the domain of the Mediterranean region, with warm, dry summers and relatively cool, wet winters (Peinado and Rivas-Martínez 1987).

A monographic description of the variability of sequences in the whole Peninsula is beyond the scope of this paper. Rather, given the high diversity of the ecosystems, our synthesis deploys a classification of fast-responding records to increasing temperatures giving place to expected vegetation dynamics (*Expected Sequences*) *versus* those cases less sensitive to climate change (*Unexpected Sequences*). We will also include within “unexpected” those situations which, despite existent vegetation reactivity, the dynamics observed do not correspond with the most frequent cases. Changes in rainfall patterns during the Lateglacial and Early Holocene periods were produced at different spatial scales and there is no agreement about their potential synchronicity in the peninsula (e.g. Valero-Garcés et al. 2004).

EXPECTED SEQUENCES: climate-sensitive vegetation changes

It is expected that during the Lateglacial and Early Holocene, a counterpart of the high-latitude European protocratic and mesocractic phases (Birks 1986) is found in the Iberian Peninsula. On a global scale, during the Last Glacial Maximum (LGM), temperature and precipitation reached minimum values, and north European landscapes were dominated by treeless tundra and prairie-steppe. Refugia for forest vegetation occurred in southern Europe (Finlayson and Carrión 2007, Leroy and Arpe 2007, Médail and Diadema 2009) and particular regions of central Europe (Willis and van Andel 2004), perhaps with cryptic refugia (areas of sheltered topography that provided suitable stable microclimates) in northern latitudes (Bhagwat and Willis 2008, Provan and Bennett 2008, Stewart and Dalén 2008). But by the Lateglacial period, *Pinus, Juniperus,* and *Betula*, and then *Quercus* spread northward from southern European localities. The Younger Dryas cold period interrupted this trend for several centuries between ca. 12,650 and 11,500 cal. yr BP. The onset of the Holocene witnessed range expansions of angiosperm trees (*Corylus, Alnus, Fraxinus, Ulmus, Acer, Abies, Fagus,* and *Quercus*). Approximately 6000 years ago northern hemisphere ice pulled back to near modern limits, and most European forests reached their maximum extent. According to this picture, as discussed by Carrión (2001a), pollen diagrams from the southern European peninsulas show most of the following characteristics: (i) increases of *Quercus* pollen since lateglacial period, with the earliest occurrences in southernmost and coastal regions and the thermomediterranean belt, (ii) evidence for the Younger Dryas cold period in the form of expansion of xerophytes, and (iii) mesic tree forest maxima during the first Holocene millennia. Vegetation sequences near the current mountain treeline were characterized by open *Pinus* and *Juniperus* woodlands (Peñalba 1994). Divergences from this basic pattern have been often considered as result of site constraints or regional climate heterogeneity (e.g. Ramil-Rego et al., 1998, Muñoz-Sobrino et al. 2001).

Abundant examples exist of sequences corresponding to this dynamic model, especially in the Eurosiberian Region and areas under the Atlantic influence; Galicia, Portugal and south-western Spain (Figs. 1 and 2). These include the pollen records of Lago Enol in the north (López-Merino 2009), Tramacastilla and El Portalet in the Pyrenees (Montserrat 1992, González-Sampériz et al. 2006), Banyoles in the northeast (Pérez-Obiol and Julià 1994) (Fig. 2), Pozo do Carballal (Muñoz-Sobrino et al. 1997) and Sanabria (Allen et al. 1996) in the northwest (Figs. 2-3), Lagoa Marinho in Sierra de Geres of northern Portugal (Ramil-Rego et al. 1993a), Lagoa Comprida (van den Brink and Janssen 1985) and Charco da Candieira in Serra da Estrela, central Portugal (van der Kaap and van Leeuwen 1995) (Fig. 4), and Padul in the southeast, northwest of the Sierra Nevada (Pons and Reille 1988) (Fig. 2). The situation in the island of Ibiza, with the pollen sequences of Prat de Vila and Prats de ses Monges (Yll et al. 2009), fits into this expected pattern. Among the charcoal records, the most complete are probably Mougás in the Eurosiberian region (Carrión-Marco 2003), and Buraca Grande, Cabeço do Porto Marinho, Cova de les Cendres and Tossal de la Roca in the Mediterranean Region (Fig. 5). Other macroremains (leaves, twigs, trunks, etc) provide information on the species involved. Thus, the Eurosiberian region is noted for the abundance of *Quercus robur, Q. petraea, Q. ilex, Salix atrocinerea, Corylus avellana, Fagus sylvatica, Abies alba, Pinus sylvestris, P. nigra, Acer pseudoplatanus, Arbutus unedo,* and *Alnus glutinosa*, among others (García-Antón et al. 2006, García-Amorena et al. 2007, 2008). For the Mediterranean region, there are macroremains of *Quercus ilex-rotundifolia, Q. pyrenaica, Q. faginea, Pinus halepensis, P. pinaster, P. nigra, P. pinea, Olea europaea,* and *Populus nigra*, among others (García-Amorena et al. 2008). Finally, marine sediment pollen records such as MD99-2331 (Naughton et al. 2007), MD03-2697 (Naughton et al. 2007), SU-8118 (Parra 1994), MD95-2042 (Sánchez-Goñi et al. 2002), SU-8113 (Parra 1994), MD95-2043 (Sánchez-Goñi et al. 2002), and SU8103 (Parra 1994) confirm that these overall trends.

Variations within the “expected” can be explained by the topographical context of the different sites. For instance, continentality, altitude and aridity may have circumstancially favoured *Pinus* in opposition to *Quercus*. Thus, the existence of *Pinus* woodlands during the Lateglacial and Early Holocene as a consequence of the orographic influence is a widespread feature in several of the Iberian mountain pollen records, such as Lago Enol (López-Merino 2009), Comeya (Ruíz-Zapata et al. 2001), Polvoredo (García-Rovés 2007), San Isidro (Fombella Blanco et al. 2003) and Lago Mayor del Valle (Allen et al. 1996) in the Cantabrian range; Lagoa Lucenza (Muñoz-Sobrino et al. 2001) in Galicia, El Portalet (González-Sampériz et al. 2006) in the Pyrenees, and Llauset (Montserrat and Vilaplana 1987), Quintanar de la Sierra (Peñalba et al. 1997, Ruíz-Zapata et al. 2002), Hoyos de Iregua (Gil-García et al. 2002, Gil-García and Ruíz-Zapata 2004) and Las Pardillas (Sánchez-Goñi and Hannon 1999) in the Iberian range (Fig. 1). Similarly, typical summer drought conditions like in the Central Ebro depression at sites like Hoya del Castillo and Laguna Guállar (Zaragoza) may have contributed to the occurrence of *Pinus* woodlands during the Lateglacial (Davis and Stevenson 2007). In southern Iberia, *Pinus* prevailed during the Early Holocene in the high-elevation Sierra de Baza (Carrión et al. 2007), the dry lowlands of Elx (Burjachs and Riera 1995) and the Guadiana Estuary in the southwest (Fletcher et al. 2007) (Fig. 2). The Atlantic coast pollen record 8057B confirms this pattern (Hooghiemstra et al. 1992).

As for the pine distribution in these records, *Pinus nigra* and *Pinus sylvestris* would have been widespread at high altitudes (Rubiales et al. 2007, García-Amorena et al. 2007, 2008), while *Pinus pinea* appeared in the south and thermomediterranean southwest, both in the Pleistocene and Holocene (Badal 1998, 2006, Carrión et al. 2008), and *Pinus halepensis* abounded in the east and Ebro Valley (Badal 2004, Badal et al. 1994, 2008, Allué 2002, Carrión-Marco 2005). *Pinus uncinata* and *Pinus sylvestris* would have formed the timberline in the Eurosiberian region (Heinz 1991, Uzquiano 1992a,1992b, Carrión-Marco 2005) (Fig. 5). The cluster pine (*Pinus pinaster*) would have been sporadically dominant in several Iberian mountains (Figueiral 1995, Figueiral and Terral 2002, Rubiales et al. 2009), and sometimes forming part of mesophytic forests with deciduous *Quercus* (Carrión et al. 2000, 2004, 2007, Rubiales et al. 2009). Charcoal analyses suggest that during the Lateglacial, alpine, subalpine, and oromediterranean pine species descended to the thermo and mesomediterranean belts, disappearing progressively throughout the Holocene (Badal et al. 2008) (Fig. 5), although exhibiting an extraordinarily long residence in some areas (Rubiales et al. 2007).

Juniperus sometimes accompanied *Pinus* and *Quercus* in the lateglacial and early Holocene woodlands of the continental Mediterranean areas. The pollen records of Salines (Giralt et al. 1999) and Salada Mediana (Valero-Garcés et al. 2000a, 2000b) and the charcoal records of Santa Maria (Carrión-Marco 2005, Aura et al. 2006), and La Falguera (Carrión-Marco 2005) illustrate this case. Other variants of the expected trend include abundance of *Betula* in humid sites of higher altitudes (Muñoz-Sobrino et al. 2004, López-Merino 2009); abundance of *Corylus* in mesothermic Eurosiberian regions such as the Cantabrian coast (Burjachs and Renault-Miskovsky 1992, Peñalba 1994, López-Merino 2009) (Fig. 3) and Mediterranean riparian areas such as Salada Mediana (Valero-Garcés et al. 2000a, 2000b); and abundance of *Olea* in the thermomediterranean belt like in Laguna de Medina (Reed et al. 2001). The colonisation by *Fagus* is generally time-transgressive, starting during the Lateglacial in Sierra de Neila, but delaying its arrival to c. 5700 cal. yr BP or even later in most of northern Spain (Ramil-Rego et al. 2000, López-Merino et al. 2008, Muñoz-Sobrino et al. 2009).

The Younger Dryas (12,650-11,500 cal. yr BP) of Iberia, as with other regions of the northern hemisphere, does not always have a clear trend in pollen diagrams. However, it can be clearly detected (e.g. increases of *Artemisia*, Poaceae, Chenopodiaceae, *Ephedra*, and/or forest depletions) in the Sierra de Geres of northern Portugal (Ramil-Rego et al. 1998), Lagoa Lucenza (Muñoz-Sobrino et al. 2001), Lagoa Lucenza (Santos et al. 2000), Pozo do Carballal (Muñoz-Sobrino et al. 1997), the Cantabrian Lago Mayor del Valle (Allen et al. 1996), Alto de la Espina (López-Merino 2009), and Lago Enol (López-Merino 2009), the Iberian Range sites of Hoyos de Iregua (Gil-García et al. 2002), Quintanar de la Sierra (Peñalba et al. 1997, Ruíz-Zapata et al. 2002, 2003a), the Pyrenees (Montserrat 1992), Cataluña in Banyoles (Pérez-Obiol and Julià 1994), Sierra de Cabrera in La Roya, Sanabria Marsh (Allen et al. 1996), Sanguijelas and Lleguna (Muñoz-Sobrino et al. 2004), Central Spain in Burgomillodo (Díez et al. 2002), and CC-17 core in Tablas de Daimiel, La Mancha Plain (Dorado-Valiño et al. 2002, Valdeolmillos 2004); Navarrés (Carrión and Dupré 1996, Carrión and van Geel 1999), Villena (Yll et al. 2003), and Tossal de la Roca (Cacho et al. 1995) in eastern Spain, and characteristically Padul in the south (Pons and Reille 1988). These, among other sites, represent a geographically wide spectrum of sensitive sites to the Younger Dryas cold-dry period.

The response in the rest of the Lateglacial biozones is not so clear, although elements are apparent in some high-resolution sequences. González-Sampériz et al. (2006) were able to correlate the environmental changes observed in El Portalet peat bog in the Pyrenees with several abrupt events observed in northern latitudes (Heinrich events 3 to 1, Oldest and Older Dryas stades, Intra-Allerød Cold Period, and 8200 cal. yr BP event). The monumental work in Serra da Estrela by van der Knaap and van Leeuwen (1997) is equally detailed at the stratigraphical level, and show palynological changes, especially with *Quercus*, that fit into the Greenland ice-core curves.

