



Taxonomic depletions and ecological disruption of the Iberian flora over 65 million years

Vascular plants do not appear to experience mass extinctions (Willis & McElwain, 2002), and, as Traverse (1988) has stressed, 'Plant evolution dances to a different beat'. This may be because of the ecophysiological and reproductive plasticity of many groups of terrestrial plants, as well as of the high frequency with which alterations in embryo development become evolutionarily fixed. It is probable that some aspects of this model will have to be reconsidered in forthcoming years as progress is made in stratigraphic resolution and as we improve the quality of the fossil record (McElwain & Punyasena, 2007). Nevertheless, it is clear that regional extinction events have occurred in plants and that these were related to changes in biome distribution and floristic composition at a continental level (Willis & McElwain, 2002). As biotic responses to climatic change have not been the same in all regions, it is crucial to gather detailed information concerning how these phenomena have varied geographically and to what extent the sequence of biodiversity loss has affected present-day floristic composition in different parts of the world.

It is for this reason that we welcome the study by Postigo *et al.* (2009), which represents a monumental effort of nomenclatural screening, bibliographic scrutiny, and a broad conceptual consideration of the history of plants in the Iberian Peninsula and the Balearic Islands over the last 65 million years. This review of Cenozoic floras will be of particular use in international palaeontological and neontological contexts because most of the information sources discussed are difficult to find by means of conventional bibliographic and data-search protocols; for example, they include symposium proceedings, conference and unpublished reports, local journals and monographs, which are mostly in Spanish and Portuguese. Postigo *et al.* (2009) provide a critical review of the floristic composition and ecology of Palaeotropical and Arctotertiary taxa in Cenozoic forest communities and detail the extinctions of a number of families and genera in relation to climate change.

Plants have often managed to escape abiotic stress through geographical redistribution, and the Mediterranean region has a number of examples illustrating this (Arroyo *et al.*, 2008). The changes described in Postigo *et al.* (2009) demonstrate this phenomenon, and it is of particular note that Iberian floras have experienced long periods of persistence compared to floras in the rest of Europe. As Postigo *et al.* (2009) postulate, this can be reasonably explained using the concept of peninsular refugia (Carrión *et al.*, 2008). However, it is also plausible that complex ecological interactions, including those derived from the enormous faunal diversity of Iberia during the Cenozoic, as well as phylogenetically

structured mutualistic networks, provide an environment particularly favourable to climatic resilience.

Looking at Postigo *et al.*'s (2009) database, several examples of the 'Lazarus effect' can be detected, that is, cases for which an apparently extinct taxon reappears in younger rocks. Among others, there are *Phaleria* and *Carpodiptera* across the Late Eocene–Early Oligocene interval; Gleicheniaceae and *Podocarpus* from the Palaeocene to the Oligocene; Chloranthaceae, Restionaceae, *Nypa*, Myrsinaceae, Simaourabaceae and Cycadaceae across the Palaeocene/Eocene up to the Miocene; Bombacaceae during the end of the Palaeocene; Menispermaceae, *Hamamelis*, *Pittosporum* and *Celastrus* from

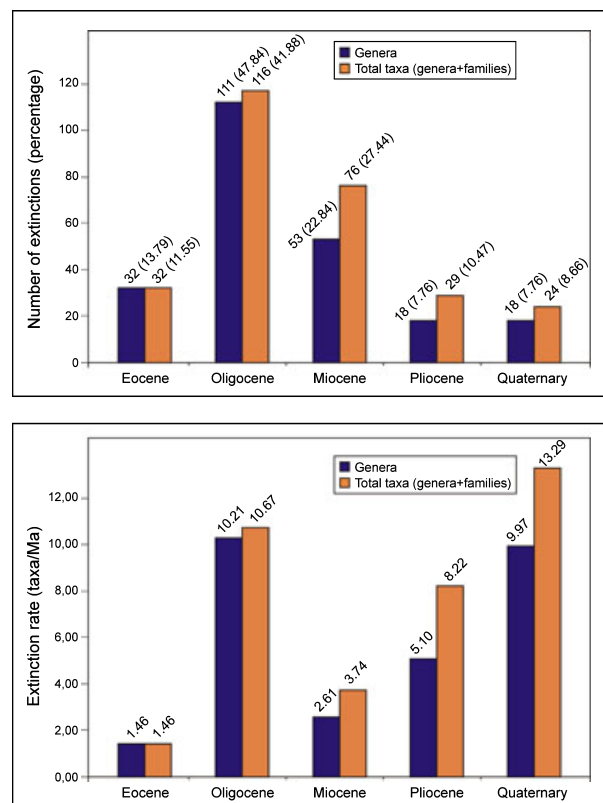


Figure 1 Number of extinctions accumulated per geological period, and extinction rate (taxa Ma⁻¹) of Iberian and Balearic vascular plants during the Cenozoic. Percentages in brackets. Data source: Postigo *et al.* (2009).

the Oligocene to the mid-Pliocene; and *Engelhardtia*, *Nyssa*, *Sciadopitys* and *Symplocos* throughout their Palaeogene records.

