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IBERIAN FLORAS THROUGH TIME: LAND OF DIVERSITY AND SURVIVAL

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Preface

Iberian floras through time: Land of diversity and survival

The current Iberian Peninsula holds palaeobotanical and palaeoecological singularities that can be situated within the geographic contexts of Europe, western Mediterranean, and western Palaearctic. Over long periods of geological time, this has been a land of transitions and physiographical heterogeneity, including the eventual occurrence of islands, and contacts with the African continent. The general outcomes of this geological scenario are both unique evolutionary histories and particular vegetation trajectories, including patterns of delayed extinction, or even survival of many taxa that became extinct in the rest of the western Palaearctic. In addition to the incorporation of new data from ongoing projects, this Special Issue of the Review collates information that has remained unpublished or was in Spanish and Portuguese specialist journals, symposia proceedings, seminar reports, PhD manuscripts, and other documentary sources of difficult access for the international audience.

This story begins 400 million years ago (Ma). During the Devonian, terranes relative to present-day Iberia embraced regions of Spain, Portugal, and west France, which were adjacent to northern Gondwana, and separated from Laurussia by a relatively narrow Rheic Ocean. Climates were generally warm, with prevalence of greenhouse type, and wide areas were eventually flooded creating marshland-like environments and land–sea ecotones without modern analogues. Devonian floras can only be reconstructed from an extremely fragmentary fossil record of plants, largely palynomorphs, thus limiting the potential of taxonomic discrimination and palaeoecological inference. Montero and Diéguez (2010) contend that Lower Devonian landscapes were probably dominated by early land plants with conducting tissue such as *Sciadophyton*, rhyniophytes (*Horneophyton*, *Cooksonia*, *Rhynia*, and *Nothia*), trimerophytes (*Pertica, and Hostinella*), and primitive lycophytes (*Drepanophycus*). A stratification of the vegetation is envisaged for the Middle Devonian with Cladoxylales (*Calamophyton*) in the superior level, and zosterophyllophytes in the basal stratum. Other groups including herbaceous and shrubby lycophytes and sphenophytes are added in the late Devonian giving the impression of floodplain ecosystems adjacent to flowing water and lakes. Revision and fieldwork are still needed to confirm these provisional reconstructions.

Fortunately the situation with the Carboniferous is different, for which Wagner and Álvarez-Vázquez (2010) provide an account of the impressive floristic diversity. The Iberian record of Stephanian floras is probably one of the most complete in the world. Although the exact linkages with the rest of current Europe are still matter of speculation, the Carboniferous of northern Iberia was deposited in the context of a Tethyan connection. In the meantime, the southern parts were amalgamating by means of strike-slip faulting. It is remarkable that the Iberian Peninsula, as we know it today, did not exist as such before the Cenozoic, while its core (Iberian Massif) was constituted in the latest Pennsylvanian.

Remaining in equatorial position, the everwet environments of Mississippian Iberia are floristically identical to the rest of Euro-American basins, explaining the occurrence of species like *Eoacanthocarpus feilitzschianus* (German floras), and *Genselia rarinervis* (North American floras). Mississippian forests are characterized in this region by arborescent lycopsids (*Archaeosigillaria*, and "*Lepidodendropsis*"), sphenophytes (*Archaeocalamites*, *Mesocalamites*, *Sphenophyllum*, *and Annularia*), and Palaeozoic foliages of eventual affinity with seed ferns, progymnosperms and ferns (*Rhacopteris*, *Eusphenopteris*, *Sphenopteris*, *Sphenopteridium*, and *Neuropteris*). Thereafter, during the Westphalian, the composition of the prevailing hyper-humid environments continues to be similar to that recorded in the Paralic Coal Belt of northern Europe and the Massif Central in France. Some particularities with regard to pteridosperms (less diversified in Iberia) exist, but these differences are interpreted to reflect local basin conditions. Prominent Westphalian taxa include *Lepidodendron mannebachense*, *L. obovatum*, and *Sigillaria tessellata*, together with characteristic species such as *Linopteris obliqua*, *Ulodendron acutum*, *Zeilleria avoldensis*, *Mariopteris muricata*, *Renaultia rotundifolia*, *Sphenophyllum majus*, *S. cuneifolium* and *Annularia radiata.*