UNEXPECTED SEQUENCES: absence of change, particular dynamics and threshold responses

The former, expected, palaeobotanical records are representative of the commonest trends in vegetation development throughout the Lateglacial and Early Holocene. They support the view that vegetation changes during this interval were generally determined by rapid shifts in the physical properties of the ecosystem. However, more than a few pollen sequences in Mediterranean Spain fail to show persistent trends through time or correlate with the major events described above (Fig. 1). Pollen-stratigraphical changes are episodic and abrupt, that is, they occur on the time scales of decades to centuries. Moreover, some pollen records show millennial-scale complacency to continental-scale climate change. All of these particular trajectories of vegetation dynamics deserve attention, and it is our view they should be conceptualized even when they may appear as less interesting or more inconclusive than the conventional histories directly assignable to climatic changes.

The vegetation sequence of Navarrés shows developments in the southern valleys of the Iberian System from about 30,900 to 3200 cal. yr BP (Carrión and van Geel, 1999) (Fig. 6). *Pinus* forests dominated the glacial landscape and resisted invasion by other species until about 5900 cal. yr BP, even though *Quercus* and other temperate trees occurred in the region several thousands of years before, as demonstrated by anthracological data (Badal et al.1994, Carrión-Marco 2005). The variation of macro- and microcharcoal throughout the core suggests that *Pinus* forests were only replaced by evergreen-*Quercus* scrub after local fire disturbance by the Neolithic populations settled in the vicinity of the study site. Although a prevailing dry climate during the first half of the Holocene may have played some role, our preferred interpretation of this vegetation sequence is that millennial-scale inertia of the established *Pinus* forests was followed by a threshold response to increased fire frequency and virulence.

Navarrés is not unique as a case of lateglacial and early Holocene dominance of pine woodlands. In other pollen sequences, these may extend further in time by reaching the Late Holocene, and this accounts for not only high- and mid-altitude mountain zones, but also coastal territories and interior platforms (Fig. 1). Examples in the vicinity of Navarrés are San Benito (Dupré et al. 1996) and Villena (Yll et al. 2003). In the Verdelpino cave pollen sequence, there is no *Quercus* colonization during the Magdalenian (lateglacial) levels, and *Quercus* only increases after c. 6000 cal. yr BP (López-García 1977). In El Carrizal, *Pinus* forests prevailed throughout the Holocene with a minor, subsidiary component of broadleaved forests (Franco-Múgica et al. 2005). In Espinosa de Cerrato, the dominance of *Pinus* is still more prolonged (Franco-Múgica et al. 2001) (Fig. 7). Similar records can be found in Gallocanta (Burjachs et al. 1996) and Ojos del Tremedal in Montes Universales (Stevenson 2000). Charcoal analyses show the coexistence of *Pinus nigra* and *P. halepensis* during the period c. 9900-8200 years BP in the rockshelter of Los Baños (Teruel), and in La Cativera (Tarragona) (Allué 2002, Badal 2004).

Other cases are even more divergent from the expected trend. The pollen assemblage in San Rafael shows that temperate trees and Mediterranean woody elements persisted during full glacial times, without any evidence of xerophytization (Pantaleón-Cano et al. 2003). In contrast, *Artemisia* increases from Lateglacial to Early Holocene. The optima of deciduous trees and Mediterranean scrub (c. 7500-4500 cal. yr BP) occur later than the mesocratic early Holocene phase of forest development in north-west Europe (Birks, 1986), and there is no record of any lateglacial expansion of *Quercus*. San Rafael, therefore, shows out-of-phase relationships in trends of meso- and xerophytic developments. Moreover, within the semi-arid southeastern province, the patterns and timing of Holocene vegetation stages differ in San Rafael, and the nearby Antas and Roquetas de Mar (Pantaleón-Cano 1997, Pantaleón-Cano et al. 2003), Elx (Burjachs and Riera 1995), Salines (Burjachs et al. 1997), Gádor (Carrión et al. 2003), Caldereros (Fuentes et al. 2005), Ubeda and Baeza (Fuentes et al. 2007), Carihuela (Fernández et al. 2007), and Baza (Carrión et al. 2007) (Fig. 1). The difficulties with the correlation of sequence events increase notably if we integrate charcoal records (Rodríguez-Ariza 1992, 2000).

In the Sierra de Segura, the Pleistocene-Holocene pollen record of Siles also exhibits its own distinctiveness (Carrión 2002). There is a first increase of *Quercus* from c. 12,000 to 10,500 cal. yr BP, then it drops while *Pinus nigra* and *P. pinaster* increase and domain the landscape until c. 7420 cal. yr BP, when deciduous *Quercus* invade abruptly the supramediterranean belt (Fig. 13). Another atypical vegetation history is seen in Bajondillo, southern Mediterranean coast. *Pinus, Quercus ilex, Betula* and *Abies* expand during the LGM and Lateglacial, while the onset of the Holocene is characterized by a partial replacement of these taxa by *Alnus, Corylus, Fraxinus, Ilex, Ulmus,* and *Quercus pyrenaica* type. The most important *Quercus* developments only occur after c. 7500 cal. yr BP (Cortés-Sánchez et al. 2008). The pollen spectra from Bajondillo, however, might be strongly influenced by the vicinity of the southeastern Baetic mountains. In charcoal analyses of similarly thermic areas of Mediterranean Iberia, tree species such as *Abies, Corylus* and *Betula* have so far not been identified (Rodríguez-Ariza 1992, 2000; Badal 1998). Although they do not go back to the very onset of the Holocene, the Early-Late Holocene pollen sequences of Algendar in Menorca (Yll et al. 1997) (Fig. 10) and Albufera de Alcudia in Mallorca (Burjachs et al. 1994) show very particular vegetation dynamics since about 7800 cal. yr BP, with *Juniperus, Pinus, Buxus* and *Corylus* as main protagonists.

Most of the cases described as “unexpected” lie in the Mediterranean Region, although in very different physiographic contexts (Fig. 1). As in the present, landscape heterogeneity could explain the occurrence of different vegetation types and moderate time lags in the response to climatic changes. When a primary climatic control is provided though, there should be certain overlap in the timing as well as in the palaeoclimatic significance of major events. Is it therefore possible that early Holocene vegetation developments were influenced by the composition and structure of the former plant communities? Could the cases of early-Holocene prevalence of pines be associated to areas where well-structured pine forests featured in the lateglacial and /or full-glacial landscapes? In general, pines show great phenotypic plasticity and resistance to invasion due to a set of ecophysiological characteristics that make them competitive in stressful environments (Rubiales et al. 2009). Facilitation is another plausible factor of species replacement, and there are case studies with *Quercus* vs. *Pinus* (Gómez-Aparicio et al. 2005, Gómez-Aparicio & Canham 2008). The climatic factor cannot be neglected, in any case, because the regions under the influence of Atlantic fronts show expected vegetation histories (Fig. 1). Palaeoecologically, what is clearly different between the Eurosiberian and Mediterranean region of Iberia is the full-glacial vegetation, with more mesothermophilous trees, and a greater extension of pine woodlands in the latter than the former (Carrión et al. 2008).

Phytogeographical hotspots of the Iberian Peninsula and Balearic Islands, as postulated by the cohesion of palaeobotanical, phylogeographical, and neoecological studies, all lie in the Mediterranean Region (Médail and Diadema 2009). So the glacial situation would be more complex in the Mediterranean, affecting not only the plants (Jiménez et al. 2004, Magri et al. 2006, Leroy and Arpe 2007, López de Heredia et al. 2007), but also the fauna (Gómez & Lunt 2007, Finlayson and Carrión 2007, Stewart and Dalén 2008), and yet not only at the population but also to the community and ecosystem levels (Arroyo et al. 2008). In this situation, subtle differences in initial conditions during the full-glacial could have affected the outcome of post-glacial events. In other words, due to the complex distribution and composition of forests during the glacial phases, a simple postglacial picture of vegetation dynamics cannot be expected.

HUMANS AS AGENTS OF DISTURBANCE (AND MORE “UNEXPECTED PATHWAYS”)

Climate has, doubtless, exerted an important influence on Holocene vegetation sequences of the Iberian Peninsula, above all into the Eurosiberian Region (Fig. 1). Palaeoecological records of the Atlantic territories exhibit directional changes suitable to correlation with the Greenland isotopic records (Mayewski et al. 2004). Thus, during the early Holocene up to 7800 cal. yr BP, pollen sequences depict at least two episodes of xerophytization paralleling the GH-11.2 and GH-8.2 events (Muñoz-Sobrino et al. 2007). The 8.2 ka cold event is also discernible in the Central Ebro River Basin where its magnitude provoked the hunter-gatherer groups to migrate to regions with more favourable conditions (González-Sampériz et al. 2009). The Cañada de la Cruz pollen record shows that the ecotones between high-elevation pine forests and xerophytic grassland-scrub have changed in altitude at least five times over the last 10,000 years, and do appear to be sensitive to temperature change, although this must be strongly related with wind exposure, continentality, and average climate xericity (Carrión et al. 2001a). These changes are synchronous with periods of abrupt oscillations and rapid transitions in the climates of north Africa and the Sahel (Gasse 2000), and the North Atlantic region (Lauritzen 1996). Aridification phases inferred from pollen ratios in Mediterranean Iberia have been established at c. 8400-7600, 5300-4200, 4300-3400, 2850-1730, and 1300-750 cal. yr BP (Jalut et al. 2000), in correlation with arid intervals at Tigalmamine, north Africa (Lamb et al. 1995). In addition, it has been shown in a number of sequences from southern Spain that the period from c. 7500-5200 cal. yr BP represents the mesophytic optimum and the period of lowest fire activity (Burjachs and Riera 1995, Pantaleón-Cano et al. 1997, Carrión 2002, Carrión et al. 2003, 2007). In contrast, the sites of Padul (Pons and Reille, 1988), and Elx and Salines (Burjachs et al., 1997) show early-Holocene (c. 11,500-8500 cal. yr BP) mesophyte maxima. Similar asymmetries are acknowledged in northern Iberia, from Galicia to the Cantabrian region (Muñoz-Sobrino et al. 2005), the Pyrenees and northeastern Spain (González-Sampériz et al. 2005, 2006). For instance, pollen data from NW Spain (Allen et al. 1996, Muñoz-Sobrino et al. 2001, 2004) depict a woodland expansion between 8000 and 2000 cal. yr BP, while the Cantabrian sequences show two forest maxima at 8000-7500 and from 5000 cal. yr BP onwards, separated by a phase of more open landscapes (Muñoz-Sobrino et al. 2005).

Regardless of the bioclimatic region, it appears, however, that the patterns of vegetation change reach maximum complexity between the Mid- and Late Holocene, and although some trends can be well-established for several territories, the timing of forest declines and expansions are spatially uneven and cannot be solely explained by current differences in physical setting (Carrión et al. 2000, Gil-Romera et al. 2009). Among the factors involved we need to consider the role of anthropogenic disturbance, which no doubt was spatially heterogeneous. Burning, pastoralism, and ploughing by agrarian and metallurgic societies, for instance, may have been historically decisive and site-specific. It is perhaps significant that this heterogeneity of environmental change increases from Mid to Late Holocene, which strongly suggests that human activities have been of crucial importance to shape current landscapes.

Figure 8 shows the Holocene pollen sites in which anthropogenic disturbance has been identified through palynological indicators and contextualized through the archaeological record. The geography of impacted sites is puzzling for any period considered. Many outstanding pollen sites show starting times of anthropogenic disturbance falling into the Neolithic period, such as Villena (Yll et al. 2003), Navarrés (Carrión and van Geel 1999), and San Benito (Dupré et al. 1996) in the east; Puerto de los Tornos and Atxuri (Peñalba 1994), Mougás (Gómez-Orellana et al. 1998), Monte Areo and Alto de la Espina (López-Merino 2009), Comeya (Jiménez-Sánchez et al. 2003), Hoyos de Iregua (Gil-García et al. 2002) in the north; Azután (Bueno et al. 2002), Barruecos (López-Sáez et al. 2005) and Dehesa Río Fortes (López-Sáez 2002) in central Iberia; Cerro de la Horca (López-Sáez et al. 2007), Prazo (López-Sáez et al. 2007), Muge Valley (van der Schriek et al. 2007), and Charco da Candieira (van der Knaap and van Leeuwen 1994, 1995,

1997) in Portugal and the southwest; Bajondillo (Cortés-Sánchez et al. 2008), and Carihuela (Fernández et al. 2007) in southern Spain; Cala´n Porter (Yll et al. 1997) (Fig. 10) and Albufera de Alcudia (Burjachs et al. 1994) in the Balearic Islands. Anthracological and palaeocarpological information confirms this early influence of man for the same regions (Uzquiano 1992a, Figueiral 1993, Buxó 1997, Rodríguez-Ariza 1992, 1995; Zapata 2002, Zapata et al. 2004, López-García et al. 2003, Carrión-Marco 2005, Peña-Chocarro et al. 2005, Piqué 2005, Badal et al. 2008). Charcoal of evergreen *Quercus*, present in north Atlantic Iberia, from Neolithic to Bronze Age levels of archaeological sites, has been interpreted as the result of human action (Zapata 2002). It must be emphasized though that the degree of landscape change that was clearly caused by human activities during the early Neolithic is low, difficult to detect, and not free from controversy (Carrión et al. 2007, López-Merino 2009).