Even more thought-provoking is the possibility of a Signor–Lipps effect in several records. These are situations in which the last occurrences precede the true times of extinction (Taylor, 2004). For example, it may be that several taxa that disappeared during the Zanclean (5.3–3.6 Ma) (e.g. *Ginkgo*, Cyatheaceae, Clethraceae–Cyrillaceae, *Andromeda*) may actually have become extinct at the Piacenzian extinction horizon (3.6–2.5 Ma). It is also worth considering whether the significant decline during the middle Chattian, about 25 Ma, in fact corresponds to an Oligocene–Miocene boundary regional extinction. Poor sampling and gaps in the fossil record may have reduced the perceived severity of peninsular extinctions during particular events.

Figure 1 summarizes the extinction record depicted by Postigo *et al.* (2009) (in their figure 4, and tables 1 and 2). The number of extinctions peaks during the Oligocene, with 41.88% of the total Cenozoic disappearances. Oligocene disappearances are even higher (47.84%) if we consider only genera. As Postigo *et al.* (2009) indicate, Miocene extinctions are also significant (27.44% of total taxa), although the Pliocene and Quaternary periods do not include high numbers of extinctions (10.47 and 8.66%, respectively). However, the situation is very different if we take into account extinction rates (Fig. 1): whereas the Oligocene has a large value (10.67 total taxa Ma⁻¹), the Pliocene (8.22 taxa Ma⁻¹) and Quaternary (13.29 taxa Ma⁻¹) also have high rates of phytodiversity loss. More specifically, as seen from data shown in Postigo *et al.*'s figure 4, major biotic crises are indicated at the end of the Oligocene (c. 28–23 Ma), at the Piacenzian (3.6–2.5 Ma), and during the Lower–Mid Pleistocene transition (1.4–0.7 Ma). The last of these was probably associated with the beginning of the 100-kyr climatic cyclicity and a general cooling trend.

Taken together, these new data open up exciting avenues for future research; for

example, a quantitative study to compare the per taxon extinction, the extinction rates, and the per taxon extinction rates in the Iberian Peninsula with those of the rest of the European continent. This may allow clarification of the post-extinction diversification dynamics and biotic interchanges in plants of the region. Lineage extinction is also a promising topic of research, considering the phylogenetic relatedness between several groups of the taxa analysed. Equally interesting would be the capability to uncouple ecological and taxonomic impacts (McGhee *et al.*, 2004) in each of the temporal extinction windows, although, in this case, it would be necessary to compare the data with the avian, terrestrial tetrapod and insect fossil records. The final aim would be to ascertain the level of collapse in the pre-existing ecosystem.

Clearly, not all taxa in an ecosystem have the same importance. In the Iberian Peninsula, few will doubt that the selective removal of the Oligocene tropical group during the Chattian (28–23 Ma; including the Bombacaceae, Nyctaginaceae and Annonaceae); of *Torreya* at c. 7 Ma; and of the Arecaceae, Ebenaceae, Magnoliaceae and Sapindaceae during the Early Pliocene, c. 3 Ma, must have had a tremendous impact on the ecological structure of communities. This is especially true for those possessing megafauna dispersal-syndrome fruits (e.g. Icacinaceae, Passifloraceae, Annonaceae, Sapotaceae) (Guimarães *et al.*, 2008). Finally, we should not forget that biodiversity losses not only result from high extinction rates, but may also result from a depression in the rate of species production, or from some combination of both processes.

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REFERENCES

- Arroyo, J., Carrión, J.S., Hampe, A. & Jordano, P. (2008) La distribución de las especies en diferentes escalas espacio-temporales. *Ecología del bosque mediterráneo en un mundo cambiante* (ed. by F. Valladares), pp. 29–70. Ministerio de Medio Ambiente, Madrid.
- Carrión, J.S., Finlayson, C., Finlayson, G., Fernández, S., Allué, E., López-Sáez, A., López-García, P., Gil, G. & González-Sampériz, P. (2008) A coastal reservoir of biodiversity for Upper Pleistocene human populations. *Quaternary Science Reviews*, **27**, 2118–2135.
- Guimarães, P.R., Jr, Galetti, M. & Jordano, P. (2008) Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE*, **3**, e1745. doi: 10.1371/journal.pone.0001745.
- McElwain, J.C. & Punyasena, S. (2007) Mass extinction events and the plant fossil record. *Trends in Ecology and Evolution*, **22**, 548–557.
- McGhee, G.R., Jr, Sheenan, P.M., Bottjer, D.J. & Droser, M.L. (2004) Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **211**, 289–297.
- Postigo, J.M., Barrón, E., Gómez-Manzanque, F. & Morla, C. (2009) Floristic changes in the Iberian Peninsula and Balearic Islands (SW Europe) during the Cenozoic. *Journal of Biogeography*. doi: 10.1111/j.1365-2699.2009.02142.x.
- Taylor, P.D. (ed.) (2004) Extinction and the fossil record. *Extinctions in the history of life*, pp. 1–34. Cambridge University Press, Cambridge.
- Traverse, A. (1988) Plant evolution dances to a different beat. *Historical Biology*, **1**, 277–301.
- Willis, K.J. & McElwain, J.C. (2002) *The evolution of plants*. Oxford University Press, Oxford.

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