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

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17  
18 Key words

19 carpological remains, phytogeographic-climatic characterization, exotic elements, climate change,  
20 late Cenozoic, Italy

21  
22 Abstract

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

35 Our analysis of fruit and seed assemblages in the San Lazzaro section (Umbria, central Italy),  
36 recently assigned to the early Pleistocene, provided contrasting evidence, which required a  
37 reconsideration of the stratigraphic and palaeontological context of two well known sites in central  
38 Italy, Cava Toppetti II and Dunarobba. Using vertebrate and continental mollusc biochronology the  
39 age of these sections was established and they were compared with other assemblages in central  
40 Italy and Europe. We show that in central Italy at least three HUTEA species (*Sinomenium*  
41 *cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) persisted after the Pliocene/Pleistocene  
42 boundary. We conclude that central-southern Italy offered a refugial niche that was warm and wet  
43 enough to assure the longer survival of some HUTEA, in contrast to central Europe.

44  
45 1. Introduction

46 In the course of the stratigraphical and palaeontological study of the San Lazzaro section in central  
47 Italy (Fig. 1), recently assigned to the early Pleistocene (Baldanza et al., 2014), one of us (A.B.)  
48 found an endocarp of *Sinomenium cantalense*. The finding of this species, readily assignable to the  
49 humid thermophilous taxa of East Asian affinity in an early Pleistocene section was the starting  
50 point for further collecting efforts to find evidence for the role of central Italy as a centre of refuge  
51 for such thermophilous taxa in the Plio-Pleistocene (Martinetto, 2001a). In this paper we adopt the

52 definition of the Pliocene and Pleistocene of Gibbard et al. (2010), with the boundary fixed at 2.6  
53 Ma, and we accept their indication for the chronologic boundaries of the four stages Zanclean,  
54 Piacenzian, Gelasian and Calabrian. Therefore, the terms middle Pliocene, late Pliocene and early  
55 Pleistocene used in previous works (among others, Ambrosetti et al., 1995a, 1995b; Abbazzi et al.,  
56 1997; Martinetto, 2001a) have a chronologic connotation which differs from that adopted here.

57 It is well known that many plant fossils found in the late Cenozoic of Europe belong to  
58 thermophilous genera or infrageneric taxa which do not grow in this continent today (Mai, 1989;  
59 Qian et al., 2006; Rodriguez Sanchez and Arroyo, 2008). Such fossils are usually called "exotic  
60 elements" (Reid, 1920) and this term corresponds more or less with "extinct plants" for the Plio-  
61 Pleistocene interval (Svenning, 2003). The climatic requirements are not considered in the  
62 definition of both exotic and extinct; however, several attempts have been made to assign the exotic  
63 (or extinct) elements to a few distinct plant groups that involve a climatic characterization and/or a  
64 phytogeographic aspect (Mai, 1989, 1991, 1995a; Grichuk, 1997; Grimsson et al., 2015). Examples  
65 of names which have been used include: "Palaeotropical flora/element", "Arcto-Tertiary" or  
66 "Arctotertiary flora/element" (Engler, 1879–1882; Mai, 1989, 1991; Grimsson et al., 2015),  
67 "subtropical elements" (Mai, 1970; Zagwijn, 1990), "Mastixioideen" (Kirchheimer, 1957; Mai,  
68 1964), "Boreotropical flora" (Wolfe, 1975), "Taxodiaceae group" (Bertoldi et al., 1994), "Tethyan  
69 plants (or Tethys flora)" (Szafer, 1961; Mai, 1989; Rodriguez Sanchez and Arroyo, 2008), "Mega-  
70 mesothermic elements" (e.g. Popescu et al., 2010), "humid subtropical elements" (Bertini and  
71 Martinetto, 2011). All these names leave some uncertainty as to what is included and what is  
72 excluded from the definition, firstly because the phytogeographic information, both past and  
73 present, is superimposed to, and variously intermingles with, the climatic one, and secondly because  
74 of the very difficult, not unambiguous, climatic characterisation of the fossil-taxa (Kvaček, 2007;  
75 Grimm and Denk, 2012; Utescher et al., 2014). Also the modern reference models may be  
76 ambiguous, for example the qualitative term "subtropical" is used with very different temperature  
77 boundaries by Chinese (e.g. Hou, 1983) and Japanese authors (e.g. Kira, 1991).

78 The different extant distribution of plant taxa that grew together in the Cenozoic of Europe have  
79 often been given considerable relevance in the analysis of palaeofloras (see Reid and Reid, 1915;  
80 Szafer, 1961; Mai, 1964, 1989, 1995a). However, in our opinion most previous analyses and  
81 descriptions of the floral change in the Plio-Pleistocene of Europe suffered from the lack of  
82 precisely defined categories whose chronological analysis would adequately point out timing and  
83 entity of the large Plio-Pleistocene mass extinction (Tallis, 1991; Svenning, 2003). Additionally, the  
84 descriptions of Plio-Pleistocene floral changes mostly relied on pollen data (e.g. Tzedakis et al.,  
85 2006; Postigo-Mijarra et al., 2009; Magri, 2010; Orain et al., 2013), particularly in Italy (Bertini,  
86 2010; Combourieu-Nebout et al., 2015). However, by combining pollen and carpological records  
87 (Bertini and Martinetto, 2011) it was noticed that pollen assemblages mainly reflect anemophilous  
88 plants, while they do not accurately represent the assemblages of "subtropical humid forest" type  
89 (*sensu* Hou, 1983, and Bertini and Martinetto, 2011), which are very rich in entomophilous plants  
90 and were present in southern Europe right at the time when major extinction events are  
91 hypothesized (Bertini and Martinetto, 2011). As recently confirmed by Goring et al. (2013), taxa  
92 that are pollinated by insect or animal vectors (entomophilous or zoophilous, respectively), and  
93 species with limited dispersal ability are rarely recorded in fossil pollen records. Some works on  
94 modern fruit and seed assemblages (e.g. Thomasson, 1991; Vassio and Martinetto, 2012 and  
95 references therein) indicate a less biased representation of plant diversity, in particular for several  
96 entomophilous (e.g. *Actinidia*, *Frangula*, *Paulownia*, *Rubus*, *Sambucus*) and herbaceous plants  
97 (e.g. *Ajuga*, *Cyperaceae*, *Hypericum*, *Potamogeton*, etc.). For these taxa, the plant elements that  
98 enter the fossil record and allow species-level identification are fruits and/or seeds. Thus, the works  
99 which exclude carpological data definitely underestimate past plant species diversity and the extent  
100 of Plio-Pleistocene plant extinctions, and the focus of this paper will be on fossil fruits and seeds.

101 The analysis of the San Lazzaro material led us to reconsider the bulk of information accumulated  
102 for the Italian late Cenozoic fruit and seed assemblages in the last 30 years (in particular: Gregor,

103 1990; Martinetto, 1994, 1995, 1999, 2001a, 2001b, 2009, in press; Bertoldi and Martinetto, 1995;  
104 Mai, 1995b; Basilici et al., 1997; Ghiotto, 2010; Martinetto et al., 2007, 2015). Consequently, we  
105 felt the need to introduce precisely defined categories, which would permit us to better appreciate  
106 the chronological steps of the dramatic southern European floral change in the Plio-Pleistocene.  
107 One of the necessary operations was to combine in a clear manner the modern phytogeography and  
108 the climatic requirements of several taxa. Therefore, we focused on geographical and ecological  
109 characteristics of modern relatives of fossil taxa: partly shared geographic range, minimum thermic  
110 tolerance and moisture requirement. Since the geographic area where most of the "exotic" taxa of  
111 the European late Cenozoic are still living today is definitely East Asia (Tralau, 1963; Martinetto,  
112 1998; Qian et al., 2006; Manchester et al., 2009), we considered it to be important for the definition  
113 of the new categories.

#### 114 1.1. Definition of "humid thermophilous extinct European taxa of East Asian affinity" (HUTEA)

115 The taxonomic similarity between Neogene European floras and modern East Asian ones are rooted  
116 at least into the Miocene (Mai, 1989). As known from various studies at a global and regional scale,  
117 Cenozoic climates were generally warmer and more humid than at present, and were characterized  
118 by shallow latitudinal gradients (Utescher et al., 2011 and references therein). Several authors  
119 (Bruch et al., 2011, Liu et al., 2011, Xing et al., 2012; Jacques et al., 2013) pointed out that the  
120 climate was wetter and warmer than the present one during the Miocene in both central Europe and  
121 China. Even central and northern Eurasian areas, such as Kazakhstan (Bruch and Zhilin, 2006) and  
122 Siberia (Popova et al., 2012), were wetter and warmer during the Miocene, despite the relatively  
123 higher seasonality and continentality.

124 This climatic situation was probably suitable for the formation of latitudinal vegetation belts with a  
125 similar floristic composition in both western and eastern Eurasia (Mai, 1989, 1991; Kovar-Eder et  
126 al., 2008), and strong floristic affinities with East Asia have also been encountered for North  
127 American floras (Liu and Jacques, 2010). Several authors explained that the modern East Asian  
128 woody flora is richer than the European (and North American) one (e.g., Kubitzki and Krutzsch,  
129 1996; Manchester, 1999; Tiffney and Manchester, 2001; Wen, 1999; Wen et al., 2010) mainly due  
130 to a minor impact of extinctions, even if several woody species got extinct also in East Asia during  
131 the Plio-Pleistocene (Momohara, 2015).