The establishment of “cultural landscapes” during the expansion of metallurgical communities (Fig. 8) is clearly depicted in pollen diagrams. Thus, during the Chalcolithic and Bronze-Age cultural periods, many sites in the Iberian Peninsula show vegetation changes more or less correlated with the timing of disturbances by humans. Several examples are Can Roqueta (Burjachs and Expósito 2007), Lago Enol (López-Merino 2009, Moreno et al., in press), Pozo do Carballal (Muñoz-Sobrino et al. 2007), San Isidro (Fombella Blanco et al. 2003), and Tramacastilla (Montserrat 1992) in the north; Carril de Caldereros (Fuentes et al. 2005), and Cova 120 (Burjachs 1988) in eastern Spain; Rascafría (Ruíz-Zapata et al. 2006), El Portalón (Ruíz-Zapata et al. 2003b), and Covatilla (Atienza 1995) in central Spain; Melides (Santos et al. 2002) in Portugal; Acebrón (Stevenson and Harrison 1992) (Fig. 11), Las Madres (Stevenson 1985), Medina (Reed et al. 2001), Baza (Carrión et al. 2007), Gádor (Carrión et al. 2003), Baeza and Úbeda (Fuentes et al. 2007) in southern Spain, and Algendar in Minorca (Yll et al. 1997) (Fig. 9). Again, this thesis is supported by anthracological and palaeocarpological information related with archaeological surveys (Grau 1990, Rodríguez-Ariza and Vernet 1991, Rodríguez-Ariza

1995, 2000, Buxó 1997, Cámalich and Martín 1999, Castro et al. 1999, Carrión-Marco 2004, 2005, García and Grau 2005, Allué et al. 2006; García et al. 2007, Ros Sala 2008).

Many of the former sites continue to be affected by anthropogenic degradation during Iron Age times, the Romanization and episodes of the last centuries. However, other pollen sites only show anthropogenic indicators after Roman times, or even only during the last centuries (Fig. 8). Alteration usually includes human-set fires often combined with overgrazing, opening of the landscapes, spread of grasslands, thorny scrub and junipers in altitude, depletion of mesophytes, increases of heaths in the Eurosiberian Region, and garrigas in the Mediterranean Region, loss of arboreal diversity and increase of heliophytic herbs. Sites like El Sabinar (Carrión et al. 2004), Siles (Carrión 2002), Daimiel (Gil-García et al. 2007), El Carrizal (Franco-Múgica et al. 2005), Espinosa de Cerrato (Franco-Múgica et al. 2001) (Fig. 7), Villaviciosa (García-Antón et al. 2006), and Leitariegos (García-Rovés et al. 2001) show these first impacts only during the last two millennia. Others, like Cañada de la Cruz (Carrión et al. 2001b), Lucenza (Santos et al. 2000), Quintanar de la Sierra (Ruíz-Zapata et al. 2002), and Villuercas (Gil-Romera et al. 2008), register human influences even later. In fact, it is remarkable that some pollen sequences lack anthropogenic pollen indicators (Pantaleón-Cano et al. 2003), and that others correspond primarily to climate changes, in spite of the noted influence of humans (e.g. Taravilla Lake by Moreno et al. 2009).

Aiming to find out whether altitude would play an important role in the distribution of sites, a frequency analysis was carried out (Fig. 9). In order to reduce the bias produced by the dissimilar abundance of sites at different altitudes, the frequency of sites in every period at any specific altitude was weighted by the abundance of total sites in that particular altitude belt. Thus the frequency is not conditioned by the number of sites found for a period but only for the altitude. According to the frequency distribution, the Iberian Peninsula shows plentiful sites with Neolithic impact of man on the vegetation landscapes, probably because of the early development of agriculture. However, the antiquity of their pastoral practices would have also demanded the occupation of rich, fresh high altitude grasslands. Within the Mediterranean Region, the sites with evidence of Chalcolithic-Bronze impacts occur largely below the oromediterranean belt, in regions that, at the time, were probably cooler and wetter than nowadays. These would represent suitable ecological conditions since they were probably providing the resources needed for the intensification of mining and agricultural activities while avoiding unnecessary risk and hazards derived from mountain occupation and facilitating the access to resources given the low altitudes. Since the Roman period onwards the land was widely occupied but, while occupying lowlands sites, the higher mountain belts were also populated.

The history of the vegetation of a number of sites seems clearly influenced by changes in local economy, but there remain technical difficulties in establishing a causal relationship between cultural and environmental changes given the imprecise chronologies available and the fragmentary character of most of the palaeoecological information. One exception is the study carried out in Sierra de Baza and Sierra de Gádor regarding the Argaric culture collapse that took place sharply about c. 3600 cal. yr BP (Carrión et al. 2003, 2007) (Fig. 12). From the fourth to the first half of the third millennia BC in southeastern Spain, the economy was a subsistence one based on mixed pastoral-agricultural strategies. Subsequently, mining is associated with a population increase during the third millennium and throughout the greater part of the second millennium BC. It is the beginning of the first metallurgic communities of the south-eastern Peninsula: the cultures of the Chalcolithic Los Millares and the Argaric Bronze. From the end of the second millennium to the Late Roman-High Medieval period, there is a depopulation that coincides with the disappearance of the Argaric world and copper-bronze-arsenic metallurgy. The palynological sequences of Baza (Carrión et al. 2007), Gádor (Carrión et al. 2003), Caldereros (Fuentes et al. 2005), in conjunction with other fragmentary palaeobotanical information (Carrión et al. 2007) suggest ecological degradation, landscape opening, fires, pastoralism, and perhaps tree cutting for mining, as the proximate causes of abandonment (Fig. 12). In the southwest Iberian Peninsula, evidence of ecological degradation has been detected from the Chalcolithic. In the beginning of the third millennium BC, intensive copper mining and smelting developed in the Iberian Pyrite Belt of southwestern Spain (Nocete al. 2005). It was of great magnitude and provoked systematic deforestation and increased erosion and the beginnings of heavy metal pollution in the estuaries of Tinto and Odiel rivers (Gulf of Cádiz). Based on a temporal correlation between the developments and dismantling of territorial networks, Nocete et al. (2005) have inferred a direct link to the development and collapse of the intersocial body of Core/Periphery relationships during this cultural period.

In northern and northwestern Iberia, Muñoz-Sobrino et al. (2005) and López-Merino (2009) found evidence of minor Neolithic-induced transformations, but the Chalcolithic, Bronze, Iron, and Roman phases are most often characterized by profound impacts on the forests, probably linked to the increase of surfaces for agriculture and livestock grazing. Forest clearance, probably linked to mining is also noticed in the Cantabrian region. More recently, a major reforestation occurred during the Christian Reconquest and the associated repopulation of the north. Other pulses of population growth include the 12th and 13th centuries (Valdeón et al. 1994) and the Late Middle Ages until the 16th century, in which the reactivation of economy was based on sheep/goat production. Deforestation increased during the 16th century due to the demand of wood for large ship construction during the Spanish colonization of America (Muñoz-Sobrino et al. 2005, and Valbuena et al., in this volume). The last five thousands years have certainly been of great impact, by human economic activity, on the vegetation landscapes of northern Iberia.

The intensity and timing of human impact on vegetation have varied from one part of the Iberian Peninsula to another. In one sense, human activities are a further “unexpected” pathway influencing vegetation dynamics. Changes in demography and economic activities represent historical accidents which may provoke peculiar trajectories in vegetation history, such as seen in the Balearic Islands of Mallorca and Minorca (Fig. 10). Yet, the interpretation of pollen-stratigraphical changes as a result of local human disturbance may be speculative if due account is not taken of the spatial scale of the impact, and of the other physical and biotic influences. How climate, ecological factors, and man activities may interact to produce similarities and divergences in Holocene vegetation sequences is illustrated in the Segura Mountains of southern Spain. Comparison between the main vegetation shifts in the sites of Cañada de la Cruz, Siles, Sabinar, and Villaverde depicts climatically-induced altitudinal displacements of vegetation belts (Carrión 2002, Carrión et al. 2001b, 2004). However, altitudinal correlation of these taxa is complicated by species interactions, mainly competitive and successional processes among *Pinus nigra, P. pinaster*, deciduous and evergreen *Quercus* (Carrión 2002). A detailed revision of the patterns and processes of vegetation change in Siles (Fig. 13) may provide us with a corollary: climate has, doubtless, exerted long-term control of the species pool, but initiating factors and the inertia of established tree populations, as well as migrational processes interconnected with competition adjustments, were responsible for important time lags in the response of vegetation to climate. Yet, fire disturbance would have been a major factor shaping interspecific relationships and vegetation change from about 4500 cal. yr BP onwards. Interestingly, the most obvious anthropogenic phase between 3000 and 1500 cal. yr BP corresponds with maximum fire activity and great sensitivity in the vegetation, as could be deduced from the rate-of-change curves (Carrión 2002).

Among all disturbances shaping the Iberian vegetation through time, the influence of fire is probably the best understood. Fire is now considered an inherent element in the Mediterranean environment, rejuvenating the system and generating new open spaces to be colonized (Carrión-Marco 2005, Ojeda et al. 2005, Pausas & Keeley 2009). As stated in the introduction, understanding the long-term role of fire would allow us to recognize the vegetation response to different forcings. The analyses of past fire regimes, although slowly gaining more importance across Europe and North-America (Carcaillet et al. 2001, 2007, Gavin et al. 2006, Tinner et al. 2006, Anderson et al. 2008, Higuera et al. 2008), are still very much needed in the southern European Peninsulas (Vannière et al. 2008), where both the climate and the pattern of human occupation create a unique fire-prone environment. Fire history reconstruction would help in assessing the post-fire response of pines and oaks, as resprouters or seeders, as this might have been a determinant factor of the ecosystem's resilience and for the competitive relation of broadleaved and coniferous forests. Fire is intimately connected to fuel availability, moisture patterns and therefore to climate changes, but it is also directly linked to human activities. This is particularly well studied in the above-mentioned sequences of the south-eastern region of Iberia (e.g. Carrión et al. 2001a-b, 2003, 2007), where the fire pattern is often independent from the climate trends and it is more subject to the abandonment and reoccupation of different areas.

As we gain more taxonomic detail and stratigraphic resolution in pollen sequences of the Iberian Peninsula, the prevailing climatic paradigm seems increasingly fragile. Vegetation stages recur in time because vegetation is subject to the consequences of physical laws and processes. But particularities must be explained and, in the cases exposed here, it seems that they may appear determined as much as by the biotic history as by abiotic site properties.