Stephanian taxa include, among others, *Odontopteris brardii*, *Alethopteris zeillerii*, *Callipteridium zeillerii*, *Dicksonites plukenetii*, *Olicocarpia leptophylla*, and *Taeniopteris* sp. pl. Near the end of the Stephanian, the conifers and allies *Ernestiodendron filiciforme*, *Walchia piniformis*, *Autunia conferta*, and other foliage types suggestive of seed fern presence (*Callipteridium rochei*, and *Mixoneura osmundaeformis*), are incorporated in the assemblage. However, the overall botanical record of the Stephanian and Autunian points to the maintenance of very humid habitats. Interestingly this contrasts with the pattern observed in the rest of the Euramerican domain, where the progressive aridification of the latest Pennsylvanian and Permian increased the areas dominated by Voltziales, primitive conifers, and Peltaspermales. It is the first time, but not the last, that southern Iberia exhibits a delay in vegetational developments in the face of climatic changes.

It is of capital importance to progress in the study of the Carboniferous floras of Iberia using the large collections available, especially that in the Palaeobotanical Centre at the Botanical Garden of Córdoba. Since the stratigraphy is now finely established and the taxonomic work detailed, further research including palaeoecological, structural and functional analyses, would allow to penetrate deeper into the evolutionary mechanisms underlying the patterns of floristic change described by Wagner and Álvarez-Vázquez (2010).

Although Wagner and Álvarez-Vázquez (2010) include some notes, the Permian floras are not specifically treated in this issue, mainly because the information is scanty. As far as is known, Early Permian landscapes were covered by conifers and Peltaspermales of

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the "*Callipteris*" type, together with local development of marshlands with *Calamites*, ferns, and seed ferns (Menéndez Amor, 1952; Wagner and Mayoral, 2007). A Cathaysian and Angaran component is noticeable in the southernmost areas (Guadalcanal, Seville), which kept higher phytodiversity (Broutin, 1986; Wagner, 2005). Upper Permian floras comprise more gymnosperms at the expense of pteridophytes. It is the time for Pentoxylales, Majonicaceae and Utrechtiaceae, while a sharp reduction in diversity is shown during the latest Permian as a result of regional extinction within Majonicaceae and Ulmaniaceae (Diéguez et al., 2007).

The floral record of the Triassic "Buntsandstein" facies is presented by Díez et al. (2010), reporting for the first time on the Anisian floras in Spain. Apart from poor palynological preservation, and scarcity of macroremains, the study of the Iberian Triassic is hampered by the repeated occurrence of sedimentary gaps, which do not necessarily mean the existence of climatically-induced erosion (Preto et al., 2010). With all these pitfalls, the available information suggests that conifers eclipsed other plant groups in the Triassic landscapes of Iberia and the Balearic Islands. As in other parts of the world, the lycophyte *Pleuromeia* may have represented a role in the vegetation recovery after the Permian/Triassic ecosystem disruption (Knoll et al., 2007). Thereafter, Iberian floras resemble the "Grès à Voltzia" flora of northern France (Grauvogel-Stamm, 1978). In the Iberian Anisian, some genera become common such as *Voltzia*, *Albertia*, *Willsiostrobus*, *Anomopteris*, *Pelourdea*, and *Neocalamites* among the macrofossils, and *Lunatisporites*, *Triadispora*, *Alisporites*, *Voltziaceaesporites*, *Hexasaccites*, *Chordasporites*, *Platysaccus*, *Protohaploxypinus*, *Brachysaccus*, *Cycadopites*, and *Calamospora*, among the microfossils. Late Triassic conifers were progressively invading and replacing pteridophytic-dominated communities. Representatives of Cheirolepidiaceae were of particular relevance (Solé de Porta et al., 1987; Doubinger et al., 1990; Sopeña et al., 2009) and some remarkable cases of floristic turnover occurred at the end of the Carnian to the benefit of *Classopollis*-producing plants (Calvet et al., 1993).