132 Some close relatives of most European extinct species were already present in the warm temperate  
133 belt of East Asia before the Pliocene (e.g., *Cathaya*, *Cephalotaxus*, *Craigia*, *Cryptomeria*,  
134 *Cyclocarya*, *Eucommia*, *Ginkgo*, *Glyptostrobus*, *Pseudolarix*, *Taiwania*: Manchester et al., 2009) or  
135 possibly migrated there during the Pliocene (e.g., *Hemiptelea*, *Rehderodendron*: Manchester et al.,  
136 2009), and could survive the Pleistocene climatic crisis because of the presence of niches that were  
137 wet (atmospheric humidity) and warm enough, even in sites not related to rivers and swamps. Based  
138 on the concept of "physiological uniformitarianism" (Tiffney and Manchester, 2001) we can  
139 assume that the climatic tolerances of the living relatives of Neogene European taxa that survived in  
140 the humid and warm temperate to tropical areas of East Asia roughly correspond (maybe only in  
141 part) to those of the extinct European forms of the same genus, subgenus or section. Svenning  
142 (2003) pointed out a deterministic effect in late Cenozoic plant extinctions and recognized three  
143 important groups of taxa for the analysis of the ancient European floras: 1) widespread taxa; 2)  
144 relictual taxa; 3) extinct taxa. In referring to extinct taxa, Svenning (2003) restricted his analysis to  
145 cool-temperate tree genera, but recently Eiserhardt et al. (2015) carried out an analysis on more  
146 thermophilous plants. Actually, several Plio-Pleistocene taxa occurring in Europe are more  
147 thermophilous than "cool-temperate" (Martinetto et al., 2015) so that we now consider it important  
148 to single out a new group of thermophilous taxa with a partly shared (as for eastern Asia) current  
149 distribution outside Europe and a common, definite climatic boundary. The thermophilous  
150 characterization of several taxa documented by fossils is provided by the minimum Mean Annual  
151 Temperature (MAT) requirement of their modern relatives (Table 1).

153 Consequently, we define as "**HU**mid **Thermophilous** extinct European taxa of **East Asian** affinity",  
154 in short HUTEA, those plant taxa which have well-**documented** fossil records in the late Cenozoic  
155 of Europe, which do not grow spontaneously in this continent and West Asia at present (unless as  
156 aliens), which do not tolerate a Mean Annual Temperature below 8°C and a Mean Annual  
157 Precipitation (MAP) below ca. 800-1000 mm/year, and which belong to genera or infrageneric taxa  
158 that presently grow in East Asia (Wang, 1961; Qian et al., 2006; Manchester et al., 2009; Fang et  
159 al., 2009, 2011; Grimm and Denk, 2012; Eiserhardt et al., 2015; Utescher and Mosbrugger, 2015).  
160 We single out the 8°C value of MAT because this is the boundary of the distribution of boreal  
161 (subarctic) and thermophilous (temperate) taxa in East Asia. The lower limit of fir and spruce forest  
162 and the upper limit of deciduous forest is 7.8 °C MAT in China (Fang and Yoda, 1989). Although  
163 the lower MAT limit of the thermophilous evergreen arboreal Fagaceae and Lauraceae (dominant  
164 tall trees of temperate broadleaved evergreen forests in East Asia) is between 9 and 12°C (Hattori  
165 and Nakanishi, 1985; Fang and Yoda, 1989; Fang et al., 2011), we decided that adding 1°C of  
166 tolerance would admit sporadic occurrences of thermophilous plants above the 9°C MAT isotherm.  
167 The focus on MAT for the definition of the HUTEA is justified by the large availability of data  
168 (Grimm and Denk, 2012; Utescher and Mosbrugger, 2015) for most of the plant genera documented  
169 by fossils in Europe, and by the determinant role of this parameter for plant extinction or survival in  
170 the late Cenozoic of Europe (Svenning, 2003; Eiserhart et al., 2015). Conversely, we did not  
171 manage to gather precise values of minimum precipitation requirements for all the exotic Neogene  
172 plant taxa of Europe; nevertheless we consider important to include in the HUTEA definition a rule  
173 that excludes those plants which tolerate a low precipitation (below ca. 800-1000 mm/year). In fact  
174 it has been pointed out that the extinction of several Neogene taxa in Europe depended from a  
175 scarce tolerance not only of low temperature, but also of low precipitation (Svenning, 2003;  
176 Eiserhart et al., 2015). The thermophilous genera that survived in southern Europe until present  
177 time (e.g. *Laurus*, *Olea*) are mainly adapted to dry (Mediterranean) climate, whereas several  
178 thermophilous genera extinct in Europe are now growing in areas affected by the East Asian  
179 Monsoon that supplies higher precipitation to plants during the growing season. In East Asia the  
180 main evergreen forest formation, dominated by Fagaceae and Lauraceae, is called "lucidophyllous  
181 forest" and differs from the south European (Mediterranean) sclerophyllous forest formation by its  
182 less xeromorphic characteristics, such as larger shiny leaves, larger tree size and higher species  
183 diversity with many epiphytes and woody lianas (Kira, 1991).  
184 We are aware that other parameters (e.g. Warmth Index, Coldness Index; Kira, 1991) could be more  
185 appropriate to define a category such as HUTEA. Nevertheless, the minimum MAT requirement is  
186 an important factor determining the possibility for a plant taxon to overcome a climatic bottleneck.  
187 The climatic characteristics of the refugia might have been decisive for the possibility of a  
188 plant species to survive (Magri, 2010; Gavin et al., 2014) and obviously it would have gone extinct  
189 if its minimal thermal or humidity requirements would no longer have been present in the last  
190 refugium. In this respect, groups of taxa with similar requirements may be expected to go extinct  
191 together (Tallis, 1991; Grichuk, 1997; Eiserhardt et al., 2015). However, some extinctions are  
192 certainly controlled by complex and multiple factors. For example it has been suggested that *Cedrus*  
193 (Su et al., 2013) and *Sequoia* (Zhang et al., 2015) disappeared from China because of seed  
194 ecological aspects, triggered by climate change.  
195  
196 Three examples, concerning genera which do not tolerate a MAT below 8°C (Table 1), may be  
197 useful to support the above definition of HUTEA: *Toddalia* is assigned to the HUTEA because it is  
198 distributed in the tropical-warm temperate zone of East Asia and in Africa, but not in Europe and  
199 West Asia (Gregor, 1979). *Symplocos* sect. *Lodhra* is assigned to the HUTEA because it is  
200 distributed in the tropical-warm temperate zone of East Asia, but not in Europe and West Asia  
201 (Fritsch et al., 2015). *Rehderodendron* is assigned to the HUTEA because it is distributed only in  
202 the "subtropical" zone (*sensu* Hou, 1983) of East Asia.

203 The genera *Cathaya* and *Pseudolarix* meet all the requirements to be classified as HUTEA, but they  
204 are excluded for their present highly relictual distribution, which may provide an inaccurate  
205 representation of their past climatic requirements, similarly as for *Tetraclinis* (Kvaček, 2007).  
206 *Azolla* is not considered a HUTEA because it is a water plant rather independent from atmospheric  
207 humidity.

208 (TABLE 1 approximately here)

209 According to the above definition and to the data (e.g., minimum thermic requirements: MAT<sub>min</sub>)  
210 reported in Table 1, the following HUTEA have so far been documented for the late Cenozoic of  
211 Italy (Martinetto, 1995, 1998, 1999, 2001a; 2001b; Follieri, 2010; Martinetto et al., 2015):  
212 *Amentotaxus*, *Cephalanthus*, *Cinnamomum*, *Craigia*, *Cyclea*, *Cyclocarya*, *Ehretia*, *Engelhardia*,  
213 *Eucommia*, *Glyptostrobus*, *Mallotus*, *Meliosma* subgen. *Kingsboroughia*, *Paulownia*,  
214 *Rehderodendron*, *Sabia*, *Sargentodoxa*, *Saurauia*, *Sinomenium*, *Stemona*, *Symplocos* sect. *Lodhra*,  
215 *Taiwania*, *Ternstroemia*, *Tetrastigma*, *Toddalia*, *Trichosanthes*, *Turpinia* and *Wikstroemia*.

216

217

218

### 219 1.2. Other categories (CTEA, TEWA)

220

221 Other taxa documented in the late Cenozoic of southern Europe have the correct geographic  
222 distribution nowadays to be considered HUTEA (i.e. embracing East Asia and excluding Europe  
223 and West Asia), but they are not considered, because the modern representatives do tolerate a Mean  
224 Annual Temperature below 8°C (e.g. *Actinidia*, *Alangium*, *Ampelopsis*, etc.: Table 1). These taxa  
225 will be named CTEA ("Cool-Tolerant extinct European taxa of East Asian affinity") in this paper  
226 and belong to the somehow ambiguous [changing on the basis of the extent of territory considered]  
227 category of the "exotic" taxa (Reid, 1920; see the more precisely defined "category E" in  
228 Martinetto, in press).

229 The HUTEA category already has a satisfactory climatic connotation, which we deem to be useful  
230 for an analysis of the climatic determinism in their extinction. Conversely, the CTEA category  
231 certainly contains a very heterogeneous mix of species with different climatic tolerances. In fact,  
232 *Magnolia* provides a good example of a cool-tolerant CTEA genus that contains several modern  
233 species (Grimm and Denk, 2012; Mosbrugger and Utescher, 2015), which are absolutely  
234 thermophilous and not cool-tolerant (tropical-subtropical). Similarly, a diversified climate tolerance  
235 has been also hypothesized for different European fossil-species (Mai, 1975). Given this situation, it  
236 is not surprising that several CTEA would show a HUTEA-like extinction pattern. However, in this  
237 paper our attention has been focused on the species that show a delayed disappearance time in  
238 comparison to the HUTEA.