CONCLUSIONS

Long-term vegetation dynamics in the Iberian Peninsula are subject to control factors equivalent to those prevailing in Northern Europe. Its landscape diversity, ecological history, fire activity and ancient human occupation, however, have often defined unexpected vegetation responses, especially in the Mediterranean-influenced climate region. Recapitulating our initial hypothesis about Iberian forest reactivity to climate change and human agency we highlight the following aspects:

- In the Eurosiberian, and often also in the Mediterranean region of the Iberian Peninsula, the Lateglacial and early Holocene are characterized by the development of *Quercus*–dominated assemblages and other angiosperm trees at the expense of pine woodlands and steppes. The earliest *Quercus* invasions occur in coastal, oceanic and thermic regions. Mesophytic maxima take place most often during the first Holocene millennia. Continental and high-altitude locations reflect pine prevalence during this period. In those sites with sufficient stratigraphical resolution, the Younger Dryas cold spell is recorded in the form of expansion of xerophytes.
- In the Mediterranean Region, a millennial-scale resilience of the established forests is often observed. Occasionally, this resilience was followed by a threshold response to increased burning in the form of competitively-mediated *Quercus* invasion during the Mid Holocene. In other cases, the *Pinus* woodlands remained as dominant landscapes until the Late Holocene or present day. Vegetational dynamics in the Balearic Islands are diverse and strongly dependent on the floristic composition and human activities.
- Human occupation has played a determinant role shaping the Iberian landscapes as we know them since the Mid-Holocene; grazing, agriculture, mining, coppicing, slash and burn, etc., are all activities exerting deep transformations. As for the climate forcing, anthropogenically induced changes have had, sometimes, unpredictable consequences and complicate the climatic reconstructions.
- As we gain temporal resolution in pollen records, we can see the concentration of the major changes into relatively short episodes; the rate of change is definitively uneven, which points to the need of a conceptualization based in an historical-contingent rather than a deterministic approach.
- In the overall picture, some areas have always been more very sensitive to climate fluctuations and human activities, although the spatial pattern is puzzling. Independent of

the area, climate has exerted long-term control of the species pool, but initiating factors and the inertia of established tree populations, as well as migrational processes interconnected with competition adjustments, were responsible for important time delays in the response of vegetation. This is so to such an extent that vegetation trajectories are sometimes intricate enough as to predict that historical contingency overwhelms the common trend. The need for more long-term vegetation studies is still very much needed in order to understand the time lags between the three-fold forcing system: climate-vegetation-humans.

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Figure Legends

Figure 1. Expected and unexpected vegetation sequences in response to lateglacial and early Holocene temperature increase (see Section: "Iberian vegetation coping with the Lateglacial-Early Holocene climatic change"). Unexpected records lie in the Mediterranean Region, from thermo and coastal areas, to high and mid-elevation mountain belts, and continental highplains as well. The areas with highest incidence of the Atlantic fronts are sensitive to climatic changes during this period. Site details in Table 1.

Figure 2. Examples of expected patterns of vegetation dynamics in the Iberian Peninsula during the Lateglacial and early Holocene. These include an increase in *Quercus* since the Lateglacial, with the earliest occurrences in southernmost and coastal regions (e.g. Padul, Guadiana Estuary), and deciduous trees (e.g. *Corylus, Fraxinus, Alnus, Fagus*) and woody scrub (e.g. *Phillyrea, Pistacia,* Ericaceae) expansion through the Holocene. Vegetation sequences in continental areas below the treeline are expected to include significant contribution of *Pinus* to the dominant oaklands, like in Sanabria. The Younger Dryas is characterized by the expansion of xerophytes.

Figure 3. Principal vegetation changes in NW Iberia during the Lateglacial and early Holocene. Note the progressive expansion of *Quercus* and other mesothermophilous trees at the expense of steppes and pine forests. This situation can be extrapolated to most of the Eurosiberian Region of Spain, although pines remained important in high-elevation areas and others of Mediterranean influence or extreme continentality. Redrawn from Muñoz-Sobrino et al. (2007).

Figure 4. Holocene vegetational developments in a montane region of the Atlantic Iberia, as shown by the synthetic pollen diagram of Charco da Candieira, central Portugal. *Quercus* prevails over *Pinus* in the forest component. The sequence includes indicators (e.g. *Cerealia, Plantago, Castanea,* among others) of anthropogenic disturbance ever since the Middle Holocene. Human activities are therefore associated with progressive opening of the landscape and increase of Cistaceae-Ericaceae scrub. Redrawn from van der Knaap and van Leeuwen (1997).

Figure 5. Main patterns of forest trees as differentiated from charcoal remains for the Mediterranean Region in the Iberian Peninsula. *Quercus* invasion of pine forests starts in the most thermic positions progressing in altitude across the early Holocene. *Pinus nigra* and *P. sylvestris* forests are inherited from glacial pine woodlands. *P. halepensis* and *Olea europaea* develop with the matorralization of ecosystems in the Mediterranean region. Human impacts are noticed from the Neolithic onwards.

Figure 6. Navarrés pollen diagram of selected types for the lateglacial and early Holocene. Full-glacial pine forests resist competition by oaks despite the lateglacial and postglacial climate changes. Mid-Holocene invasion by oaks is coherent with threshold response of local forests to increased fire virulence and correlates archaeological evidence of the first Neolithic settlements in the vicinity of the study site. Redrawn from Carrión and van Geel (1999).

Figure 7. Synthetic pollen diagram of a small group of ecologically relevant types from the Espinosa de Cerrato sequence in Palencia. Pine forests show a millennial-scale resilience and prevail as main vegetation type at about 800-900 m a.s.l. in north-central Spain. Redrawn from Franco-Múgica et al. (2001).

Figure 8. Starting times of anthropogenic disturbance according to palynological indicators in the Iberian Peninsula and Balearic Islands. The data do not suggest a clear relationship between the timing of the first cultural landscapes and the bioclimatic belts. Most of the “delayed” (Iron Age to present) sites occur in high-elevation areas, while from the coasts to the mountains there are sites with Neolithic impact of man on the vegetation landscapes, probably because of the early agricultural activities and antiquity of pastoral activities. Anthropogenic palynological indicators include not only pollen types indicative of agriculture and ruderalization (*Cerealia, Polygonum aviculare, Rumex, Vitis*, etc) or arboriculture (*Juglans, Castanea, Fraxinus, Eucalyptus*), but also spores (Sordariaceae, *Riccia*, Glomaceae) and non-pollen microfossils (*Pseudoschizaea*, Acari Oribatidae, etc). See section of “Palaeoecological indicators” for further detail. Site details in Table 1.

Figure 9. Frequencies of site type per bioclimatic belts following altitudinal gradients in the Eurosiberian and Mediterranean regions. Values for every site type per bioclimatic belt have been weighted by the total number of sites at a particular altitude.

Figure 10. Synthetic pollen diagram of Algendar (Minorca, Balearic Islands). A particular combination of taxa (*Pinus, Juniperus, Corylus*, and *Buxus*) dominate the mid-holocene

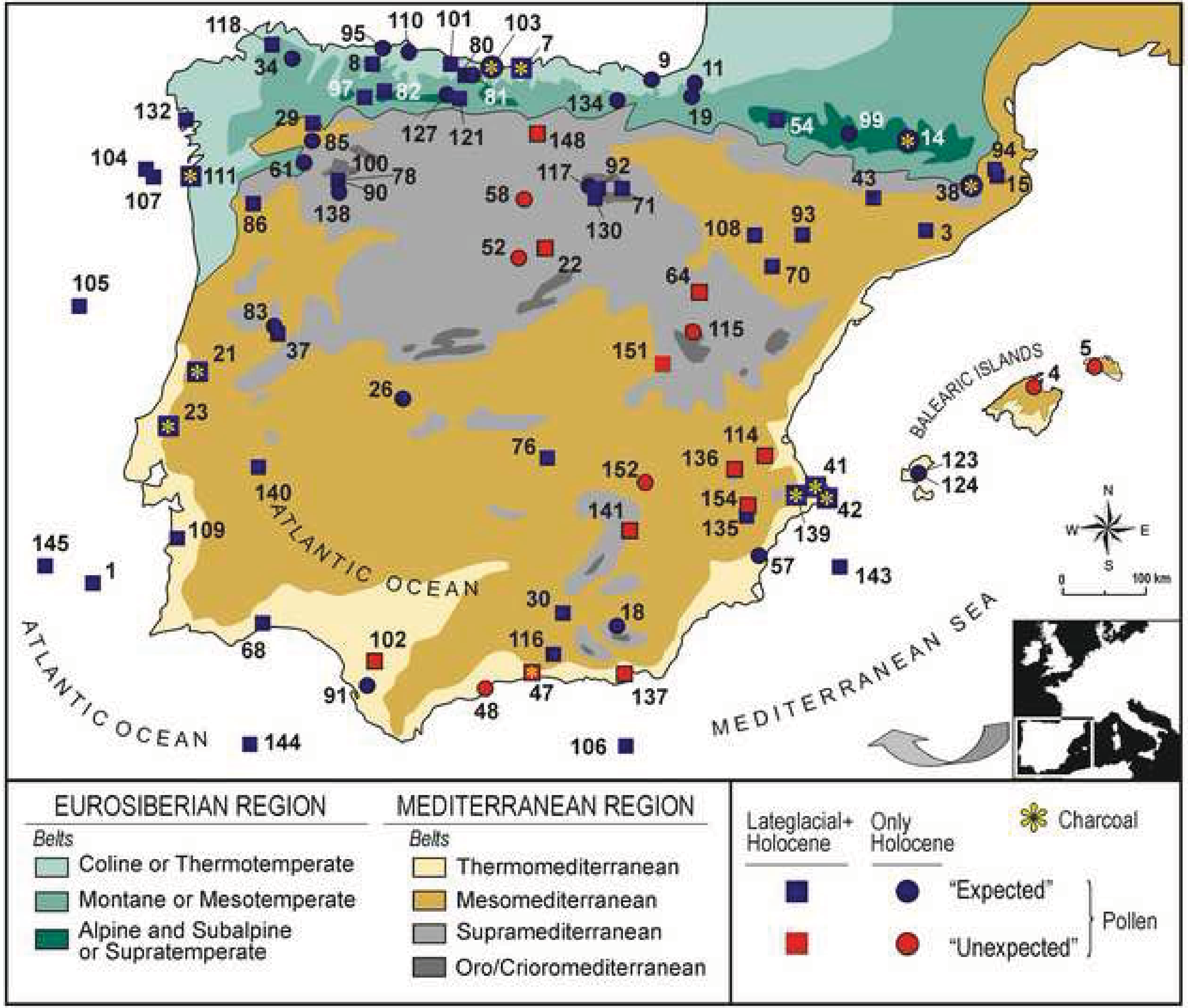
assemblages, while evergreen *Quercus* rises in the phase of more intense human activities, accompanied by *Olea, Plantago*, and *Vitis*. Redrawn from Yll et al. (1997).

Figure 11. Oak-dominated landscapes may have been selected by humans, probably linked to the dehesa economy, which has been dated from Bronze Age times in southwestern Spain. This is illustrated in several pollen records such as El Acebrón, Doñana, where *Quercus* replaces the former pine woodlands while indicators of agriculture and ruderalization (*Vitis, Echium, Plantago, Rumex, Galium*) are present from c. 4510 cal. BP. Redrawn from Stevenson and Harrison (1992).

Figure 12. Vegetational developments in the Sierra de Baza (Carrión et al. 2007) and Sierra de Gádor (Carrión et al. 2003) of southern Spain, and correlation with patterns of human settlement. In both records, increased fire frequency (c. 4200-4100 cal. yr BP) and a change from mixed forests to sclerophyllous forest-scrub (c. 3940-3800 cal. yr BP) precedes the collapse of the Argaric Bronze culture at c. 3600 cal. yr BP. A climate trend towards greater aridity is observed ever since c. 5500 cal. yr BP. Ages in black boxes represent the dates of main changes in both sequences.

Figure 13. Temporal relationships between vegetation zones, and hypotheses for the main processes and controls of vegetational developments in the Siles sequence, Segura Mountains of southern Spain. Climatically-influenced changes occur as rapid, gradual or threshold responses to competitive interactions, aridity crises, increased water availability, grazing pressure, and fire disturbance. Lags in vegetational developments occur at the centennial scale. Biotically-induced changes of vegetation are mainly shown at the intrazonal variation level. Modified from Carrión (2002).

