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Late persistence and deterministic extinction of "humid thermophilous plant taxa of East Asian affinity" (HUTEA) in southern Europe

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ABSTRACT

Several terrestrial plant fossils found in the late Cenozoic of Europe belong to thermophilous genera or infrageneric taxa which do not grow in this continent today, and are usually called "exotic elements". Within this large group we singled out three more precisely defined categories based on the hypothesis that the change of geographic distribution between the late Cenozoic and the present is the result of deterministic extinctions caused by climate change. Among the taxa shared by the modern East Asian and the Plio–Pleistocene European flora, the "humid thermophilous taxa of East Asian affinity" (HUTEA) represent the central category in our study. These were traditionally considered "Pliocene" elements in Europe. In our analysis of 13 reliably dated Italian assemblages the percentage of species belonging to the HUTEA category was found to be higher in Pliocene sites, and very low to null in Pleistocene ones. Also early Pleistocene assemblages across all of Europe did not contain any HUTEA, apart from *Eucommia*, and *Symplocos* sect. *Lodhra* in the refugial area of the Colchis.

Our analysis of fruit and seed assemblages in the San Lazzaro section (Umbria, central Italy), recently assigned to the early Pleistocene, provided contrasting evidence, which required a reconsideration of the stratigraphic and palaeontological context of another well known site in central Italy, Cava Toppetti II. Using vertebrate and continental mollusc biochronology the early Pleistocene age of this section was confirmed and its palaeontological records were compared with other assemblages in central Italy and Europe. We show that in central Italy at least three HUTEA species (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) persisted after the Pliocene/Pleistocene boundary. We conclude that central-southern Italy offered a refugial niche that was warm and wet enough to assure the longer survival of some HUTEA, in contrast to central Europe.

1. Introduction

In the course of the stratigraphical and palaeontological study of the San Lazzaro section in central Italy (Fig. 1), recently assigned to the early Pleistocene (Baldanza et al., 2014), one of us (A.B.) found an endocarp of *Sinomenium cantalense*. The finding of this species, readily assignable to the humid thermophilous taxa of East Asian affinity, in an early Pleistocene section was the starting point for further collecting efforts to find evidence for the role of central Italy as a centre of refuge for such thermophilous taxa in the Plio–Pleistocene (Martinetto, 2001a). In this paper we adopt the definition of the Pliocene and Pleistocene of Gibbard et al. (2010), with the boundary fixed at 2.6 Ma, and we accept their indication for the chronologic boundaries of the four stages Zanclean, Piacenzian, Gelasian and Calabrian. Therefore, the terms middle Pliocene, late Pliocene and early Pleistocene used in previous works (among others, Ambrosetti et al., 1995a,b; Abbazzi et al., 1997; Martinetto, 2001a) have a chronologic connotation which differs from that adopted here.

It is well known that many plant fossils found in the late Cenozoic of Europe belong to thermophilous genera or infrageneric taxa which do not grow in this continent today (Mai, 1989; Qian et al., 2006; Rodríguez-Sánchez and Arroyo, 2008). Such fossils are usually called "exotic elements" (Reid, 1920) and this concept corresponds more or less with "extinct plants" for the Plio–Pleistocene interval (Svenning, 2003). The climatic requirements are not considered in the definition of both exotic and extinct; however, several attempts have been made to assign the exotic (or extinct) elements to a few distinct plant groups that involve a climatic characterization and/or a phytogeographic aspect (Mai, 1989, 1991, 1995a; Grichuk, 1997; Grímsson et al., 2015). Examples of names which have been used include: "Palaeotropical flora/