Due to tectonic subsidence during the Jurassic and Cretaceous, a system of shallow marine carbonate platforms developed in a great part of the Iberian Block. The context was one of intracratonic basins, and eventually insular, plausibly favouring allopatric speciation and giving place to a particular composition of regional floras. Another outstanding geological event takes place during the Cenomanian when the Iberian Peninsula rotated almost 26° in an anticlockwise direction with respect to the current North Pole and to Europe, moving towards 30°N in palaeolatitude. These changes certainly influenced the biological history of Iberia during the last 200 Ma. Diéguez et al. (2010) bring to this issue a detailed discussion of the floristic and vegetation changes during the period from Triassic–Jurassic to Cretaceous–Paleocene boundaries. Xerophytic forests dominated by microphyllous conifers are typical of Jurassic and early Cretaceous periods, while most of the Cretaceous is characterized by mixed forests of gymnosperms and angiosperms within a generally subtropical climate interrupted by two warm–dry episodes in the Jurassic–Cretaceous and Aptian–Albian transitions.

Lower Jurassic Iberia, as based on palynological assemblages, is still characterized by *Classopollis*-producing plants, with striking differences in the regional balance of other element such as Araucariaceae, Pinaceae, Ginkgoales, Cycadales and Bennettitales (Diéguez et al., 2010). The Triassic/Jurassic humid interval is postulated to have increased the presence of hydrophytic lycopsids, ferns and Taxodiaceae. Plant communities during the Lower Jurassic were most likely dominated by gymnosperms in the arboreal stratum, with small lycophytes and ferns in the understorey. Swamp environments are inferred from the growing frequencies of *Spheripollenites* between c. 195 and 185 Ma. The gymnosperm fossil record increases during the Upper Jurassic, probably in the context of a winter-wet biome in the Iberian Massif. The vegetation is still characterized by cheirolepids in the canopy, but pteridosperms and Bennettitales may have entered into competition with ferns and lycophytes in the understorey.

Cretaceous macrofloras until the Albian are rich in xeromorphic ferns (*Ruffordia*, *Onychiopsis*, and *Weichselia*), and microphyllous conifers (*Brachyphyllum*, *Sphenolepis*, and *Cupressinocladus*), with occasional macrophyllous such as *Podozamites*, and scarcity of Ginkgoales, Caytoniales and other pteridosperms (Diéguez et al., 2010). It is also worth mentioning the enhanced provincialization of the floras. The coexistence of Araucariaceae, Taxodiaceae, Cupressaceae, Pinaceae, Podocarpaceae, Ginkgoaceae, Matoniaceae, and Dicksoniaceae is a remarkable feature of the Aptian to Cenomanian interval. From c. 83 to 65 Ma (Campanian–Maastrichtian), several regions were already dominated by angiosperms (e.g. Fagales, Combretaceae, and Arecaceae), which had been gaining ecological preponderance at the expense of Cheirolepidiaceae and conifers.

Cretaceous diversification of angiosperms is spatially transgressive along the Peninsula, with the Lusitanian Basin (largely current Portugal) preceding the rest, and providing fossil records of such importance as to change many long-standing views about the "abominable mystery" (following Darwin's quote) about the radiation of angiosperms during the early Cretaceous. Friis et al. (2010) contribute new findings to the existing palaeodatabase of angiosperms to produce a coherent picture of the radiation. Mesofossil floras start as early as during the Late Barremian–Early Aptian (125 Ma) in the Torres Vedras locality, with a number of monoaperturate pollen-producing plants (e.g. *Appomattoxia*, and *Hedyosmum*-like flowers) assigned to Chloranthaceae, Piperales, Nymphaeales, Alismatales, and other basal angiosperms. By the Late Aptian–Early Albian (110 Ma), eudicotyledon diversification is well under way and during the Late Cretaceous (95–65 Ma) the *Normapolles* complex prevails in the pollen spectra and remains of their flowers and fruits (*Normanthus*, *Endressianthus*, and *Caryanthus*) among the reproductive structures (Friis et al., 2006, 2010).

Palynological assemblages from the Sant Just site in the Escucha Formation (Villanueva-Amadoz et al., 2010) show that these rapid patterns of speciation have a counterpart in eastern Iberia during the Albian. New species (e.g. *Pennipollis escuchensis*) are described, but overall, the record of microfossils conforms with other southern Laurasian localities, although retaining some Gondwanan component. For the west, however, Friis et al. (2010) describe strong divergences in systematic composition of the Iberian floras in line with those from the rest of Europe and North America. The diversity of Late Cretaceous core eudicotyledons and reproductive innovations are astonishing in the Portuguese floras. SEM micrographs and synchrotron-radiation X-ray tomographic microscopy join to provide highly-resolved images of the internal structures of Cretaceous flowers.