Figure 1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BALEARIC ISLANDS
114
136
123
124
76
152
41
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154
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141
140
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143
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ATLANTIC OCEAN
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137
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ATLANTIC OCEAN
144
106
MEDITERRANEAN SEA
EUROSIBERIAN REGION
Belts
Coline or Thermotemperate
Montane or Mesotemperate
Alpine and Subalpine or Supratemperate
MEDITERRANEAN REGION
Belts
Thermomediterranean
Mesomediterranean
Supramediterranean
Oro/Crioromediterranean
Lateglacial+ Holocene
Only Holocene
Charcoal
"Expected"
"Unexpected"
Pollen

Figure 2

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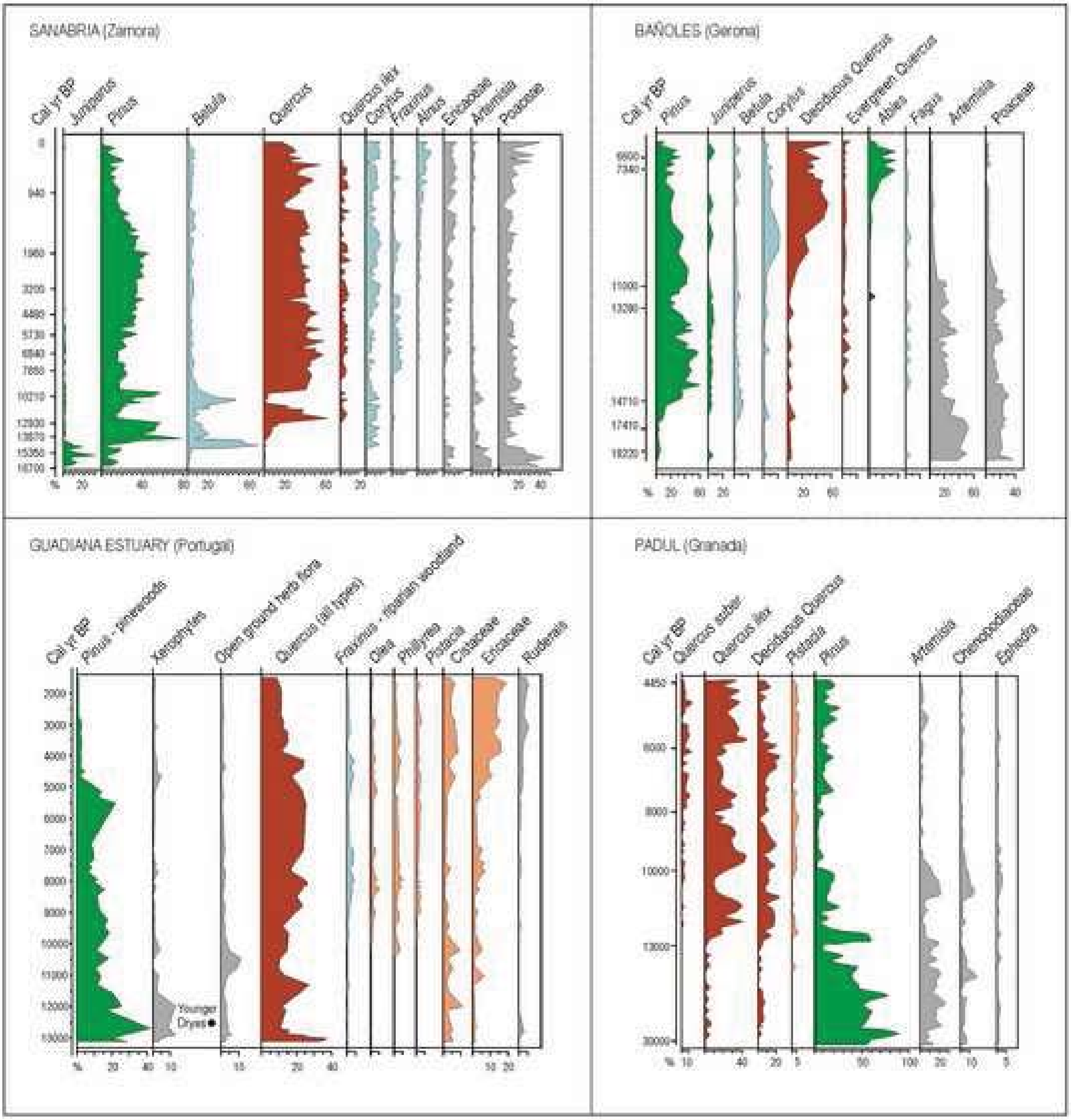
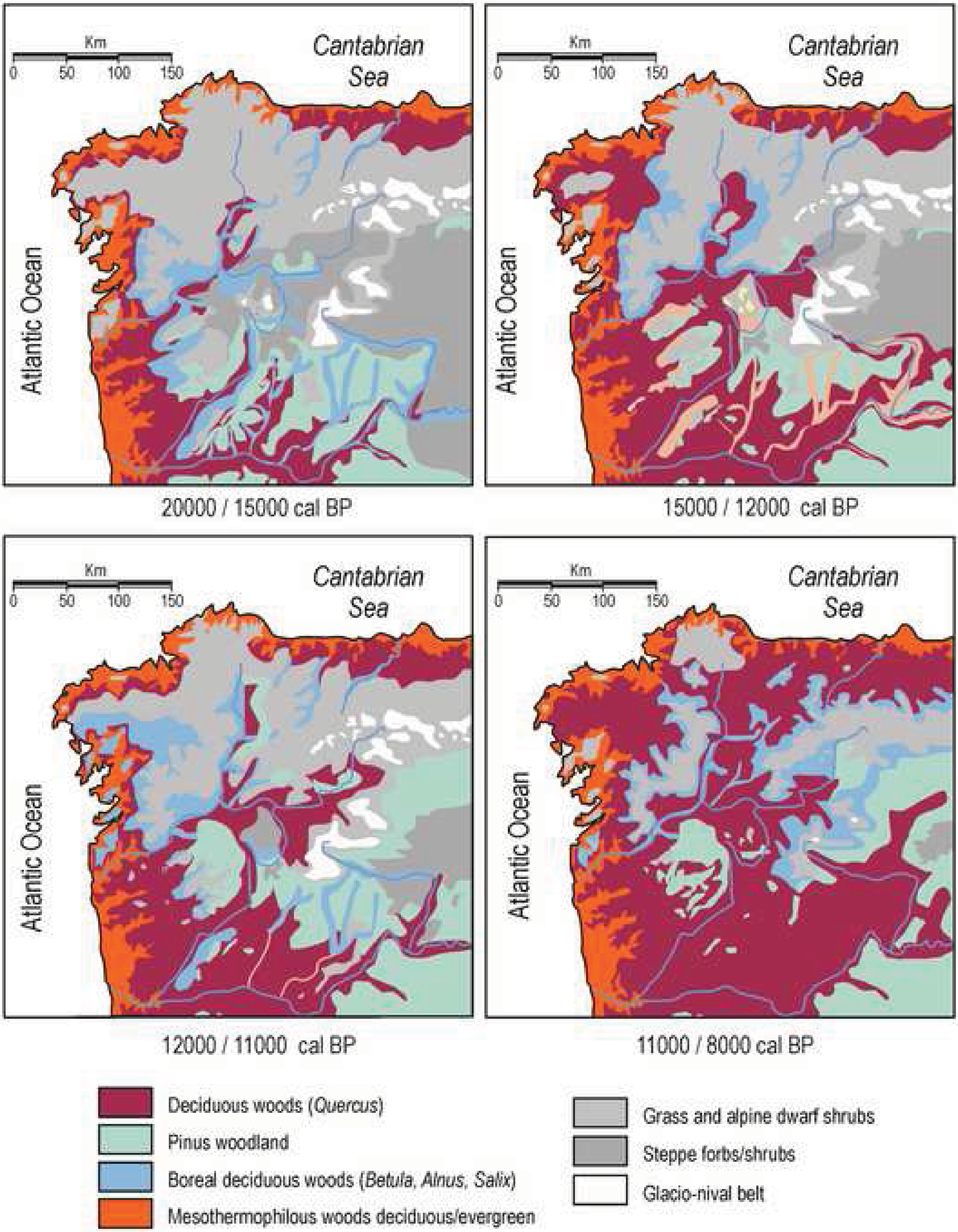


Figure 3


Km
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50
100
150
Cantabrian Sea
Atlantic Ocean
20000 / 15000 cal BP
15000 / 12000 cal BP
12000 / 11000 cal BP
11000 / 8000 cal BP
Deciduous woods (*Quercus*)
Pinus woodland
Boreal deciduous woods (*Betula, Alnus, Salix*)
Mesothermophilous woods deciduous/evergreen
Grass and alpine dwarf shrubs
Steppe forbs/shrubs
Glacio-nival belt

Figure 4

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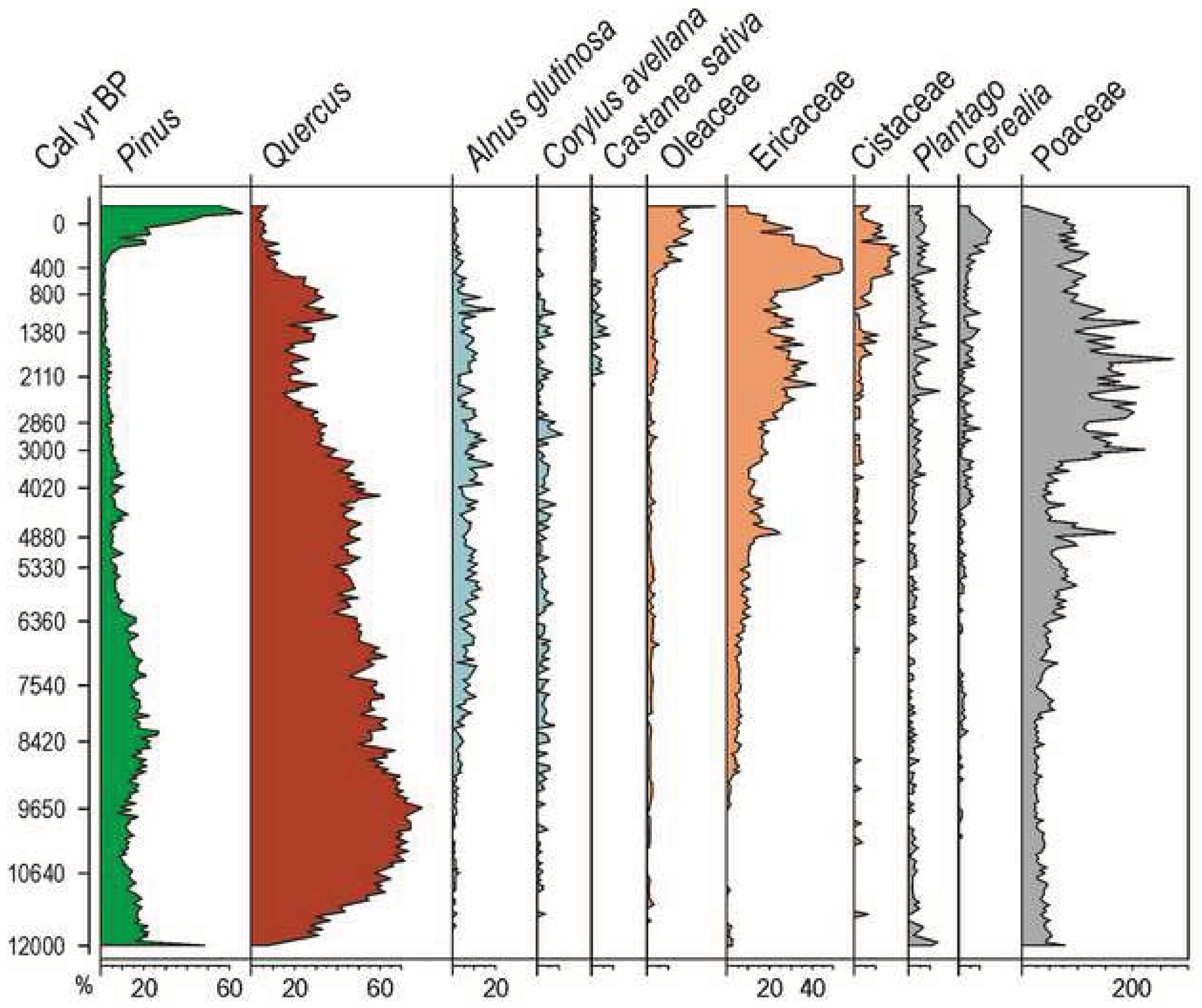