239 Finally, a few taxa which do not tolerate a MAT below 8°C are not assigned to the HUTEA because  
240 of the modern geographic range: *Coriaria*, *Datisca*, *Ficus*, *Laurus*, *Liquidambar*, *Morella*, *Ocotea*,  
241 *Olea*, *Platanus*, *Sideroxylon*, *Styrax*, *Tetraclinis* and *Visnea* grow in southern Europe, North Africa  
242 (incl. Macaronesia) and/or West Asia. These taxa will be indicated as TEWA, Thermophilous  
243 European, West Asian and/or African elements, in this paper. *Pterocarya*, *Parrotia* and *Zelkova* are  
244 not assigned to the HUTEA nor to the CTEA or TEWA, because they grow in relict niches of  
245 south-eastern Europe and/or West Asia (southern shores of the Black Sea and Caspian Sea),  
246 commonly including sites with a Mean Annual Temperature below 8°C.

247 Finally, late Cenozoic south European taxa that today only survive in America are not many  
248 (*Decodon*, *Dulichium*, *Leitneria*, *Proserpinaca*, *Sequoia*, *Taxodium*) and will not be specifically  
249 dealt with in this paper.

250 It is apparent that the HUTEA and CTEA concepts have much to do with a change of geographic  
251 distribution between the Plio-Pleistocene and the present. The main aim of this work is to present  
252 new fossil data from Italy and an updated state-of-the-art regarding the timing of disappearance of



253 HUTEA and CTEA species from Europe. Furthermore, we newly consider the possibility of  
254 deterministic extinctions (Svenning, 2003; Eiserhardt et al., 2015).

255

## 256 2. Geological setting

257 The post-Miocene, NW-SE oriented South Valdichiana Basin (Fig. 1), enclosed between the Meso-  
258 Cenozoic Rapolano-Mt. Cetona and Narnese-Amerina Apennine anticlines and bounded by  
259 extensional faults, occupies a wide area between south-eastern Tuscany and western Umbria, in  
260 central Italy. In the Pliocene-Pleistocene interval, the Narnese-Amerina ridge separated the mainly  
261 marine domain of South Valdichiana from the continental deposits of the Southern Tiberino Basin  
262 (Figs. 1, 2), while, during the early Pleistocene, a wide delta in what is now the Città della Pieve  
263 area divided the continental (northwards) and the marine Valdichiana (southwards) (Bizzarri and  
264 Baldanza, 2009; Bizzarri et al., 2015).

265

(FIGURE 1 approximately here)

266 South Valdichiana marine deposits in the study area, including the San Lazzaro section (Fig. 1),  
267 clearly mark a regressive trend, from offshore transition silty sands to lower shoreface sands, and  
268 finally to a gravel beachface with evidence of a river mouth in the uppermost part (Baldanza et al.,  
269 2011). The same main trend is recognized in other sections nearby, such as the Monteleone section  
270 and the Città della Pieve section (Bizzarri and Baldanza, 2009). All these sections are referred to  
271 alternatively river- and wave-dominated shallow coastal marine environments (Bizzarri et al.,  
272 2015), and attributed to the “Deltaic coast” inside the “Chiani-Tevere” Unit (Fig. 2, Baldanza et al.,  
273 2014; Martinetto et al., 2014). On the other hand, through late Pliocene and early Pleistocene, the  
274 Southern Tiberino Basin evolved from a wide lacustrine environment to a river-drained valley  
275 system (Ambrosetti et al., 1995a; Basilici, 1997, 2000a, 2000b; Martinetto et al., 2014). The  
276 sections Cava Toppetti II (Abbazzi et al., 1997) and Dunarobba (Ambrosetti et al., 1995b) are  
277 representative of this second context.

278

(FIGURE 2 approximately here)

## 279 3. Materials and methods

280 This work integrates the analysis of freshly collected material from the San Lazzaro section with the  
281 reinterpretation of the stratigraphic and palaeontological data from the sites Cava Toppetti II  
282 (Abbazzi et al., 1997; Argenti, 1999, 2004; Martinetto, 2001a; Petronio et al., 2003; Sardella et al.,  
283 2003) and Dunarobba (Ciangherotti et al., 1998; Manganeli and Giusti, 2000; Manganeli et al.,  
284 2008; Martinetto et al., 2014).

285 In the San Lazzaro section, as well as in the neighbouring sections (Fig. 3), a close, about 1 m  
286 spaced, sampling for marine microfossils ("biostratigraphic samples") was carried out in the  
287 lowermost deposits, in order to provide an integrated biostratigraphical datum. Similarly, more  
288 widely spaced biostratigraphic samples were collected in the upper part of the section, in  
289 correspondence of fine-grained deposits. For each sample, 100 g of sediment were processed with  
290 H<sub>2</sub>O<sub>2</sub> solution, washed through a 63 μ size mesh, and the residue observed using a  
291 stereomicroscope. Smear slides for nannoplankton analysis were prepared using the standard  
292 technique proposed by Bown and Young (1998), and observed under a polarizing-light microscope  
293 at 1000x magnification.

294

(FIGURE 3 approximately here)

295 The above-mentioned finding, in a biostratigraphic bulk sample (FU6, ca. 100 g) collected at 14 m,  
296 of a fruit part (endocarp) of *Sinomenium cantalense* was the starting point for a more extensive  
297 sampling effort in the San Lazzaro section. A few concentrations of compressed plant fragments  
298 were noticed in the portion from 5.5 m to 8.5 m of the section (Fig. 4), and three bulk sediment  
299 samples FU3 and FU4, ca. 400 g, and FU5, ca. 2000 g; these are named "carpological samples")  
300 have been collected there and processed with the palaeocarpological method illustrated in Basilici et  
301 al. (1997).

302 The methods for the identification of plant materials are the same as those recently described in  
303 Martinetto et al. (2015). However, the climatic characterisation of each plant fossil-species was



304 carried out differently. We did not use only the data available in the Paleoflora Database (PFDB:  
305 Utescher and Mosbrugger, 2015) and in the GrimClim Database (CG: Grimm and Denk, 2012),  
306 because these data have several biases depending from their literature sources: the PFDB does not  
307 indicate references for the thermal boundary values referred to each taxon, and the boundary  
308 temperatures of Fang (2011), largely used by the CG, were defined from very rough distribution  
309 data at county level (several Chinese provinces are larger than Japan). Therefore, whenever  
310 possible, we used in Table 1 the more precise data from different literature sources (Alternative  
311 MATmin in Appendix 1). Those include local floras and vegetation survey reports in China and  
312 Japan, in which distribution of taxa are described and/or mapped on the altitudinal scale of at least  
313 100 m based on herbarium specimens and/or field observations (Appendix 1).

314  
315 (FIGURE 4 approximately here)

316 Deposits in the area of Fabro Scalo (Fig. 1) have been investigated with the aim to: 1) reconstruct a  
317 lithostratigraphic section for the area, 2) better document the palaeofloral assemblages inside the  
318 phytodebris-rich horizons of the San Lazzaro outcrop, 3) establish the age of these deposits, and 4)  
319 compare the plant assemblages with other possibly coeval assemblages in central Italy, first of all  
320 those of the dated Cava Toppetti II section (Abbazzi et al., 1997; Martinetto, 2001a), and secondly  
321 those of poorly dated Dunarobba succession (Martinetto et al., 2014). To reevaluate the age of these  
322 three sections, data on vertebrate and continental mollusc biochronology were reconsidered  
323 (Abbazzi et al., 1997; Gliozzi et al., 1997; Ciangherotti et al., 1998; Petronio et al., 2003; Sardella et  
324 al., 2003; Argenti, 2004; Manganelli et al., 2008).

325 In addition, continental mollusc and vertebrate records were investigated as complementary  
326 palaeoclimatic evidence to terrestrial plants. In particular we analysed the history of the HUTEA  
327 plants in parallel with that of the terrestrial ectothermic vertebrates, whose distribution is clearly  
328 related to historical variations of temperature and humidity more directly than that of other  
329 vertebrates (Delfino, 2002; Kotsakis et al., 2004; Venczel and Sanchiz, 2005; Delfino et al., 2006;  
330 Delfino and Sala, 2007; Piras et al., 2007; Delfino et al., 2008).

331  
332 Even if we base our analysis on the climatic determinism of plant extinctions, the correlation of the  
333 disappearance events with the standard climatic curves (e.g. Zachos et al., 2001; Lisecki and Raymo,  
334 2005; De Shepper et al., 2013; Prescott et al., 2014) requires more information and is beyond the  
335 scope of this work.

### 336 337 3.2. Carpological and floristic analyses

338  
339 The San Lazzaro sediment samples FU3, FU4 and FU5 were prepared according to a standard  
340 palaeocarpological method (Martinetto, 1994; Basilici et al., 1997). The definition of the HUTEA  
341 category allowed us to carry out a new floristic analysis, both for the San Lazzaro assemblage and  
342 for several other Pliocene and early Pleistocene floras of Italy: we selected 13 reliably dated  
343 assemblages (2 of the Zanclean, 5 of the Piacenzian, 2 of the Gelasian, 3 Calabrian, 1 early Middle  
344 Pleistocene) and we analysed the percentage of species belonging to the HUTEA category, referred  
345 to the total number of species (Table 2). Furthermore, since our focus was on the early Pleistocene,  
346 we also analyzed the floral lists of all the main carpofloras of the rest of Europe (Baas, 1932;  
347 Chochieva, 1965; Buzek et al., 1985; Mai and Walther, 1988; Günther and Gregor, 1990;  
348 Velichkievich and Zastawniak, 2003; Mai and Velitzelos, 2007) whose age was proved or supposed  
349 to fall within that time interval (Table 3).