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0031-0182/

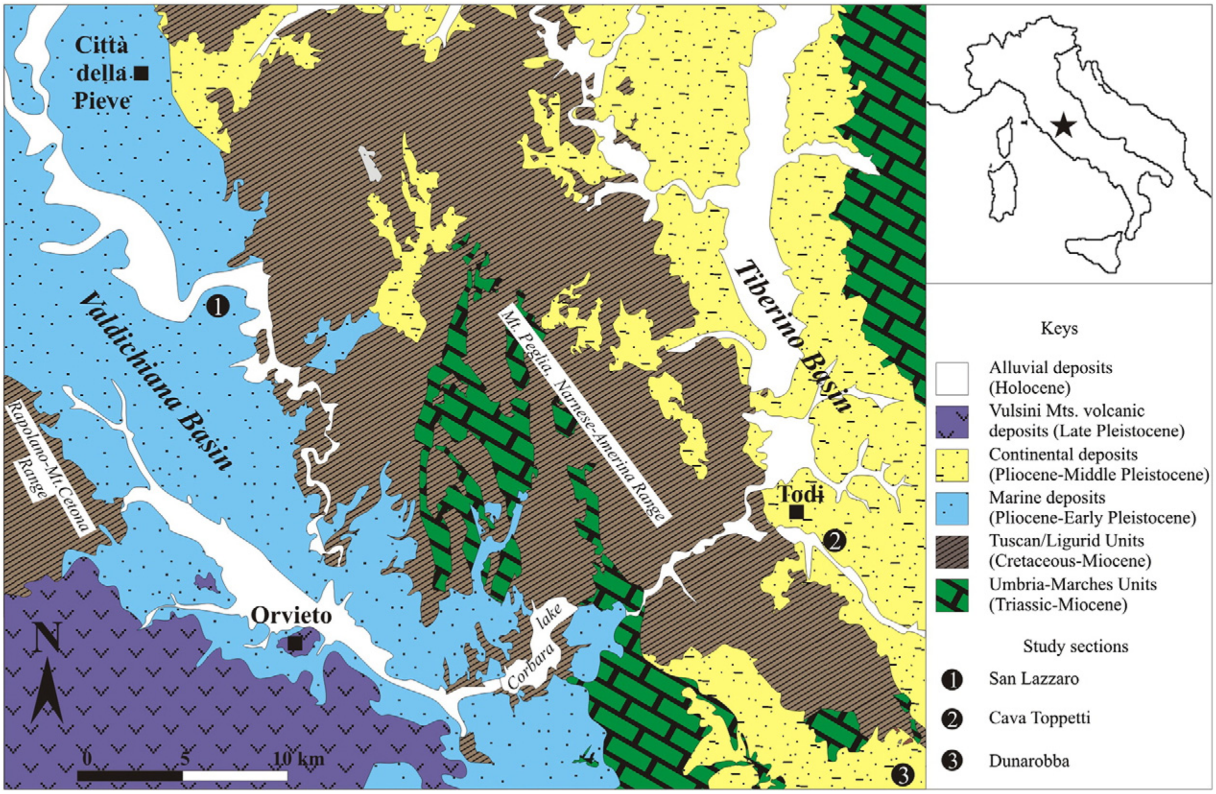

Fig. 1. Simplified geological scheme for the area of the San Lazzaro, Cava Toppetti and Dunarobba sections.

element", "Arcto-Tertiary" or "Arctotertiary flora/element" (Engler, 1879–1882; Mai, 1989, 1991; Grímsson et al., 2015), "subtropical elements" (Mai, 1970; Zagwjin, 1990), "Mastixioideen" (Kirchheimer, 1957; Mai, 1964), "Boreotropical flora" (Wolfe, 1975), "Taxodiaceae group" (Bertoldi et al., 1994), "Tethyan plants (or Tethys flora)" (Szafer, 1961; Mai, 1989; Rodríguez-Sánchez and Arroyo, 2008), "Mega-mesothermic elements" (e.g. Popescu et al., 2010), and "humid subtropical elements" (Bertini and Martinetto, 2011). All these names leave some uncertainty as to what is included and what is excluded from the definition, firstly because the phytogeographic information, both past and present, is superimposed to, and variously interfingers with, the climatic one, and secondly because of the very difficult, not unambiguous, climatic characterization of the fossil-taxa (Kvaček, 2007; Grimm and Denk, 2012; Utescher et al., 2014). Also the modern reference models may be ambiguous, for example the qualitative term "subtropical" is used with very different temperature boundaries by Chinese (e.g. Hou, 1983) and Japanese authors (e.g. Kira, 1991).

The different extant distribution of plant taxa that grew together in the Cenozoic of Europe have often been given considerable relevance in the analysis of palaeofloras (see Reid and Reid, 1915; Szafer, 1961; Mai, 1964, 1989, 1995a). However, in our opinion most previous analyses and descriptions of the floral change in the Plio–Pleistocene of Europe suffered from the lack of precisely defined categories whose chronological analysis would adequately point out timing and entity of the large Plio–Pleistocene mass extinction (Tallis, 1991; Svenning, 2003). Additionally, the descriptions of Plio–Pleistocene floral changes mostly relied on pollen data (e.g. Tzedakis et al., 2006; Postigo-Mijarra et al., 2009; Magri, 2010; Orain et al., 2013), particularly in Italy (Bertini, 2010; Combourieu-Nebout et al., 2015). However, by combining pollen and carpological records (Bertini and Martinetto, 2011) it was noticed that pollen assemblages mainly reflect anemophilous plants, whilst they do not accurately represent the assemblages of "subtropical humid forest" type (sensu Hou, 1983, and Bertini and Martinetto, 2011), which are very rich in entomophilous plants and were present in southern Europe right at the time when major extinction events are hypothesized (Martinetto, 2001a; Bertini, 2010; Bertini and Martinetto, 2011; Biltekin et al., 2015; Combourieu-Nebout et al., 2015). As recently confirmed by Goring et al. (2013), taxa that are pollinated by insect or animal vectors (entomophilous or zoophilous, respectively), and species with limited dispersal ability are rarely recorded in fossil pollen records. Some works on modern fruit and seed assemblages (e.g. Thomasson, 1991; Vassio and Martinetto, 2012 and references therein) indicate a less biassed representation of plant diversity, in particular for several enthomophilous (e.g. *Actinidia*, *Frangula*, *Paulownia*, *Rubus*, *Sambucus*) and herbaceous plants (e.g. *Ajuga*, Cyperaceae, *Hypericum*, and *Potamogeton*). For these taxa, the plant elements that enter the fossil record and allow species-level identification are fruits and/or seeds. Thus, the works which exclude carpological data definitely underestimate past plant species diversity and the extent of Plio–Pleistocene plant extinctions, and the focus of this paper will be on fossil fruits and seeds.

The analysis of the San Lazzaro material led us to reconsider the bulk of information accumulated for the Italian late Cenozoic fruit and seed assemblages in the last 30 years (in particular: Gregor, 1990; Martinetto, 1994, 1995, 1999, 2001a,b, 2009, in press; Bertoldi and Martinetto, 1995; Mai, 1995b; Basilici et al., 1997; Fischer and Butzmann, 2000; Ghiotto, 2010; Martinetto et al., 2007, 2015). Consequently, we felt the need to introduce precisely defined categories, which would permit us to better appreciate the chronological steps of the dramatic southern European floral change in the Plio–Pleistocene. One of the necessary operations was to combine in a clear manner the modern phytogeography and the climatic requirements of several taxa. Therefore, we focused on geographical and ecological characteristics of modern relatives of fossil taxa: partly shared geographic range, minimum thermic tolerance and moisture requirement. Since the geographic area where most of the "exotic" taxa of the European late