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Quaternary disappearance of tree taxa from Southern Europe: Timing and trends

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ABSTRACT

A hundred pollen and plant macrofossil records from the Iberian Peninsula, Southern France, the Italian Peninsula, Greece and the Aegean, and the southwestern Black Sea area formed the basis for a review of the Quaternary distribution and extirpation of tree populations from Southern Europe. Following a discussion of the caveats/challenges about using pollen data, the Quaternary history of tree taxa has been reconstructed with attention to *Taxodium*/*Glyptostrobus*, *Sciadopitys*, *Cathaya*, *Cedrus*, *Tsuga*, *Eucommia*, *Engelhardia*, *Carya*, *Pterocarya*, *Parrotia*, *Liquidambar*, and *Zelkova*. The timing of extinction, distributed over the whole Quaternary, appears very diverse from one region to the other, in agreement with current biodiversity in Southern Europe. The geographical patterns of persistence/disappearance of taxa show unexpected trends and rule out a simple North to South and/or West to East trend in extirpations. In particular, it is possible to detect disjunct populations (*Engelhardia*), long-term persistence of taxa in restricted regions (*Sciadopitys*), distinct populations/species/genera in different geographical areas (*Taxodium* type). Some taxa that are still widespread in Europe have undergone extirpation in Mediterranean areas in the lateglacial period and Holocene (*Buxus*, *Carpinus betulus*, *Picea*); they provide an indication of the modes of disappearance of tree populations that may be useful to evaluate correctly the vulnerability of modern fragmented plant populations. The demographic histories of tree taxa obtained by combined palaeobotanical and genetic studies is a most challenging field of research needed not only to assess species/population differentiation, but also to reach a better understanding of extinction processes, an essential task in the current global change scenario.

1. Introduction

The progressive disappearance of tree taxa from Europe in the course of the late Cenozoic, and their persistence in East Asia and/or eastern North America, has long been recognized. The first papers highlighting the question, based on seed floras, date back to more than one century ago (Reid and Reid, 1907, 1915). Starting in the 1950s, several "fathers" of the European palynology published pioneering studies dealing with Quaternary extinctions of plants, including van der Hammen (1951), van der Hammen et al. (1971), Zagwjin (1957, 1963, 1974), West (1962, 1970), and Lona (1950). Since then, following a considerable increase in the number of published Early and Middle Pleistocene pollen records in Europe and a significant refinement of the chronological setting of the Quaternary stages, our knowledge of the timing of disappearance of tree taxa from Europe has much improved. Recently, a number of synthesis works on the history of vegetation and the Quaternary progression of plant extirpations (or regional extinctions, hereafter called extinctions) in Southern Europe have been published, describing the state of knowledge in different regions: Spain (González-Sampériz et al., 2010; Postigo-Mijarra et al., 2010), Italy (Bertini, 2003, 2010; Magri and Palombo, 2013; Martinetto, 2015), Greece (Tzedakis et al., 2006; Velitzelos et al., 2014), and Anatolia (Biltekin et al., 2015). In addition, several studies have examined the

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history of taxa currently extinct, or severely reduced in Europe, including *Taxodium* (Biltekin et al., 2015), *Cathaya* (Liu and Basinger, 2000), *Cedrus* (Magri, 2012), *Carya* (Orain et al., 2013), *Aesculus* (Ravazzi, 1994; Postigo Mijarra et al., 2008), *Zelkova* (Follieri et al., 1986), and *Parrotia* (Bińka et al., 2003). The present review paper is intended to summarize the available information obtained from the Pleistocene pollen records and from the synthesis papers, and to provide a holistic view of the timing and trends of tree taxa disappearance in Southern Europe.

Previous works dealing with plant extinctions in Europe have mainly focused on two main problems:

1. Usage of abundances and/or last occurrences of extinct plant taxa as biostratigraphical markers. This practice has been rather common since the beginning of pollen analysis of Plio-Pleistocene deposits. In the absence of, or in support of other chronostratigraphical constrains, the presence of locally extinct taxa in pollen records may provide useful indications about the age of study sites. Many such cases can be quoted, especially before the development of advanced chronostratigraphical tools, but the presence of extinct taxa in the pollen records is still considered an important biostratigraphical indicator. For example, the pollen record from La Côte in the western French Alps has been ascribed to the temperate Holsteinian interglacial, corresponding to Marine Isotope Stage (MIS) 11, on the basis of the occurrence of *Pterocarya* and the dominance of *Abies* (Field et al., 2000), according to the records of the Velay maar in the French Massif (Reille et al., 2000). Similarly, the record from Torre Mucchia (Central Italy) has been correlated to MIS 17 on the basis of the underlying Brunhes/Matuyama magnetostratigraphic boundary coupled with a significant abundance of *Tsuga* (Pieruccini et al., 2016), which is only sporadically found in Central and Southern Italy after MIS 16 (Russo Ermolli et al., 2015). On the other hand, this approach may be rather weak and may lead to misleading interpretations. A classic example is the setting of the “Tiberian boundary” between the Gelasian (formerly in the Upper Pliocene) and the Calabrian (Early Pleistocene) with respect to a significant reduction of Taxodiaceae (Lona and Bertoldi, 1972; Suc, 1973). Recent pollen studies have shown that this event is not clear-cut or synchronous over a large region as previously believed, suggesting that biostratigraphical schemes need to be constantly updated and that they may be considered valid only for regions of limited extension. Thoughtful discussions on the stratigraphical potentiality and risks of palynology in the study of late Neogene and Quaternary deposits may be found in Leroy (2007) and Bertini (2010).
2. Relation between plant extinctions and climate changes. This was first raised by Reid and Reid (1915), who considered the presence of barriers to migration in the form of west-east oriented mountain ranges (e.g., Pyrenees, Alps, and Carpathians) the main cause for the extinction of taxa in NW Europe, preventing plant population migrations in response to Quaternary climate oscillations (West, 1970). Huntley (1993) suggested that the enhanced rate of extinction of genera and families in Europe during the Quaternary climate changes may depend on a much smaller area of forest vegetation persisting during glacial stages in Europe compared to eastern North America and East Asia. This reduced area is due, on the one hand, to the considerable extent of glaciated and periglacial surfaces at high latitudes, and, on the other hand, to a trend of increasing seasonality and dryness in the Mediterranean regions since the Pliocene, which according to Suc (1984) is at the origin of the Mediterranean evergreen vegetation, although with clear latitudinal and longitudinal gradients (Suc and Popescu, 2005). In Central and Northern Europe, most temperate trees are believed to have disappeared during the Quaternary glacial periods and migrated back during interglacial periods, but a number of them were extirpated (see list in Svenning, 2003; Suppl. Materials), and some of them are still living in Southern Europe in a relictual state (e.g., *Zelkova*, *Aesculus*, *Castanea*, *Celtis*, *Cercis*, *Cupressus*, *Styrax*, *Juglans*, *Ostrya*, *Platanus*). Svenning (2003) has found that genera of woody plants that are currently widespread in Europe have greater tolerance to cold growing season and winter temperatures with respect to regionally extinct and relictual genera, while relictual genera are more drought tolerant. This indicates that the persistence (or extinction) of tree populations in Europe is largely controlled by a deterministic ecological sorting process. Bhagwat and Willis (2008) showed that biogeographical traits (geographical distribution, habitat preference and life-history) of woody plants may have determined their ability to survive in inhospitable climates, so influencing their persistence (or extinction) in response to Pleistocene climate change. Eiserhardt et al. (2015) showed that late Cenozoic climate change induced phylogenetically selective regional extinction of northern temperate trees, leading to significant losses of phylogenetic diversity. Studying the relationships between climate oscillations and ecological traits, as well as the genetic characteristics of plants that went extinct in Europe during the Quaternary is especially important in terms of modern biodiversity conservation. This is a hot topic, as a better understanding of the ability of species to survive abrupt warming is indispensable in view of predicted global climate changes (Dawson et al., 2011). Linking studies of modern biodiversity and ecosystem patterns with palaeoclimate dynamics may offer important scientific advances in both reconstructing the climatic conditions under which past extinction events happened, and inferring how present-day biodiversity patterns may be affected by climate change (Svenning et al., 2015).

Biostratigraphical and palaeoclimatic aspects have been often considered together, in connection to the question of whether Quaternary climate changes may have determined the extinction of plants in Southern Europe, in particular specific events including the Pliocene/Pleistocene transition (Popescu et al., 2010; Bertini, 2010; Jiménez-Moreno et al., 2010; Martinetto et al., 2015; Biltekin et al., 2015), the Gelasian/Calabrian transition (Combourieu-Nebout, 1993; Bertini, 2010; Martinetto et al., 2015; Combourieu-Nebout et al., 2015), the Middle Pleistocene Revolution (Suc and Popescu, 2005; Leroy, 2007; Postigo Mijarra et al., 2009, 2010; Bertini, 2010; Magri and Palombo, 2013), and specific glacial stages corresponding to MIS 22, 16 and 12 (Muttoni et al., 2003; Tzedakis et al., 2006). Moreover, this question implicitly involves the still open problem of whether plant extinctions were step-wise (e.g., Svenning, 2003; Martinetto et al., 2015) or progressive (e.g., Bertini, 2010; Combourieu-Nebout et al., 2015; Biltekin et al., 2015).

Other aspects related to the Pleistocene disappearance of tree taxa have not been adequately discussed yet, and will be encompassed in the present paper. Starting from the compilation of schematic regional records of past tree populations spanning the whole Quaternary, we intend to examine the following issues:

- value and limitations of pollen data for reconstructing the Pleistocene extinction of tree taxa,
- state of the art of the Early and Middle Pleistocene palaeofloristic data available from Southern Europe,
- Quaternary history of tree taxa no longer present in the Southern Europe mainland,