350 (TABLE 2 approximately here)

351 (TABLE 3 approximately here)

352  
353 In order to get an overview of the disappearance times of thermophilous plants at the south European  
354 scale, the occurrence and suggested extinction time of HUTEA were also checked in synthetic

355 palynological papers dealing with the following areas: whole area (Popescu et al., 2010), Iberian  
356 peninsula (Postigo-Mijarra et al., 2009), Italy (Bertini, 2010; Magri, 2010; Combourieu-Nebout et  
357 al., 2015), Balkan Peninsula (Tsedakis et al., 2006; Biltekin et al., in press), Colchis area (Shatilova  
358 et al., 2014) and Turkey (Biltekin et al., in press).

359

## 360 4. Results

361

### 362 4.1. The San Lazzaro section and its age constraints

363

364 The composite sedimentological and stratigraphic reconstruction proposed for the Fabro Scalo area  
365 integrates old observations (Baldanza et al., 2011, 2014; Bizzarri et al., 2015) and newly collected  
366 data. The general geological and sedimentological pattern, from the base to the top, is organized as  
367 follows (Fig. 3):

368 - about 10 m (cropping out) of structureless, mollusc-rich clayey and silty sand (offshore transition  
369 deposits); the lowermost layers are covered by recent alluvial deposits;

370 - up to 30-40 m of highly fossiliferous (mainly molluscs) fine sand (lower shoreface deposits);

371 - up to 25 m of intermingled coarse sand and gravel (gravel beachface deposits);

372 - a minimum of 20 m of channelled gravel with minor sand (river mouth deposits).

373 The about 27 m-thick San Lazzaro section represents approximately the lower/intermediate part of  
374 this composite section (Fig. 3); deposits grade up from poorly sorted silty sand, referred to the  
375 offshore transition, to moderately sorted fine sand of lower shoreface. Throughout the section, a  
376 rich and diversified fossil record (Baldanza et al., 2014; Bizzarri et al., 2015), dominated by  
377 molluscs, echinids, lunulite bryozoans, benthic foraminifera and decapod crustaceans was  
378 documented; both macro- and micropaleontological assemblages are dominated by benthic taxa,  
379 mostly referred to warm shallow water conditions.

380 As for the Monteleone and the Città della Pieve sections, deposits in the Fabro Scalo area are  
381 mainly referred to the MNN 18 - MNN 19a zones (*sensu* Rio et al., 1990) on the basis of  
382 nannofossil assemblages: rare small-sized *Gephyrocapsa* spp. (*sensu* Raffi, 2002), *Helicosphaera*  
383 *sellii*, *Calcidiscus macintyreii*, very rare and broken *Discoaster brouweri* and *Coccolithus pelagicus*.

384 Through the composite lithostratigraphic section, two calcareous nannofossil biostratigraphic events  
385 are recognized (Fig. 3): the LO of *Discoaster brouweri* (top of MNN 18 zone, *tDb sensu* Raffi,  
386 2002) in the lowermost part of the Fabro-Carnaiola section, and the FO of medium-sized  
387 *Gephyrocapsa* spp. (base of MNN19b subzone, *bmG sensu* Raffi, 2002) at about the top (22 m) of  
388 the San Lazzaro section. Therefore, the biostratigraphic data permit to assign deposits to the  
389 Gelasian *pro parte* - Calabrian *p.p.* interval. This transition is also marked by the occurrence, in the  
390 lowermost deposits, of marine ostracods such as *Aurila cruciata*, *Loxoconcha glabra*, *Argilloecia*  
391 sp., and *Ruggieria longecarenata*, usually documented from the end of the Gelasian and the base of  
392 the Calabrian (Faranda and Gliozzi, 2008). The occurrence, throughout Gelasian-Calabrian sections,  
393 of taxa of previously supposed “Pliocene affinity”, such as *Amphistegina* spp. and *Persististrombus*  
394 cf. *coronatus*, is not surprising, nor sufficient to suggest an older (Piacenzian) age: in fact, the  
395 persistence of these taxa into Gelasian to Calabrian deposits has been documented in other sites of  
396 this area (Bizzarri and Baldanza, 2006; Monaco et al., 2011). The two horizons with carpological  
397 remains, inside the San Lazzaro section (Fig. 3), are attributed to the MNN 19a subzone, well inside  
398 the early Pleistocene, and are still referable to the Gelasian stage.

399

#### 400 4.1.1. The San Lazzaro carpological assemblage

401 The preparation of the San Lazzaro carpological samples yielded plant assemblages mainly made  
402 up of woody fragments, particularly abundant in sample FU5. However, a careful observation  
403 allowed us to separate also a few, mostly fragmentary, fruits and seeds. Samples FU3 and FU4 had  
404 a very poor carpological content, reported in Table 4, whereas FU5 yielded more abundant  
405 carpological material that allowed us to identify five definite fossil-species (ICN, McNeill et al.,

406 2012) well-known in the Pliocene of Italy (see Table 4 for the number of specimens): *Magnolia*  
407 *allasoniae*, *Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana* and *Zanthoxylum*  
408 *ailanthiforme*. The occurrence of 3 HUTEA out of 6 species forming the San Lazzaro plant  
409 assemblage (Table 4) represents a very high percentage (50%). So, the precise identification at  
410 species level allowed by fruit morphology give to these few remains a relevant importance, due to  
411 the stratigraphic context in which they have been found. These taxa have been described and  
412 figured in Martinetto (2001a, 2001b), Mai and Martinetto (2006) and Martinetto et al. (2014, 2015).  
413 A single species has been left in open nomenclature for the reason discussed below:  
414 - *Vitis* cf. *vinifera* L. subsp. *sylvestris* Gmelin - seeds of *Vitis* with distinct similarities to the modern  
415 Mediterranean wild grape *V. vinifera* subsp. *sylvestris* are abundant in several tens of Italian fossil  
416 sites spanning from the Zanclean to the Holocene (Martinetto, 1994; Basilici et al., 1997; Cavallo  
417 and Martinetto, 2001). However, their assignment to the modern species (and subspecies) is not  
418 straightforward because a similar fossil-species has also been described (*Vitis parasylvestris*  
419 Kirchheimer 1957) and often reported in the Neogene of Europe (Geissert et al., 1990; Martinetto,  
420 1994; Mai, 2001). The diagnostic features of this last species are said to be the length up to 7 mm  
421 and the small seed body associated to a narrow cylindrical basis, somehow similar to that of the  
422 Holocene cultivated forms of *V. vinifera* subsp. *vinifera*. The consistent variability of morphological  
423 characters observed in rich fossil populations makes a precise assignment at species level  
424 problematic, in the absence of a detailed statistical and morphometric study. However, the  
425 dimensions and the shape of the base in the Plio-Pleistocene Italian seeds is mostly the same as in  
426 the modern Mediterranean species, so that a major affinity to *Vitis vinifera* subsp. *sylvestris* than to  
427 *V. parasylvestris* is suggested also for the specimen of San Lazzaro.

428  
429 (TABLE 4 approximately here)  
430

#### 431 4.1.2. Taphonomical considerations

432 Almost the whole carpological record of San Lazzaro comes from a thin lens of mixed shells and  
433 compressed phytodebris (FU5 in Table 4). Several lenses of this type are usually well exposed and  
434 recognizable after periods of intense rain (Fig. 5). Each lens is concave upwards, up to 40 cm wide,  
435 less than 10 cm thick, and filled by structureless clastic-bioclastic very fine sand, just a little coarser  
436 than the enclosing silty sand deposits. Mollusc shells and fragments are usually found at the bottom  
437 or in the lateral parts, while thin wood fragments are more randomly dispersed. In the 4-9.5 m  
438 interval (Fig. 3), such lenses are frequent, interposed to both shell lags and spotted mollusc  
439 specimens. Millimetric, isolated wood fragments (compressions) are locally spread through the rest  
440 of the section. A speditive anatomical analysis (stereomicroscope) proves that most of the  
441 phytodebris consists of heteroxylous and homoxylous xylem fragments, thus proving their origin  
442 from terrestrial or at least coastal woody plants. The abundance of such plant remains in a shallow  
443 marine nearshore environment probably reflects river flood events from neighboring areas. Distally,  
444 from the prodelta to the offshore marine environment, major events may trigger remobilization of  
445 sediments (sediment-gravity flows *sensu* Lowe, 1982 and Nemec and Steel, 1984), including  
446 density currents (turbidity currents). Several plant fragments horizons inside massive to laminated  
447 sandy sediments are interpreted as part of turbidites *s.l.* and even diagnostic of hyperpycnal flows  
448 (hyperpycnites: Zavala et al., 2012). On the other hand, the San Lazzaro deposits were referred to  
449 lower shoreface/offshore transition by means of sedimentological features (Baldanza et al., 2014;  
450 Bizzarri et al., 2015), and no evidences of deposits related to turbidity currents and/or hyperpycnal  
451 flows was found. Thus, the depositional models proposed by Zavala et al. (2012) to account for the  
452 richness of plant remains, leaves, charcoal or other very light land-derived materials in distal to  
453 deep marine deposits cannot be applied here. As well as the shell lags, these lenses can be  
454 interpreted as storm layers: plant remains transported to the sea during intense floods (in mass  
455 transport) by small rivers, depending on their size and density, may more or less longer float or  
456 quickly settle to the seafloor. As for other bioclasts, woody fragments and even larger branches and

457 trunks (Monaco et al., 2011) are remobilized during storm events, and redistributed inside storm  
458 layers. The small dimensions of fragments (up to few centimetres, usually <1 cm), the lack of whole  
459 leaves, the partially abraded aspect of carpological remains, their concentration inside lenses of very  
460 fine sands, surrounded by silty sand-dominated deposits, all indicate discontinuous, wave-induced  
461 sedimentation events (tempestites) in a relatively low energy environment. The possibility of  
462 reworking of plant material in marine environments was already discussed in Martinetto et al.  
463 (2015).