Figure 5

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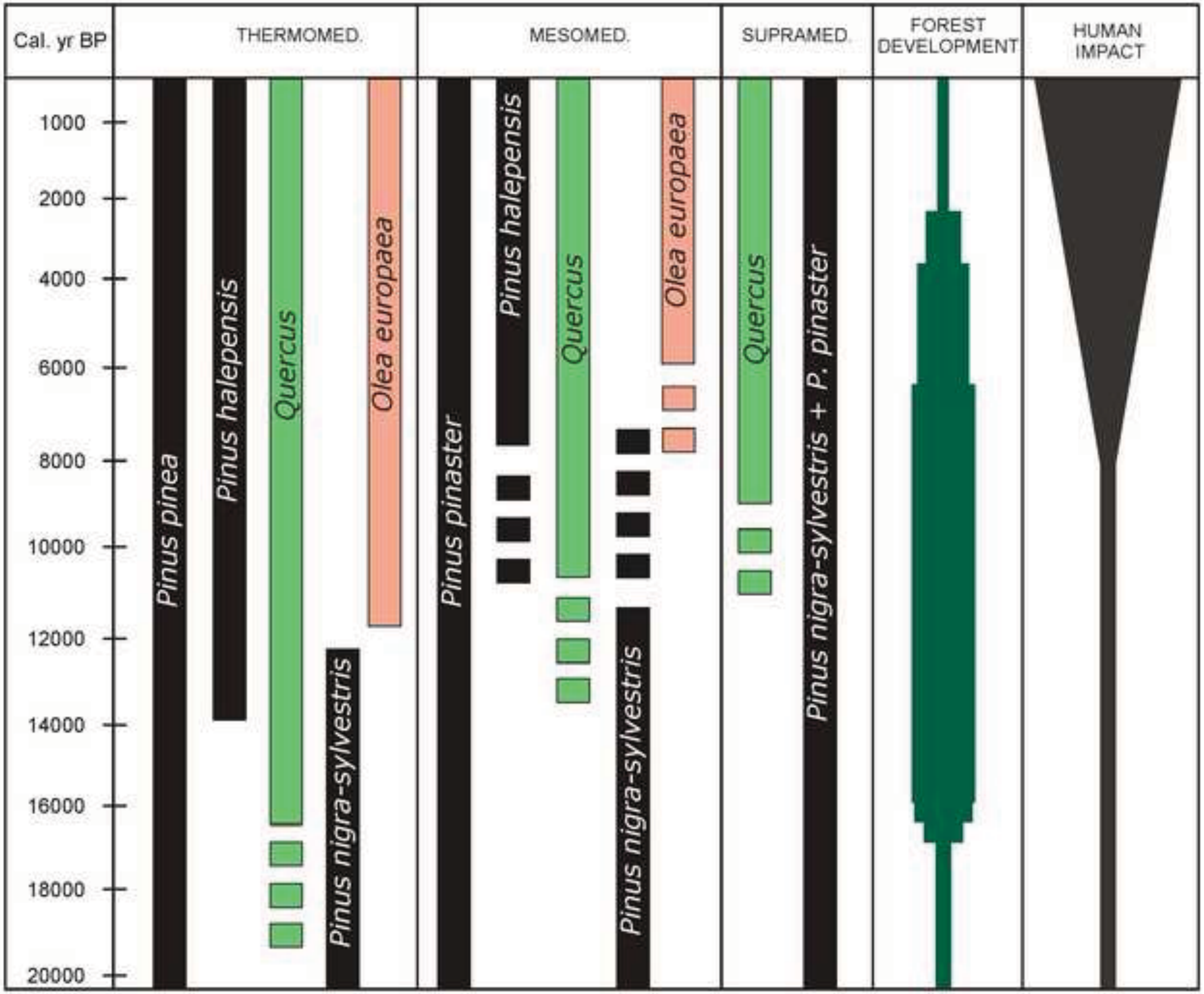

Figure 6

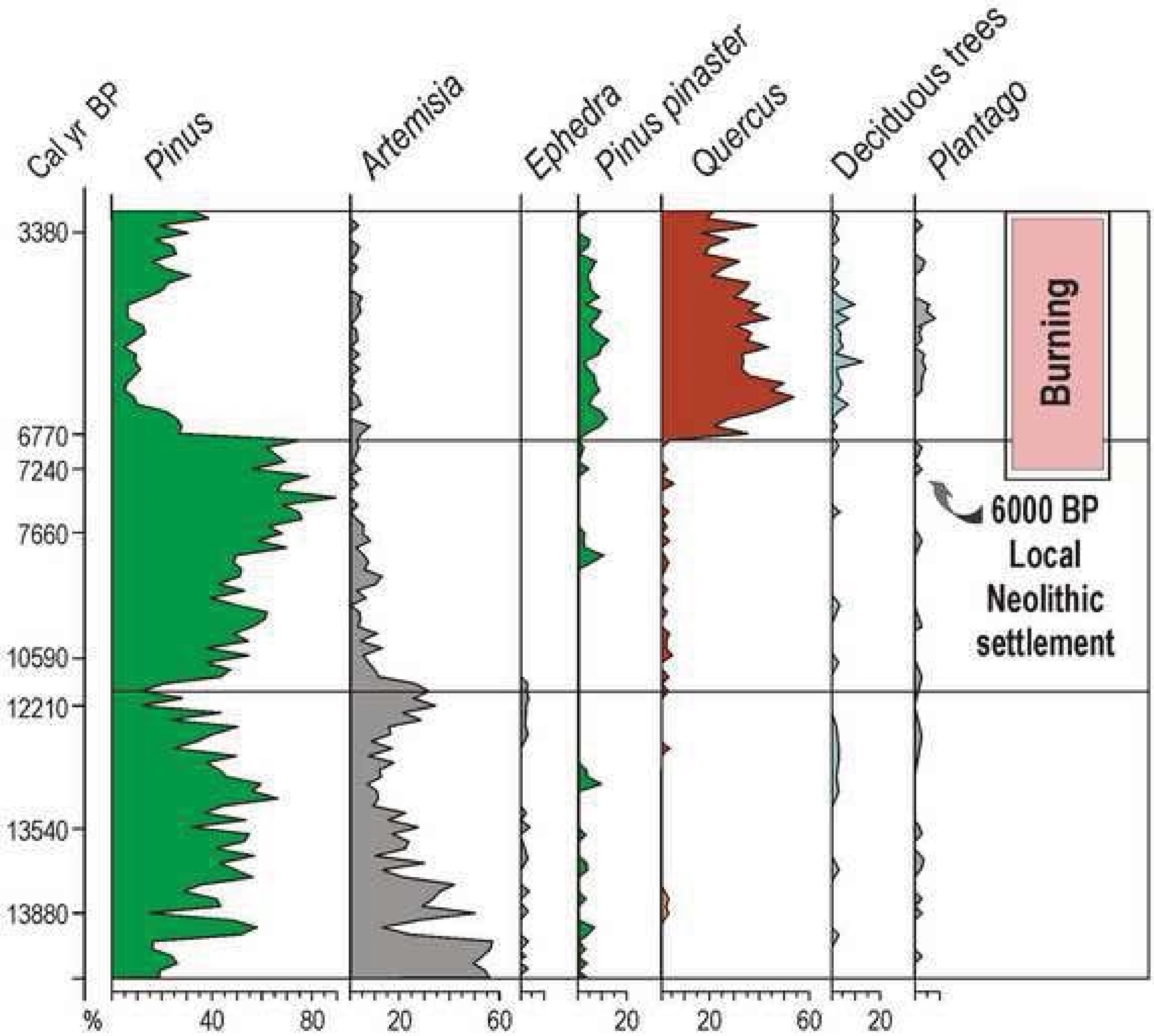
Cal yr BP
Pinus
Artemisia
Ephedra
Pinus pinaster
Quercus
Deciduous trees
Plantago
3380
6770
7240
7660
10590
12210
13540
13880
%
40
80
20
60
20
20
60
20
Burning
6000 BP
Local
Neolithic
settlement

Figure 7

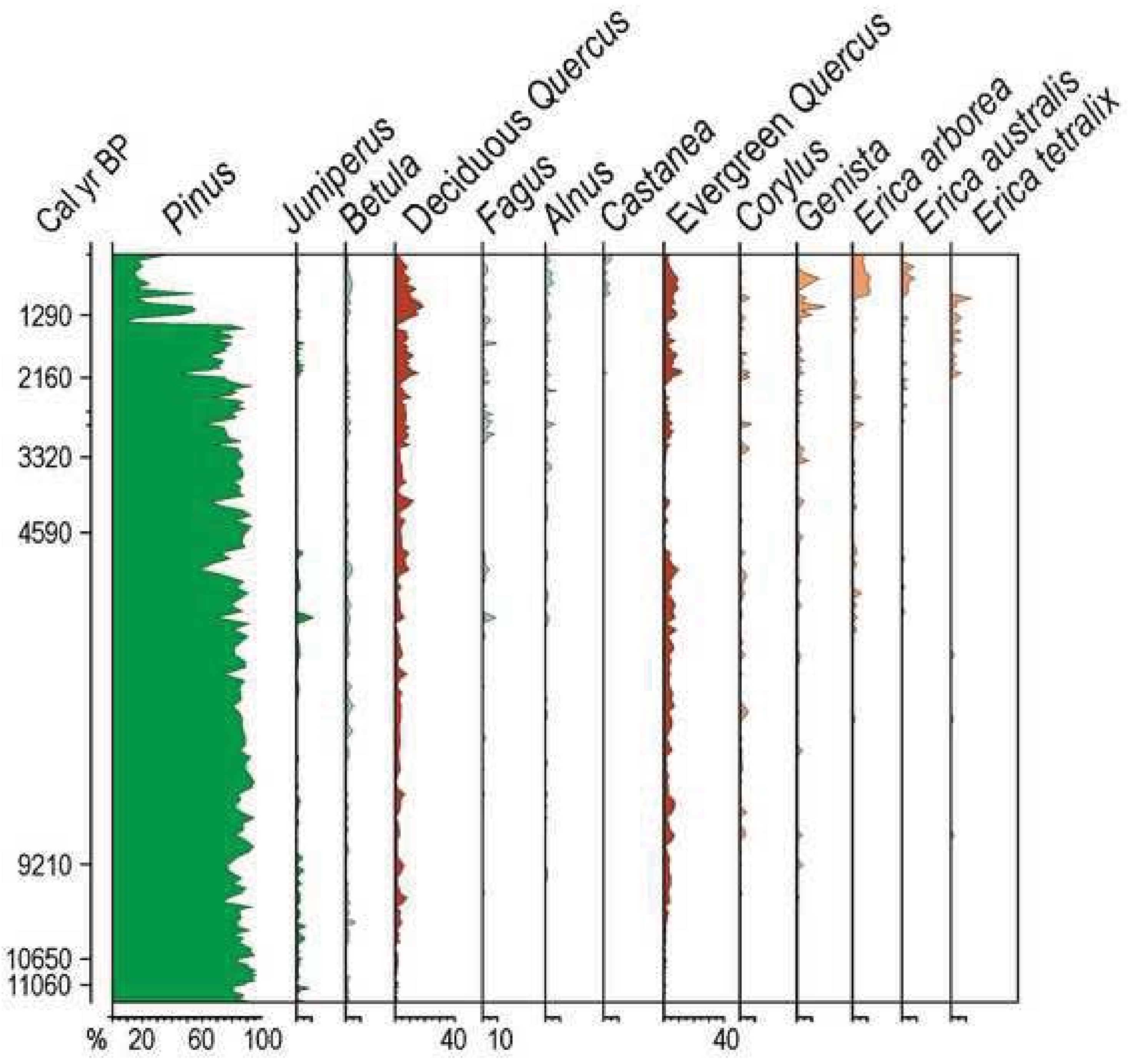
Cal yr BP
Pinus
Juniperus
Betula
Deciduous Quercus
Fagus
Alnus
Castanea
Evergreen Quercus
Corylus
Genista
Erica arborea
Erica australis
Erica tetralix
1290
2160
3320
4590
9210
10650
11060
%
20
60
100
40
10
40