The last c. 65 Ma in Iberia shows intense geological activity and consequent evolutionary events (Barrón et al., 2010). While during the Upper Cretaceous, the Iberian plate was relatively uniform, from Palaeocene to Miocene several important tectonic events took place (Pyrenees, Cantabrian, Iberian and Betic ranges). Other features of this period include the formation of the Guadalquivir basin during the Neogene, the closing of the North Betic straits about 5.9–5.6 Ma leading to the salinity crisis of the Messinian and land communication between Iberia, Africa and Asia. The opening of the Gibraltar Strait took place during the Lower Pliocene.

Barrón et al. (2010)'s paper is the first comprehensive approach to the Iberian palaeobotany during the Cenozoic. The Palaeogene is shown to be dominated by Palaeotropical elements in the context of rainforests, mangroves (*Acrostichum*, *Avicennia*, *Aegiceras*, *Browlonia*, and *Pelliceria*), laurisilvae, and sclerophyllous communities characterized by Rhamnaceae (*Ziziphus*, *Rhamnus*, and *Paliurus*) and legumes (*Acacia*, *Albizzia*, *Caesalpinia*, *Cassia*, *Mimosa*, and *Gleditsia*). A dramatic change occurs during the Miocene owing to cooling and aridification, which allowed heliophytic communities (*Ephedra*, Chenopodiaceae, Asteraceae, *Combretum*, and Thymeleaceae) to spread. This is also the time for the peninsular invasion of Arctotertiary plants (e.g. *Alnus*, *Castanea*, *Salix*, *Ulmus*, *Abies*, *Corylus*, *Tsuga*, *Zelkova*, *Acer*, and *Juglans*) which moved across mountain chains and fluvial courses. The coexistence of Arctotertiary and Palaeotropical components was less and less frequent across the Tertiary, the culmination of a first background extinction of the latter being obvious by the Late Miocene. Carrión and Fernández (2009), based on a Cenozoic database by Postigo-Mijarra et al. (2009), showed that the extinction rates of Iberian vascular plants are relatively high during three phases, namely the Oligocene (10.67 total taxa/Ma), the Pliocene (8.22 taxa/Ma) and the Quaternary (13.29 taxa/Ma). It is, however, worth mentioning that some thermophytes survived during the late Neogene and Pleistocene to present day, such as the Palaeotropical *Laurus nobilis*, *Rhododendron ponticum*, *Prunus lusitanica* and *Myrica faya*.

The quality of the Iberian pollen record from Miocene to Pliocene has allowed Jiménez-Moreno et al. (2010) to reconstruct vegetation and climatic changes for this interval. This analysis postulates a gradual reduction in plant diversity that parallels the expansions of Mediterranean taxa, high-elevation conifers and xero-heliophytic groups. The development of patches of steppe-like vegetation is shown to root as deep in time as in the Oligocene, while the onset of contrasted seasonality in temperature may have started in the Middle Pliocene superimposed on a pre-existing seasonality in precipitation. The Mediterranean climatic rhythm is proposed to have been established around 3.4 Ma. This paper also provides evidence for strong physiographical gradients in the Iberian Peninsula ever since the Middle Miocene.

Although it is unlikely that vascular plants have experienced mass extinction in the way marine and terrestrial faunas did (Willis and McElwain, 2002), regional events have occurred. Since they provoke changes in distribution, it is important to gather detailed information as to how the extinction varied geographically, and to what extent the sequence of biodiversity loss has affected present-day floristic composition. Yet, to which extent this is influenced by survival of some taxa. This is a principal theme that inspirates Postigo-Mijarra et al. (2010)'s paper in this issue. It is therefore remarkable that, instead of the expected Plio-Pleistocene transition, the Early to Mid Pleistocene boundary shows extinction for taxa like *Cathaya*, *Elaeagnus*, *Engelhardia*, *Eucommia*, *Keteleeria*, *Liquidambar*, *Nyssa*, *Parrotia*, *Parthenocissus*, *Pterocarya*, *Sciadopitys*, *Symplocos*, *Aesculus* and Taxodiaceae. Other taxa survived until the Middle Pleistocene such as *Carya*, *Ostrya* and Mimosaceae.