(FIGURE 5 approximately here)

#### 464 4.2. The Dunarobba section

465 An updated overview of the stratigraphic information on several sections of the Dunarobba site can  
466 be found in Martinetto et al. (2014), and here we concentrate on two types of rich and well-  
467 diversified molluscan assemblages from the Dunarobba Forest Section (DF). The first, coming from  
468 the silty clays encrusting the trunks, is dominated by extinct hygrophilous land prosobranchs and  
469 pulmonates, such as *Hydrocena dubrueilliana*, *Carychium (Saraphia) pachyichilum*, *C. (S.)*  
470 *pseudotetrodon*, *Negulus villafranchianus*, *Leiostyla gottschicki*, *Gastrocopta (Albinula) acuminata*  
471 *fossanensis* (= *G. (A.) acuminata*), *Gastrocopta (Vertigopsis) dehmi* (= *G. (V.) moravica*),  
472 *Eostrobilops aloisii*, *Staurodon cianfanellianus*, *Laminifera (Laminiplicata) villafranchiana* (= *Laminiplicata villafranchiana*) (Manganelli et al., 1989, 1990; Esu and Girotti, 1991, Esu et al., 1993; Ciangherotti et al., 1998; Manganelli and Giusti, 2000; Manganelli et al., 2008). These species are of high palaeobiogeographical and biochronological interest. Most of them, such as *H. dubrueilliana*, *C. pseudotetrodon*, *N. villafranchianus*, *G. (V.) dehmi* (= *G. (V.) moravica*), *G. (A.) acuminata fossanensis* (= *G. (A.) acuminata*), *L. gottschicki*, *E. aloisii*, *L. villafranchiana*, are in common with the NW Italian assemblages of the late Pliocene (Piacenzian of the marine chronostratigraphy) deposits of Villafranca d'Asti (RDB section) or Ceresole d'Alba and other Pliocene sites (Ciangherotti, 1997; Esu and Ciangherotti, 2004, Ciangherotti et al., 2007), and mostly got extinct during the late Pliocene (Piacenzian)/early Pleistocene (Gelasian) transition.

483 The second assemblage, coming from the sediments around the trunks of the Forest Section  
484 (Martinetto et al., 2014), is characterized by aquatic prosobranchs, such as *Theodoxus groyanus*,  
485 *Emmericia umbra*, *Prososthenia paulae*, *Tournouerina belnensis*, *Melanopsis affinis*, *Micromelania*  
486 (*Goniochilus*) *zitteli*, mainly endemic to central Italy and getting extinct in the late early Pleistocene  
487 (Ambrosetti et al., 1995b; Ciangherotti et al., 1998; Esu and Girotti, 2001).

488 Thanks to a high percentage of extinct molluscs of Pliocene character and to the findings of land  
489 species common to the late Pliocene molluscan fauna of NW Italy and other European Pliocene  
490 sites, it is possible to suggest a late Pliocene age (Piacenzian) for the Dunarobba molluscan fauna,  
491 even if a late Pliocene-earliest Pleistocene age (Piacenzian-Gelasian) cannot be excluded. The  
492 climatic indications of these molluscs, based on the modern relatives, indicate a warm temperate  
493 climate with a high atmospheric humidity, e.g. the genus *Eostrobilops* lives in East Asia, South of  
494 40° N, and *Negulus* in East Africa (Ethiopia) (Esu and Ciangherotti, 2004).

495 The occurrence of several fruit and seed assemblages in different sections of the Dunarobba site has  
496 been recently reported by Martinetto et al. (2014). The most diverse plant assemblage, originating  
497 from a sandy bed indicated as DC1b, included 41 species, 8 of which are recognized as HUTEA  
498 with a resulting percentage of 20%.

#### 499 500 4.3. The Cava Toppetti II section

501 The Cava Toppetti site, a few kilometers south-west of Todi (Fig. 1), was comprehensively  
502 investigated during the two last decades, and several sedimentological, stratigraphic,  
503 palaeontological and palaeoenvironmental data were collected (Ambrosetti et al., 1995a; Basilici,  
504 1995; Abbazzi et al., 1997; Gliozzi et al., 1997; Pontini, 1997; Leone et al., 2000; Pontini et al.,  
505 2002; Martinetto et al., 2014). Due to the presence of two completely different successions, cut  
506 through by a main extensional fault, the various records were referred to either Cava Toppetti I, the  
507 older succession made up by the Fosso Bianco Unit (FBU), or Cava Toppetti II, the younger

508 succession made up by the Ponte Naja Unit (PNU). Both the FBU and PNU (Fig. 2: Ambrosetti et  
509 al., 1995a; Basilici, 1995) were well exposed through the quarry fronts in the 1980s-1990s, but later  
510 the outcrop was deteriorated by the lack of quarrying activities, the successive backfilling and the  
511 slope restoration.

(FIGURE 6 approximately here)

513 The about 150 m thick Cava Toppetti II section pertained to the uppermost PNU; it was composed  
514 (Fig. 6) of prevailing clayey-sandy silt deposits (fine-grained sheet flow deposits), with interposed  
515 silty clay (palaeosol), planar-concave sandy gravel (stream ribbon channels) and tabular sandy  
516 gravel deposits (coarse-grained sheet-flow deposits). A complete sedimentological description and  
517 interpretation of PNU deposits can be found in Basilici (1995) and Abbazzi et al. (1997). The  
518 palaeoenvironment was reconstructed on a sedimentological basis as the medial and distal portion  
519 of an alluvial fan. Several types of sediments locally bear molluscs, whereas fragments of large  
520 vertebrates and micromammals were mainly collected inside palaeosols. According to Abbazzi et  
521 al. (1997), deposits of Cava Toppetti II section originally overlie the about 300 m thick lacustrine  
522 laminated silty clay deposits of the FBU, attributed to late Pliocene-early Pleistocene by means of  
523 magnetostratigraphy (Late Gauss to Early Matuyama Chrons).

524 At Cava Toppetti II an important biochronological datum is given by the occurrence of the  
525 micromammal *Apodemus dominans* (Argenti, 1999; Sala and Masini, 2007). In the southwestern  
526 branch of the Tiberino Basin such occurrence has been recorded also at the Pantalla site, together  
527 with a diversified vertebrate assemblage (Gentili et al., 1997; Cherin et al., 2013a, 2013b, 2014a,  
528 2014b). All the vertebrate data support a biochronological framework with Cava Toppetti II and  
529 Pantalla referable to the middle-late Villafranchian transition (Coste San Giacomo or Olivola  
530 Faunal Units), i.e. to the late Gelasian (Cohen et al., 2013). Recently, Bellucci et al. (2014) provided  
531 new data on the Coste San Giacomo faunal assemblage, including also small vertebrates. The age of  
532 this deposit, reference locality of the Coste San Giacomo Faunal Unit, has been approximately  
533 assessed at 2.1 Ma. The ongoing researches will allow a more detailed comparison of the Cava  
534 Toppetti II mammal assemblage to those of Coste San Giacomo and of the other Umbrian localities  
535 mentioned above.

536 The molluscs collected in the alluvial fan deposits of the Cava Toppetti II section (Abbazzi et al.,  
537 1997) are characterized by a few extinct freshwater prosobranchs, such as *T. groyanus*, *E. umbra*,  
538 *Choerina tudertis*, *M. affinis*, *Prososthenia augusti*, *P. tassoii*, which are endemic to central Italy,  
539 and by a few extinct species of land snails, such as *Carychium (Carychiella) puisseguri*, *Carychium*  
540 (*Saraphia*) *pachychilum*, *Carychium (S.) pseudotetrodon* and *Negulus villafranchianus*. Among  
541 these, only three species are shared with the Dunarobba assemblage, whilst all the species of  
542 freshwater prosobranchs were recovered also at Dunarobba. The PNU land molluscan fauna results  
543 impoverished in extinct molluscs compared with the Dunarobba one indicating a slightly younger  
544 age, that is early early Pleistocene (Gelasian). The lack of most of the thermophilous taxa occurring  
545 at Dunarobba, such as the representatives of the genera *Hydrocena*, *Eostrobilops*, *Staurodon*,  
546 *Laminiplica*, suggests a cooler climate during the deposition of the PNU unit in comparison to the  
547 Dunarobba Fossil Forest one (Ciangherotti et al., 1998). Furthermore, these taxa are also less  
548 exigent in terms of atmospheric humidity.

549 As for the macroscopic plant remains, the record of the Cava Toppetti II section is rather poor, but  
550 an important fruit and seed-bearing deposit (Fig. 7) has been located in the middle part of the  
551 section (Fig. 6) and the occurrence of several species had been reported by Martinetto (2001a). As a  
552 whole 40 species have been identified, 8 of which are recognized as HUTEA with a resulting  
553 percentage of 7%.

(FIGURE 7 approximately here)

555  
556  
557 All the data presented above call for a reconfirmation of the chronological position of the Cava  
558 Toppetti II section. We know that some recent papers challenged the reliability of several old



559 paleomagnetic data, due to some bias on magnetic minerals (e.g. the issue related to the Jaramillo  
560 subchron discussed in Muttoni et al., 2014). However, the bulk of data collected in the Tiberino  
561 Basin, their correlation with part of the Valdarno Basin sequence, which is also time-calibrated by  
562 means of radiometric data (Bertini, 2013), and the magnetic susceptibility-based high-resolution  
563 cyclostratigraphy (Pontini et al., 2002; Napoleone et al., 2003, 2004), make the chronologic  
564 interpretation of the Cava Toppetti II succession reliable in the light of current knowledge. Thus, on  
565 the basis of its palaeontological content and stratigraphic position, the section is thought to be early  
566 Pleistocene (Gelasian) in age, younger than the Reunion Event and older than the Olivola Faunal  
567 Unit, which is placed at the end of the normal polarity subchron Olduvai (Torre et al., 1996;  
568 Napoleone et al., 2003; Bellucci et al., 2014). The sedimentological features suggest a high  
569 sedimentation rate (>1.3 mm/y: Basilici, 1995; Abbazzi et al., 1997), and a time span of about 100  
570 ky to 300 ky is presumed for the whole Cava Toppetti II section, inside the 2.1-1.9 Ma range;  
571 (Abbazzi et al., 1997; Leone et al., 2000; Martinetto et al., 2014).