Figure 8

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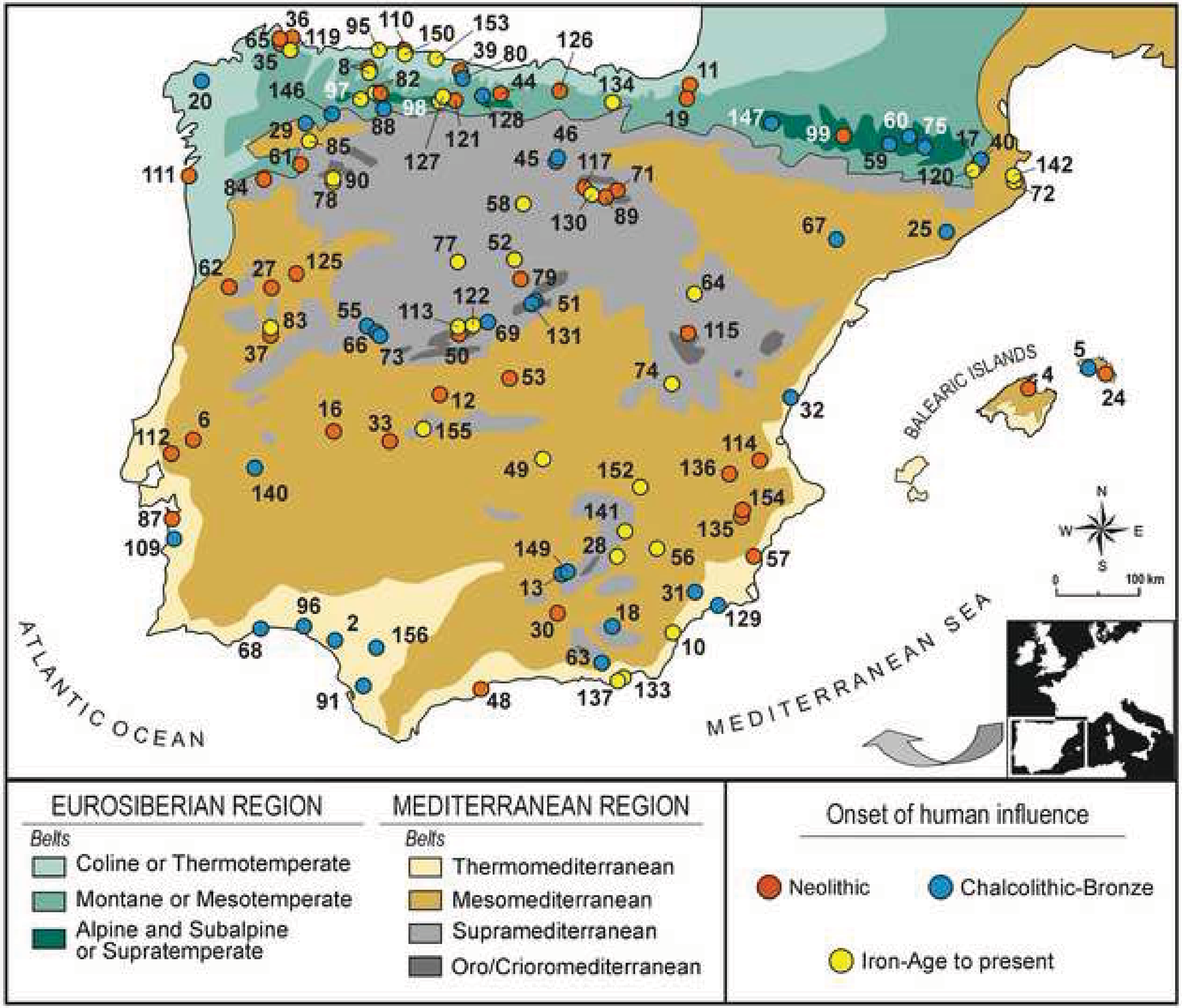

Figure 9

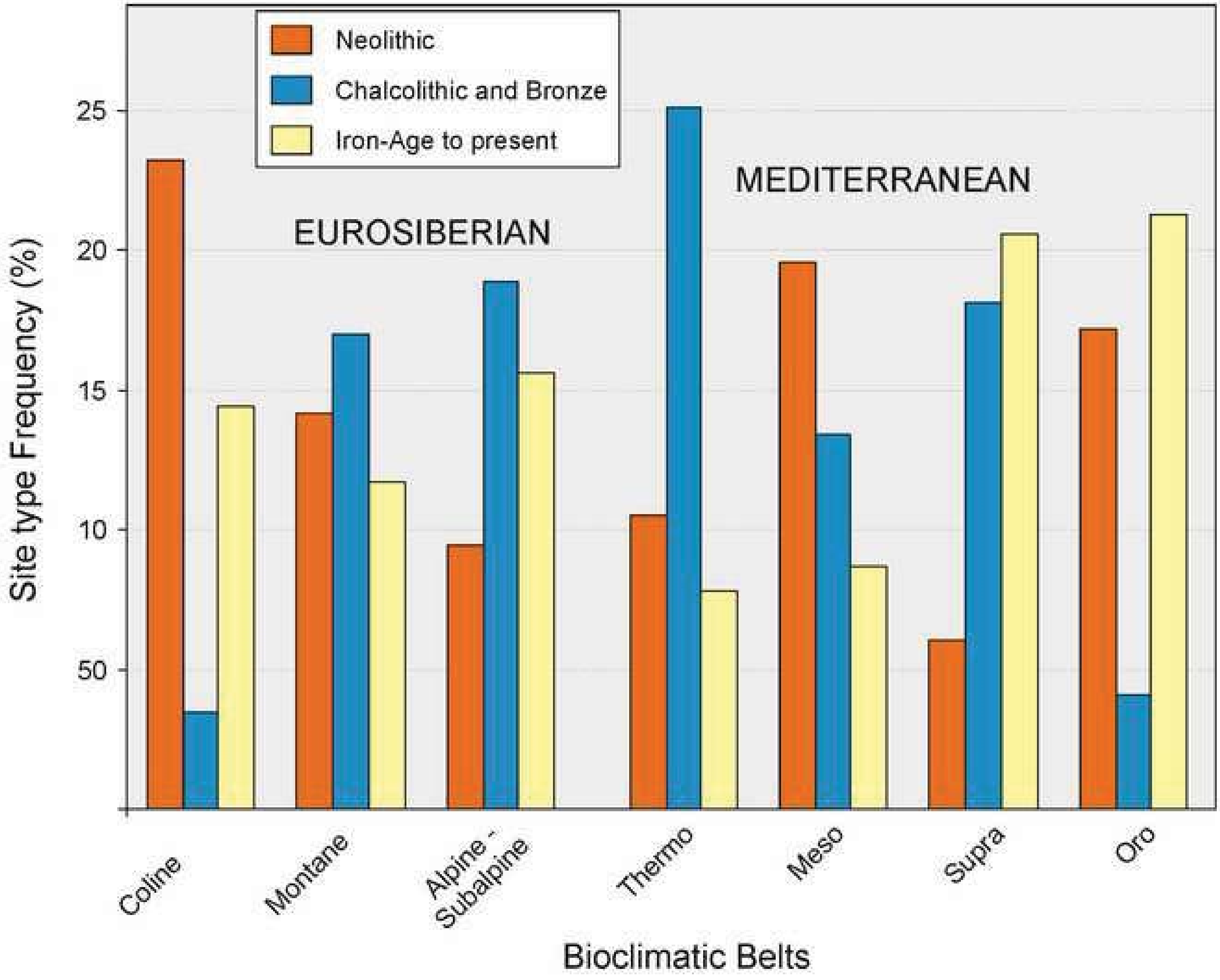
Neolithic
Chalcolithic and Bronze
Iron-Age to present
EUROSIBERIAN
MEDITERRANEAN
Site type Frequency (%)
25
20
15
10
50
Coline
Montane
Alpine - Subalpine
Thermo
Meso
Supra
Oro
Bioclimatic Belts

Figure 10

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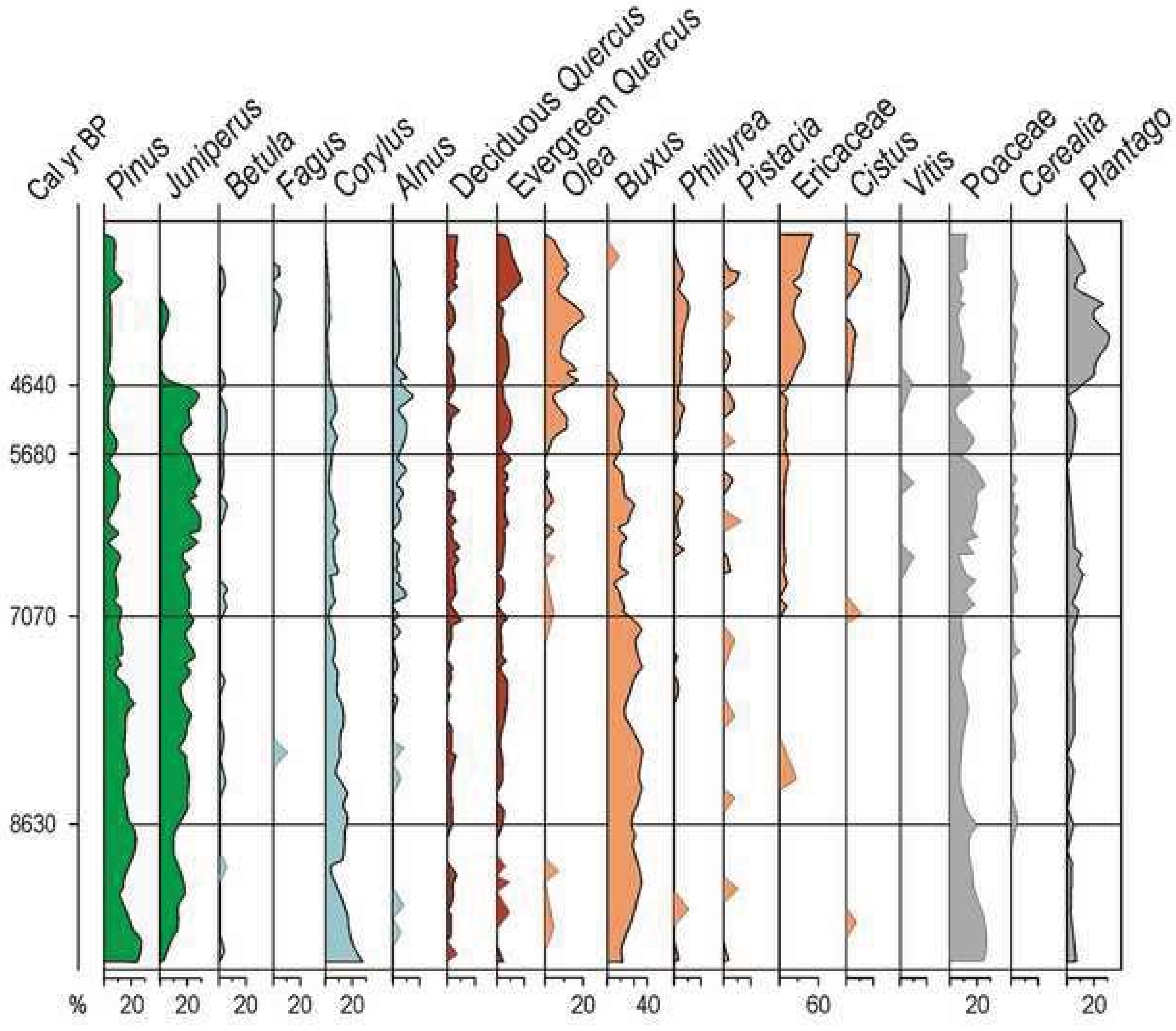