Pleistocene vegetation deserves attention on its own. A detailed examination of the location and composition of glacial refugia for temperate and Mediterranean angiosperm woods, suggests that the Iberian Pleistocene was a period of complexity in landscapes, ecosystems, and biotic responses to climate changes forced by orbital and suborbital variability (González-Sampériz et al., 2010). Stepp landscapes extended during the cold spells of the Quaternary. Coastal shelves and intramountain valleys are spots of floristic diversity and nuclei of population expansion during climatic ameliorations. Vegetational landscapes were highly heterogeneous, so suitable to fast recovery after disturbance. The diversity of Pleistocene landscapes includes savannah-like ecosystems, pine woodlands, deciduous and mixed forests, shrublands, steppes and grasslands. The survival of broad-leaf trees, Mediterranean and Ibero-North African taxa (e.g. *Periploca*, *Osyris*, *Maytenus*, and *Whitania*) can be satisfactorily explained by resource to multi-refugia models which are supported by studies of genetic structure of modern populations (Rodríguez-Sánchez et al., 2010). Cases with rapid response of vegetation to orbital and suborbital variability are also shown by González-Sampériz et al. (2010).

Pleistocene plant geography critically shaped vegetation dynamics during the early to mid Holocene, provoking local situations of millennial-scale resilience of the established communities. Carrión et al. (2010) make a conceptual experiment by separating the vegetation histories of directional change through time from those that exhibit accidental trajectories. The emergence of anthropogenic events is detected in some sequences from the mid Holocene, but is extraordinarily delayed in others. In the Mediterranean region, a threshold response to increased burning in the form of competitively-mediated *Quercus* invasion of pine forests during the Mid Holocene, is sometimes observed. The succession in the Balearic Islands seems strongly dependent on the starting (early Holocene) floristic composition. Finely resolved pollen records show that major changes in vegetation may occur concentrated into relatively short episodes and that the rate of change is generally uneven. This points to the convenience of a historical-contingent rather than a deterministic approach.

In connection with the former, and using new data on macroremains in addition to existing palynological information, Rubiales et al. (2010) debate the role of pinewoods as native forests in the Iberian Mountains during the Lateglacial and Holocene. *Pinus*-dominated formations, largely *P. nigra*, *P. sylvestris*, and *P. pinaster*, are interpreted on the basis of life history traits and patterns of plant dynamics derived from ecological studies, e.g. incumbency, frugality, and ability to disperse.

In support of this thesis is the paper by Valbuena-Carabaña et al. (2010), which brings historical sources of vegetation change into the arena. These authors show how Spanish forests have been shaped by human activities including clearance for mining, charcoal, shipbuilding and caulking. From this paper, it is clear that there is no possible return to a hypothetical pristine woodland, as no forest in the region can be considered free of human influence. Times and spatio-temporal pathways of agriculturization, pastoral uses, social and administrative changes, are here detailed. This definition of Iberian cultural landscapes is now ineluctable for environmental management policy.

The closing paper of this Special Issue (Rodríguez-Sánchez et al., 2010) is a successful case study on how palaeobotany may join phylogeography and species distribution modelling in order to shed light on past tree range dynamics. The focus is on major Iberian forest types, and special attention is given to *Quercus*, *Pinus*, *Fagus*, *Laurus*, *Abies*, *Fraxinus*, *Corylus*, *Betula*, *Frangula*, *Salix*, *Alnus*, *Populus*, *Castanea*, *Olea*, *Juniperus*, *Ilex* and *Hedera* species. Some outstanding conclusions are (i) that the Mediterranean and Atlantic regions of the Peninsula have independently sustained viable populations of trees over multiple glacial cycles, (ii) that different species, and populations within species, have responded idiosyncratically to past climatic changes under a variety of influences including life histories, dispersal abilities, ecological requirements, and the initial geographical contexts; and (iii) that the Iberian Peninsula appears to be one of the most significant sources for postglacial range expansions of forest trees. Finally, Rodríguez-Sánchez et al. (2010) show examples of suitable areas that could have sustained so far undetected refugia. The implications for conservation policies are also formidable: these long persisting, evolutionarily unique populations should be considered high-priority targets.

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