#### 572 573 574 4.4. Frequency of the HUTEA since 5 Ma and last occurrence of CTEA

575  
576 The percentages of species belonging to the HUTEA category in the well-dated reference floras of  
577 Italy (Fig. 8, Table 2) show that the Zanclean-Piacenzian assemblages have a higher value (7-31%),  
578 and the HUTEA are constantly present in all the floras that are well dated within this time interval,  
579 and also in those tentatively assigned to it (Martinetto et al., 2015; Martinetto, in press). A single  
580 HUTEA (*Eucommia*) occurs in one (Arda-AD3) of the two Gelasian reference assemblages (2%  
581 HUTEA), whereas the other Gelasian assemblage (Casnigo) and all of the Calabrian-Middle  
582 Pleistocene ones are devoid of HUTEA. Also the main European carpofloras definitely or possibly  
583 dated to the Gelasian-Calabrian would be devoid of HUTEA (Table 2), if not for the occurrence of  
584 *Eucommia* at Tegelen and Schwanheim.

585 Another late occurrence of two HUTEA species has been reported for a fossil flora of the Colchis  
586 area (Kvarbeti, Georgia): *Glyptostrobus europaeus* and *Symplocos casparyi* (*Symplocos* sect.  
587 *Lodhra*). This flora was referred by Chochieva (1975) to the Gurian local stage, which is now  
588 correlated to the Calabrian (Shatilova et al., 2014). Biltekin et al. (in press) even suggest the  
589 persistence of *G. europaeus* in the Holocene of the southern Black Sea.

590 (FIGURE 8 approximately here)

591 Our newly recovered Gelasian assemblage of San Lazzaro, with 50% HUTEA, is an exception at  
592 the European scale, but it must be considered that the low number of species may have biased this  
593 value. The other Gelasian assemblage available in central Italy, Cava Toppetti II, has 7% HUTEA  
594 and the Piacenzian or Gelasian Dunarobba assemblage has 20% HUTEA. These floras, similar to  
595 other Gelasian-Calabrian ones of Italy (Girotti et al., 2003, Martinetto, 2001a; Martinetto et al.,  
596 2015) and Europe (Table 2) are still very rich in CTEA, commonly associated with *Parrotia*,  
597 *Pterocarya* and *Zelkova*. By merging the occurrence data of HUTEA (Fig. 9), CTEA (compare  
598 Table 1 with data in Martinetto, 2001a, and Martinetto et al., 2015) and TEWA (Martinetto, 2001a;  
599 Martinetto et al., 2015) it is apparent that at least 70 plant species disappeared from southern Europe  
600 in the time interval between latest Zanclean (3.7 Ma) and early Middle Pleistocene (0.5 Ma).

601 (FIGURE 9 approximately here)

#### 602 603 4.5. Ectothermic vertebrate record (amphibians and reptiles)

604 The Italian peninsula hosted in the past a few reptile genera that went locally extinct (with a timing  
605 different from that of the HUTEA) and now survive in a stripe that extends eastward from the  
606 Balkan Peninsula to Indonesia, but still preserves in an exclusive way some amphibians that once  
607 had a much larger range. Examples are *Agama s.l.*, *Pseudopus*, *Tomistoma*, *Vipera* (oriental group),  
608 among thermophilous reptiles (Delfino, 2002; Kotsakis et al., 2004; Piras et al., 2007; Delfino et al.,  
609 2008), and *Salamandrina* and plethodontid salamanders among the amphibians that are tied to



610 humid terrestrial, non lentic or lotic, niches (Delfino, 2002; Venczel and Sanchiz, 2005; Delfino et  
611 al., 2006; Delfino and Sala, 2007). Particularly interesting is the case of the fully terrestrial  
612 plethodontid salamanders of the genus *Hydromantes* that have in the Italian biogeographic region  
613 the only Palaearctic representatives with their sister taxon living in Korea (Buckley et al., 2010).  
614 These lungless salamanders are tied to environments with high environmental humidity that allow  
615 gas exchanges through their skin, but the fact that they have interstitial habits could imply the  
616 influence of factors that go beyond those that controlled the survival of plants. It should also be  
617 mentioned that the last European occurrence of the frog genus *Latonia*, known since the Oligocene,  
618 is the one of Pietrafitta (Delfino, 2002; Rage and Rocek, 2003), a Calabrian site in Central Italy  
619 (Martinetto et al., 2014) and that this genus, described on the basis of fossil material and long  
620 considered extinct, was recently found alive in Israel (Biton et al., 2013).

## 621 5. Discussion

622 Depending on the concepts of "physiological uniformitarianism" (Tiffney and Manchester, 2001)  
623 and deterministic late Cenozoic plant extinctions in Europe (Svenning, 2003) we singled out three  
624 groups of plant fossil-species occurring in southern Europe: CTEA, HUTEA, TEWA. The CTEA  
625 and HUTEA include several species extinct in Europe, belonging to supraspecific plant taxa with a  
626 partly shared modern distribution in East Asia. The HUTEA are the descendants of the "exuberant  
627 laurophyllous flora" (Kubitzki and Krutzsch, 1996) growing in the warm temperate belt of southern  
628 Laurasia during the Eocene. At this time many taxa now distributed in eastern Asia were present in  
629 North America and Europe, but later survived only in the first and, partly, in the second continent.  
630 For this reason it would be more appropriate to speak about taxa "conserved in East Asia" rather  
631 than "of East Asian affinity".

632 Several taxa that tolerated cooler conditions (including many CTEA) tended to occupy a higher  
633 latitudinal belt during the Eocene and Early-Middle Miocene, and were able to survive both in  
634 eastern Asia and eastern North America, but not in Europe (Tiffney and Manchester, 2001; Wen et  
635 al., 2010). In fact, the present Asian-American biogeographic disjunction of several plant taxa  
636 (*Hamamelis*, *Liquidambar*, *Liriodendron*, *Magnolia*, ecc.) "mostly represents relict distributions of  
637 a wider distribution in the Tertiary. It is a product of complex processes such as migration/dispersal,  
638 extinction, speciation, vicariance, and perhaps also evolutionary convergence and stasis" (Wen et  
639 al., 2010).

640 Phylogenetic studies based on disjunct eastern Asian-eastern North American living plants (e.g.  
641 Magnoliaceae: Nie et al., 2008) pointed out that the divergence times mostly date back to Eocene-  
642 Miocene (Wen et al., 2010). The divergence times of extinct European taxa and their extant eastern  
643 Asian sister taxa is poorly understood, even if a few recent studies incorporated fossils in the  
644 phylogenies (e.g. Xiang et al., 2006; Denk and Grimm, 2009; Zhang et al., 2013; Fritsch et al.,  
645 2015).

646 Despite this lack of information, the available literature is sufficient to explain why it is convenient  
647 to separate the groups CTEA, HUTEA and TEWA: during the Eocene and/or Early-Middle  
648 Miocene, under equable climatic conditions (Wing and Greenwood, 1993; Zachos et al., 2001;  
649 Tiffney and Manchester, 2001; Grímsson et al., 2015), a north-south differentiation of the flora (and  
650 vegetation) was already present, so that the boreal regions were covered by cool-tolerant taxa (e.g.  
651 *Fagus*, *Juglans*: Aradhya et al., 2007; Denk and Grimm, 2009), some of which can be classified as  
652 CTEA (e.g. *Chamaecyparis*: Liu et al., 2009), and the middle latitudes were covered by more  
653 thermophilous taxa, including many HUTEA and TEWA, not adapted to regular and severe frost  
654 (e.g. *Cinnamomum*, *Engelhardia*, *Mastixia*, *Ocotea*, *Sideroxylon*, *Symplocos* sect. *Lodhra*,  
655 *Tetraclinis*, *Toddalia*, etc.). However, also several CTEA grew in these warm mid-latitude forests:  
656 in fact, even if we indicated the CTEA as a group of cool-tolerant plants, this applies only to the  
657 supraspecific taxa, and several CTEA species were probably as thermophilous as the HUTEA (see  
658 above the example of *Magnolia*). This hypothesis is corroborated by the observation that several  
659

660 CTEA species display a HUTEA-like pattern of disappearance in Italy (see CTEA2 and CTEA3 in  
661 Fig. 9), which could suggest a similar thermophilous attitude.

662 The analysis of the percentage of HUTEA species in some well-dated early Pliocene to early  
663 Pleistocene carpofloras of Italy (excluding those newly analysed here) provided an interesting  
664 picture: values above 15% in the Zanclean, above 7% in the Piacenzian, 2-0% percent in the  
665 Gelasian and invariably 0% in the Calabrian (Figs 8, 9). Furthermore, an analysis of the early  
666 Pleistocene carpofloras of Europe (Table 2) showed that most of them do not contain HUTEA, apart  
667 *Eucommia* and possibly *Glyptostrobos* and *Symplocos* sect. *Lodhra* in the Colchis refugial area  
668 (Chochieva, 1975; Shatilova et al., 2014). Thus, our new record of the San Lazzaro section is of  
669 particular relevance, because for the first time an assemblage containing a very high percentage  
670 (50%) of HUTEA is documented in European sediments independently dated to the early  
671 Pleistocene. This is in agreement with a previous record (Martinetto, 2001a) of the same species  
672 occurring at San Lazzaro (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) in the  
673 continental sediments of another early Pleistocene site of central Italy, Cava Toppetti II, even if in  
674 this second site the percentage of HUTEA is definitely lower (7%). The reconsideration of the  
675 stratigraphic data, in particular the biochronologic indications of continental molluscs and  
676 vertebrates, allows us to confirm a Gelasian age for the Cava Toppetti II section, the flora-bearing  
677 layer being most likely deposited between 2.1 and 1.9 Ma. The independent age assignments of the  
678 Cava Toppetti II and San Lazzaro sections point to a time-correlation of the warm and humid  
679 HUTEA-bearing phase detected in both of them. The combined record of the two sections is  
680 fundamental to prove that the three above-mentioned HUTEA species actually survived in central  
681 Italy after the Pliocene/Pleistocene boundary, and to rule out the suspect that the occurrence of their  
682 carpological remains in the marine San Lazzaro section could be due to the reworking from older  
683 (Pliocene) sediments (Martinetto et al., 2015).