Figure 11

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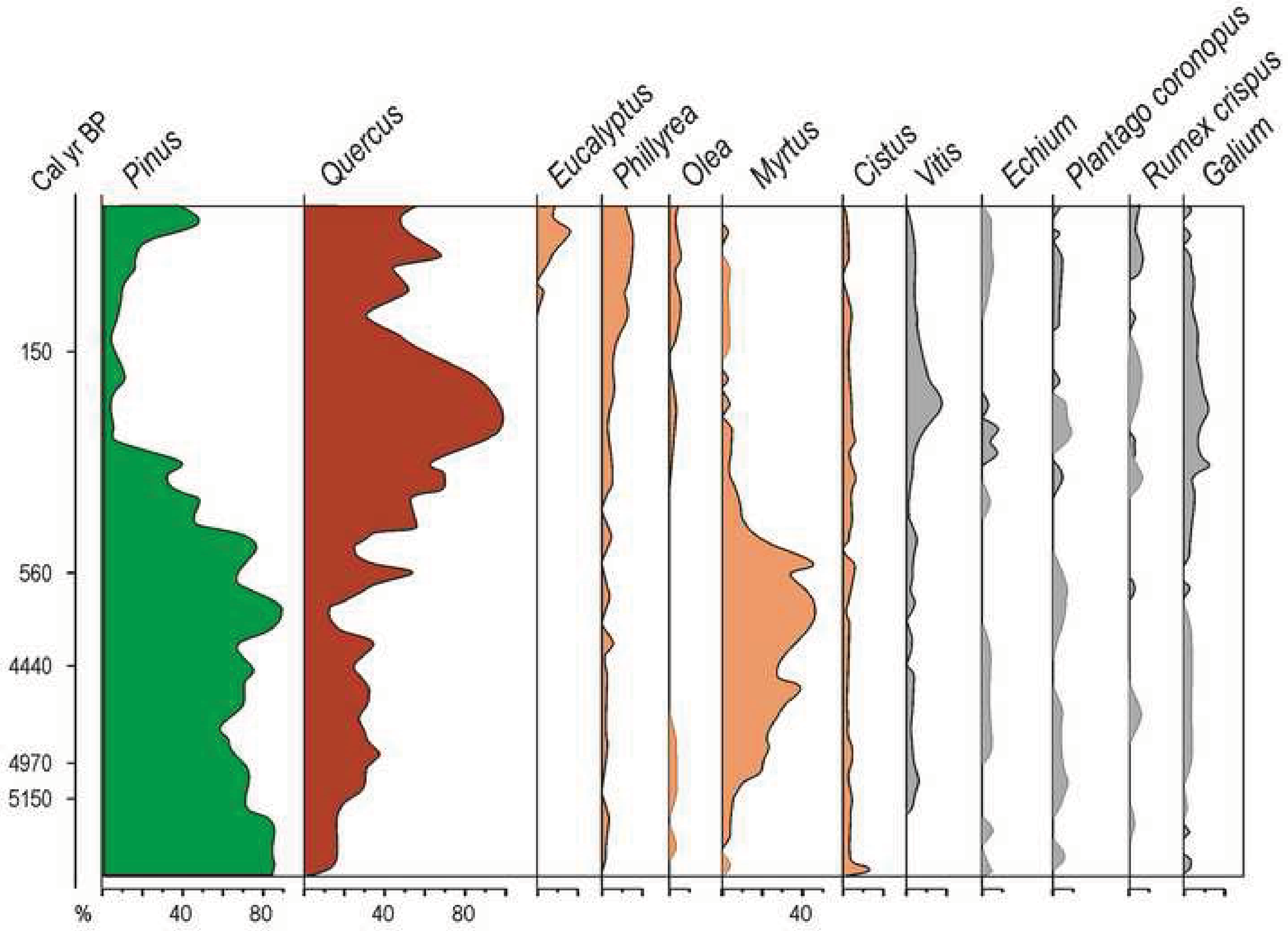
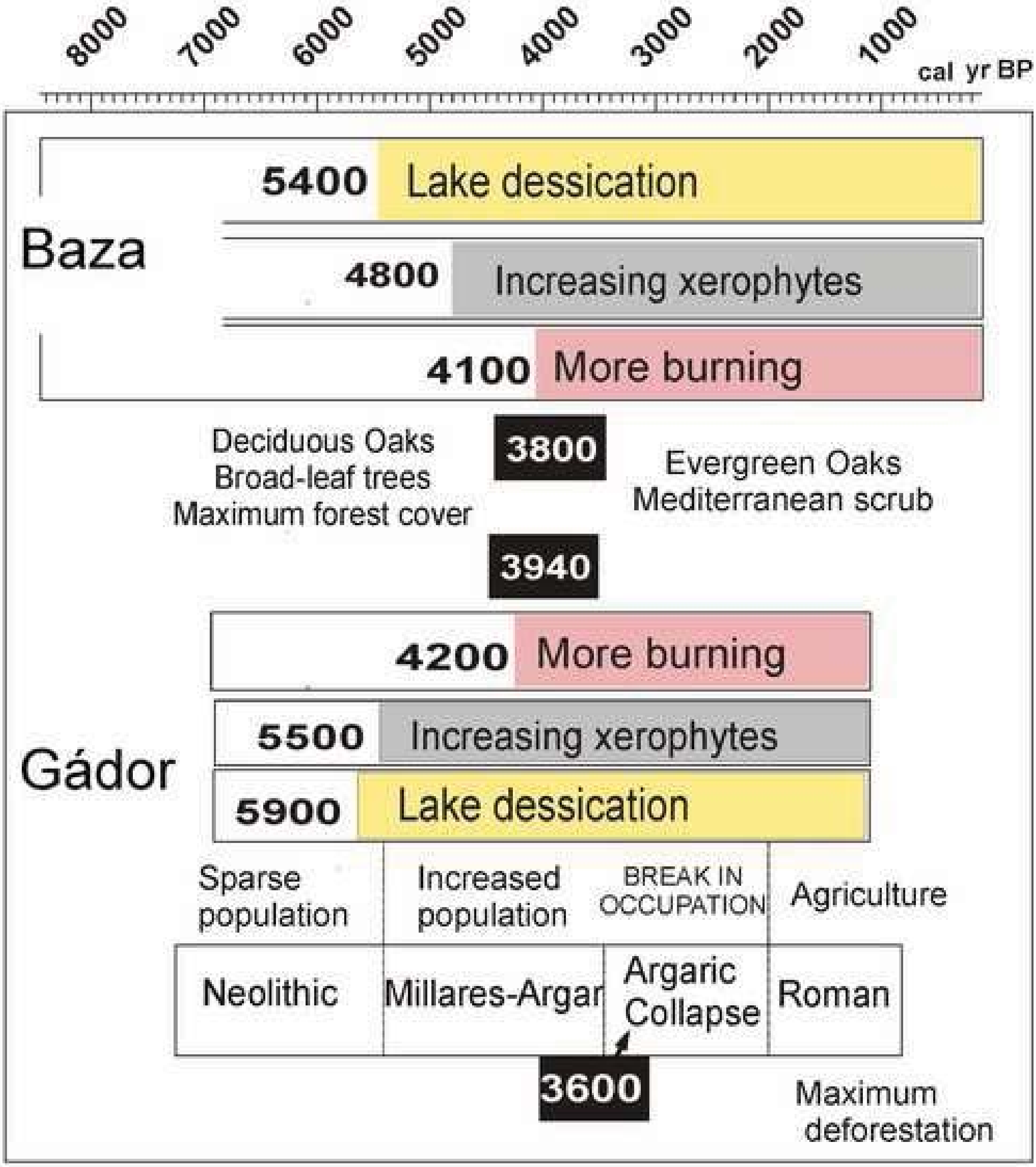


Figure 12


8000
7000
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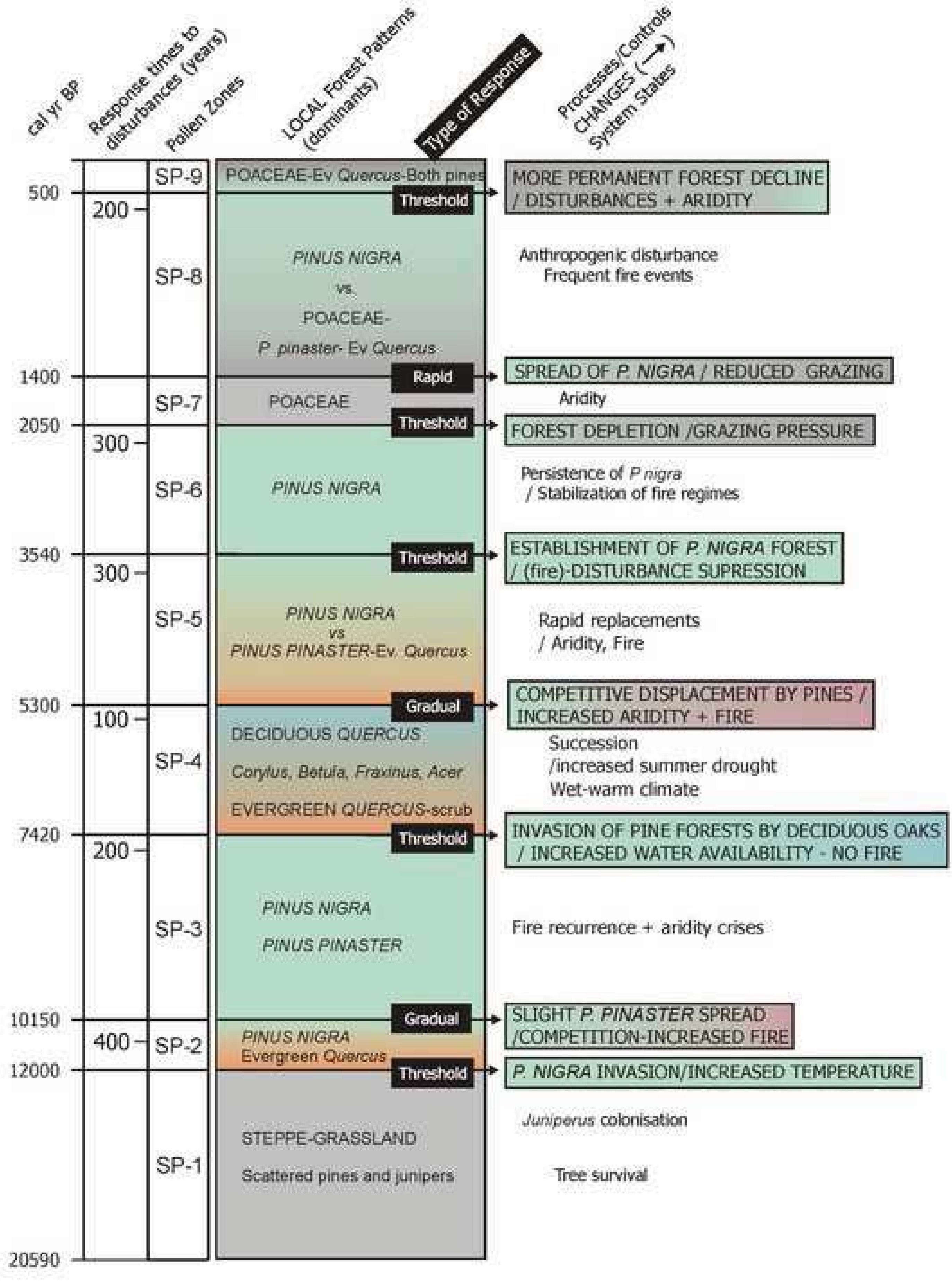
5000
4000
3000
2000
1000
cal yr BP
Baza
5400
Lake dessication
4800
Increasing xerophytes
4100
More burning
Deciduous Oaks
Broad-leaf trees
Maximum forest cover
3800
Evergreen Oaks
Mediterranean scrub
3940
Gádor
4200
More burning
5500
Increasing xerophytes
5900
Lake dessication
Sparse population
Increased population
BREAK IN OCCUPATION
Agriculture
Neolithic
Millares-Argar
Argaric Collapse
Roman
3600
Maximum deforestation

Figure 13


cal yr BP
Response times to disturbances (years)
Pollen Zones
LOCAL Forest Patterns (dominants)
Type of Response
Processes/Controls CHANGES (⟶) System States
500
200
SP-9
POACEAE-Ev Quercus-Both pines
Threshold
MORE PERMANENT FOREST DECLINE / DISTURBANCES + ARIDITY
SP-8
PINUS NIGRA vs. POACEAE- P. pinaster- Ev Quercus
Anthropogenic disturbance
Frequent fire events
1400
Rapid
SPREAD OF P. NIGRA / REDUCED GRAZING
SP-7
POACEAE
Aridity
2050
Threshold
FOREST DEPLETION /GRAZING PRESSURE
300
SP-6
PINUS NIGRA
Persistence of P nigra / Stabilization of fire regimes
3540
Threshold
ESTABLISHMENT OF P. NIGRA FOREST / (fire)-DISTURBANCE SUPRESSION
300
SP-5
PINUS NIGRA vs PINUS PINASTER-Ev. Quercus
Rapid replacements / Aridity, Fire
5300
Gradual
COMPETITIVE DISPLACEMENT BY PINES / INCREASED ARIDITY + FIRE
100
SP-4
DECIDUOUS QUERCUS
Corylus, Betula, Fraxinus, Acer
EVERGREEN QUERCUS-scrub
Succession /increased summer drought
Wet-warm climate
7420
Threshold
INVASION OF PINE FORESTS BY DECIDUOUS OAKS / INCREASED WATER AVAILABILITY - NO FIRE
200
SP-3
PINUS NIGRA
PINUS PINASTER
Fire recurrence + aridity crises
10150
Gradual
SLIGHT P. PINASTER SPREAD /COMPETITION-INCREASED FIRE
400
SP-2
PINUS NIGRA
Evergreen Quercus
12000
Threshold
P. NIGRA INVASION/INCREASED TEMPERATURE
Juniperus colonisation
SP-1
STEPPE-GRASSLAND
Scattered pines and junipers
Tree survival
20590