684 Even if most of the HUTEA documented in the Pliocene (Fig. 9) are not yet reported in the early  
685 Pleistocene, it may be argued that this is a bias due to the scarcity of records. Indeed, the proved  
686 occurrence in the early Pleistocene of such thermophilous and humidity-requiring plants as  
687 *Symplocos* sect. *Lodhra* and *Toddalia* suggests the possibility that also other HUTEA would have  
688 crossed the Pliocene/Pleistocene boundary. Chiarini et al. (2009) reported fruits of *Engelhardia*  
689 from a poorly dated section that could be of early Pleistocene age. Pollen data suggest the  
690 persistence of *Engelhardia* in central Italy until the Middle Pleistocene (Biltekin et al., in press) and  
691 in Spain till to the early Pleistocene (Postigo-Mijarra et al., 2009). These late occurrences are in  
692 agreement with the suggestion by Kvaček (2007) that the European *Engelhardia* is an extinct  
693 phylogenetic clade that was more cool-tolerant than the extant Asian species, and possibly it should  
694 be excluded from the HUTEA in future analyses.

695 The possible late occurrence of a few potential HUTEA is also implicit in other South European  
696 palynological assemblages (Tsedakis et al., 2006; Postigo-Mijarra et al., 2009; Bertini, 2010; Magri,  
697 2010; Popescu et al., 2010; Orain et al., 2013; Shatilova et al., 2014; Biltekin et al., in press;  
698 Combourieu-Nebout et al., 2015), reporting *Eucommia*, *Symplocos* and "Taxodiaceae" pollen up to  
699 the Calabrian, and in some areas to the Middle Pleistocene (Shatilova et al., 2014; Biltekin et al., in  
700 press) or Holocene ("Taxodiaceae": Biltekin et al., in press). However, the identification at genus  
701 (for the "Taxodiaceae") or section level (for *Symplocos*), which is necessary for the assignment to  
702 the CTEA or HUTEA, is mostly not provided in such works (except Biltekin et al., in press).

703 To our knowledge the single macrofossil of a HUTEA in the Middle Pleistocene of Europe is a  
704 wood of *Amentotaxus* sp. (Follieri, 2010) from central Italy, associated to several taxa that later  
705 went extinct in Europe (*Taxodium*, the CTEA *Cephalotaxus* and *Torreya*, and the TEWA *Ocotea*).  
706 We cannot exclude that central-southern Italy may have offered a refugial niche that was warm and  
707 wet enough to assure the longer survival of a few HUTEA, in contrast to central Europe. In fact  
708 pollen data document the persistence of potential HUTEA ("Taxodiaceae") and humidity-requiring  
709 CTEA (*Carya*) till to the Middle Pleistocene in central and southern Italy (Manzi et al., 2011; Magri  
710 and Palombo, 2013; Orain et al., 2013; Biltekin et al., in press). However, most of the CTEA have

711 the last macrofossil record (Martinetto, 1999, 2001a; Martinetto et al., 2015) in the time span from  
712 1.4 to 0.8 Ma (Fig. 9).

713 Also a simple comparison of the fossil record and the current distribution of the terrestrial  
714 ectothermic vertebrates suggests that the Italian biogeographic region acted as a humid refugium. It  
715 is actually tempting to associate the history of plants with that of these animals, whose distribution  
716 is clearly related to historical variations of temperature and humidity more directly than that of  
717 other vertebrates. However, it seems that despite the possibility of identifying a general common  
718 trend there are significant differences that are only partly related to the incompleteness of the fossil  
719 records of both groups. Conversely, a particularly intriguing argument is the concomitant  
720 persistence in the San Lazzaro section of thermophilous terrestrial plants and unexpected (for the  
721 early Pleistocene) thermophilous marine benthic taxa, such as *Amphistegina* spp. and  
722 *Persististrombus* cf. *coronatus* (Bizzarri and Baldanza, 2006; Harzhauser and Kronenberg, 2008;  
723 Monaco et al., 2011).

724 It is well known that the Pliocene is characterized by intense climatic oscillations of increasing  
725 amplitude, also at the middle latitudes (De Shepper et al., 2013), with cold pulses at 3.7-3.6 Ma, 3.3  
726 Ma (Zanclean/Piacenzian transition) and intense glaciations during late Piacenzian-early Gelasian,  
727 at 2.7-2.4 Ma (Zachos et al., 2001; Lisecki and Raymo, 2005; Prescott et al., 2014). The early  
728 Pleistocene is characterized by ~40 kyr lower-amplitude glacio-eustatic oscillations (Combourieu-  
729 Nebout et al., 2015), terminating in the mid Pleistocene 'climate revolution' with an abrupt shift to  
730 ~100 kyr higher-amplitude oscillations in the late Calabrian, between 0.9 and 0.8 Ma (MIS 23 and  
731 MIS 22: Muttoni et al., 2011). This event brought a cooler climate during glacial maxima at the  
732 middle latitudes (Ravazzi et al., 2005; Bertini, 2010; Muttoni et al., 2011).

733 The above-mentioned climatic crises were probably responsible for terrestrial plant extinctions  
734 (Svenning, 2003; Eiserhardt et al., 2015). In the Italian record (Martinetto, 1999, 2001a; Martinetto  
735 et al., 2015) the HUTEA still show a very high percentage in correspondence of the late Piacenzian  
736 "warm blip" (CQ1 assemblage: 31%), but a marked decrease in the percentage and number of  
737 species (Fig. 8) occurs soon after, in the transition from the Piacenzian to the Gelasian. The north  
738 Italian plant assemblages formed during the late Piacenzian cooling (Irace et al., 2012) are totally  
739 devoid of HUTEA, but this is not the time of their definitive disappearance from Europe. The new  
740 record from the independently dated marine section of San Lazzaro and the related continental  
741 record from Cava Toppetti II show that at least three species of HUTEA persisted in central Italy in  
742 the Gelasian (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*). Further macrofossil  
743 studies in the Calabrian and Middle Pleistocene are needed for a better assessment of the  
744 disappearance time of these and other HUTEA species. In parallel, a more precise dating of  
745 important fruit and seed bearing sections should be obtained. If the Dunarobba section would be  
746 proven to have an early Pleistocene age (Bizzarri et al., 2011; Martinetto et al., 2014), this would  
747 imply that at least 8 HUTEA species (20% of the species in Dunarobba's assemblage DC1b)  
748 overcome the Plio/Pleistocene boundary in central Italy (Fig. 9), and the warmest Gelasian peaks  
749 still had a flora of definite "Pliocene" character. Actually, the evidences provided by continental  
750 molluscs and the fruit and seed assemblages (Fig. 9) suggest a Piacenzian (or transitional  
751 Piacenzian-Gelasian) age of the Dunarobba deposits, but also in this case we cannot rule out the  
752 persistence of Pliocene taxa in a climatic refugium. In fact, uncertainties in the disappearance time  
753 from central Italy of several thermophilous and humid requiring organisms still exist, and further  
754 data should be collected. As for plants, particular attention should be addressed to southern Italy,  
755 where pollen assemblages (Biltekin et al., in press; Combourieu-Nebout et al., 2015) suggest a  
756 longer persistence of thermophilous exotic taxa. However, the lack of palaeocarpological  
757 investigations in such an area did not permit a verification of the eventual presence of several  
758 HUTEA that do not have a recognizable pollen record (Table 1).

759 The new data collected and the use of the new categories HUTEA, CTEA and TEWA allow us to  
760 provide a description of the massive late Cenozoic plant extinction in southern Europe, which is  
761 more detailed and effective than the previous ones. For example, Rodriguez Sanchez and Arroyo

762 (2008) recently provided this version of the story: "in the Piacenzian relict genera of the Tethyan  
763 flora still coexisted in southern Europe with ancestors of extant Mediterranean taxa. The onset of  
764 the Mediterranean climate in the Pliocene, with hot and dry seasons, and the glacial–interglacial  
765 cycles of the Quaternary, with recurrent periods of cold and arid conditions, ultimately caused the  
766 extinction of many members of the Tethyan Palaeogene flora in Europe and North Africa (Mai,  
767 1989; Svenning, 2003)".

768 We suggest here a more articulated scenario: during the Miocene the humidity-requiring  
769 descendants of both the Palaeotropical ("Tethyan") and Arctotertiary floras coexisted in Europe  
770 (Mai, 1989, 1991), and most of them (TEWA excluded) did not develop an adaptation to aridity. A  
771 consistent group of plants, namely our HUTEA, also did not adapt to cool climate, whereas in other  
772 groups (our CTEA) cool-tolerant forms had been selected in the course of various Cenozoic cool  
773 phases (Zachos et al., 2001). The climatic tolerances of the HUTEA, TEWA (e.g. *Ficus*, *Laurus*,  
774 *Liquidambar*, *Ocotea*) and likely thermophilous CTEA species (i.e. CTEA2 in Fig. 9) were  
775 probably fixed by a selection under globally equable climates in the Eocene-Miocene time span  
776 (Mai, 1989; Wing and Greenwood, 1993; Svenning, 2003; Rodriguez Sanchez and Arroyo, 2008;  
777 Manchester et al., 2009; Grímsson et al., 2015), when some HUTEA (*Sargentodoxa*, *Sinomenium*)  
778 also grew in North America (Manchester et al., 2009), persisting into the Mio/Pliocene transition  
779 (Liu and Jacques, 2010).

780 In southern Europe the HUTEA, TEWA and thermophilous CTEA species still grew together in the  
781 same plant communities (see Martinetto and Vassio, 2010; Martinetto et al., 2015) during the  
782 Zanclean, Piacenzian and the Gelasian warm peaks, when the climate was favourable for all of  
783 them. Later, thanks to their major drought tolerance (Svenning, 2003; Grimm and Denk, 2012;  
784 Utescher and Mosbrugger, 2015), the TEWA found some relatively warm refuges in the  
785 Mediterranean (*Coriaria*, *Laurus*, *Liquidambar*, *Olea*, *Styrax*, *Tetraclinis*), North Africa (*Laurus*,  
786 *Olea*, *Tetraclinis* and, possibly, *Morella*, *Ocotea*, *Sideroxylon*, *Visnea*) and West Asia (*Olea*,  
787 *Sideroxylon*). Some TEWA are today conserved in Macaronesia (*Morella*, *Ocotea*, *Sideroxylon*,  
788 *Visnea*) but their arrival there could be as recent as Pleistocene (Kondrasov et al., 2015).

789 Conversely, the HUTEA did not manage to adapt either to the dry and cool European conditions  
790 (Manzi et al., 2011) or to the too dry North African-East Asian ones and survived only in East Asia;  
791 just a few of them also survived in wet parts of tropical Africa (e.g. *Toddalia*) and/or America (e.g.  
792 *Meliosma* subgen. *Kingsbouroghia*, *Sassafras*, *Saurauia*).

793 As for the chronology of the disappearance, the Italian record would suggest that the HUTEA were  
794 constantly present in the Zanclean-Piacenzian flora of southern Europe, had a small retreat at the  
795 Zanclean-Piacenzian transition, possibly affecting four species of HUTEA (Fig. 9), and a larger one  
796 at the Piacenzian-Gelasian transition (18 species of HUTEA: Fig. 9); three species of HUTEA  
797 (*Toddalia latisiliquata*, *T. rhenana*, *Sinomenium cantalense*) seem to disappear at the  
798 Gelasian/Calabrian transition, and there is poor evidence in Italy for the few HUTEA which  
799 survived in the Calabrian, even if at least two HUTEA species (*Glyptostrobus europaeus* and  
800 *Symplocos casparyi*) were still present during the Calabrian in the Colchidian refugium (Chochieva,  
801 1975). *Engelhardia* and *Eucommia* still occurred in the Calabrian of Italy and Spain (Postigo-  
802 Mijarra et al., 2009; Bertini, 2010; Biltekin et al., in press; Martinetto in press PalB); the last  
803 southern European macrofossil record of an HUTEA which is presently known is that of  
804 *Amentotaxus* sp. in the Middle Pleistocene of central Italy (Follieri, 2010).

805 Similarly to the HUTEA, also the CTEA did not tolerate dry conditions (Svenning, 2003), but a few  
806 ones (*Carya*, *Tsuga*) still survived in the Middle Pleistocene of central-southern Italy (Magri, 2010),  
807 Turkey (Biltekin et al., in press) and the Balkan (Tsedakis et al., 2006; Biltekin et al., in press) and  
808 Iberian (Postigo-Mijarra et al., 2009) peninsulas, due to the presence of refugia (Combourieu-  
809 Nebout et al., 2015) which were humid enough, as demonstrated by the continuous presence of the  
810 draught-intolerant *Fagus* until today (Magri, 2008). *Parrotia*, *Pterocarya* and *Zelkova*, which had  
811 climatic requirements similar to the CTEA, survived until the present around the Black and Caspian

812 seas (*Zelkova* also in the Mediterranean). Another plant extinct in Europe, *Cedrus*, has particular  
813 requirements and histories (Magri, 2012; Su et al., 2013; Biltekin et al., in press).  
814 As a whole the carpological data, in connection with the abundant pollen data available, testify that  
815 in the late Piacenzian-Middle Pleistocene interval at least 70 plant species (Table 1), including  
816 HUTEA (Fig. 9), CTEA (Fig. 9, Table 1) and TEWA (Martinetto et al., 2015), disappeared from the  
817 fossil record. However, such a disappearance is not readily interpretable as extinction. By  
818 comparing our results with those of Bertoldi et al. (1994), Martinetto (1999, 2001a), Martinetto et  
819 al. (2007) and Bertini (2010) it is apparent that the rapidly increasing fossil evidence provided by  
820 the Italian carpological and pollen records determined a progressive shift of the last occurrence data  
821 of several taxa (e.g.: *Liriodendron*, *Magnolia*, *Sinomenium*, *Symplocos*, *Toddalia*), and there is still  
822 space for further changes based on new fossil evidence. We propose that, based on the present  
823 evidence, only the concomitant disappearance events of several species, such as the HUTEA2 +  
824 CTEA2 (Fig. 9), should be considered as reliably assessed. These concern only two main phases:  
825 The Piacenzian/Gelasian transition (main crisis of the HUTEA2 and CTEA2) and the late  
826 Calabrian/Middle Pleistocene (main crisis of the CTEA4, last occurrence of the HUTEA  
827 *Amentotaxus*). The disappearance events of plant macrofossils at the Zanclean/Piacenzian transition  
828 (a few HUTEA1) and Gelasian/Calabrian transition (a few HUTEA3 and CTEA3) appear of minor  
829 scale, as also confirmed by the relatively continuous pollen records (Tzedakis et al., 2006; Postigo-  
830 Mijarra et al., 2009; Bertini, 2010; Magri, 2010; Orain et al., 2013; Shatilova et al., 2014; Biltekin  
831 et al., in press; Combourieu-Nebout et al., 2015). These last events are not univocally interpretable  
832 as extinctions, since the taxa which seem to disappear could have become silent for the macrofossil  
833 record, though perhaps still present in small relict niches, as suggested by the late occurrence of  
834 *Eurya* cf. *stigmosa* (CTEA), *Glyptostrobys europaeus* (HUTEA) and *Symplocos casparyi* (HUTEA)  
835 in the Calabrian of the Colchis refugium (Chochieva, 1975; Mai and Martinetto, 2006) and also of  
836 *Amentotaxus* (HUTEA), *Cephalotaxus* (CTEA) and *Torreya* (CTEA) in the Middle Pleistocene of  
837 central Italy (Follieri, 2010).

## 838 839 6. Conclusions

840 New data on early Pleistocene fossil fruit and seed assemblages from Italy allowed us to detect  
841 several extinct taxa that commonly went unnoticed in pollen analyses. The combined analysis of  
842 Pliocene and early Pleistocene occurrence data provided a detailed picture of the reduction of plant  
843 diversity in southern Europe. The possible explanation of the causes of plant extinction requires an  
844 excursion into deeper times: Several Neogene plants were mainly adapted to grow in thermophilous  
845 mesic forests, whose consistent water supply was guaranteed by atmospheric humidity more than  
846 groundwater. The climate deterioration of the Plio-Pleistocene cancelled the ecological space of  
847 growth of most thermophilous and humidity-requiring taxa. Provided that habitat shift occurred  
848 very rarely, most taxa did not manage to adapt to the harsh conditions either from 2.7 to 2.4 Ma or  
849 from 1.0 to 0.3 Ma, and went extinct. The chance to avoid extinction was not only a question of  
850 temperature, but a combination of this with humidity requirements. Southern Europe became  
851 extremely dry during the Pleistocene glacials and those plants requiring both higher temperature  
852 and consistent water supply had no chance to find a niche to survive, if not adapted to live along  
853 rivers (*Liquidambar*, *Parrotia*, *Platanus*, *Pterocarya*). A few humidity-requiring plants that had  
854 already developed an adaptation to cold climate in the Oligocene or Miocene, like *Carya*, could  
855 temporarily survive into the Middle Pleistocene also in the inhospitable Europe, possibly in small,  
856 not too dry refugia. A similar niche may have saved *Parrotia*, but in the south Caspian area.  
857 Our carpological data, in connection to the abundant pollen data available from the literature, testify  
858 that the late Zanclean-Middle Pleistocene interval has really been the theatre of a stepwise mass  
859 extinction in southern Europe: at least 70 plant species disappeared in two main phases: Piacenzian-  
860 Gelasian transition (main crisis of the HUTEA and CTEA2) and late Calabrian-Middle Pleistocene  
861 (main crisis of the CTEA4, last occurrence of the HUTEA *Amentotaxus*). The disappearance events  
862 at the Zanclean-Piacenzian transition (mostly HUTEA1) and Gelasian/Calabrian transition (a few



863 HUTEA3 and CTEA3) appear of minor entity and are not univocally interpretable as extinctions.  
864 The chronological positions of the two main collective disappearance events coincide with two  
865 well-known intervals of major climatic deterioration and support a climatic determinism in the  
866 south European extinctions of the investigated plant taxa.

867

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880

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1340  
1341 Figure captions

1342 Figure 1 - Simplified geological scheme for the area of the San Lazzaro, Cava Toppetti and  
1343 Dunarobba sections.

1344 Figure 2 - Reference lithostratigraphic schemes for the South Valdichiana and Tiberino Basins  
1345 (modified after Baldanza et al., 2014). 1=San Lazzaro; 2=Cava Toppetti II; 3=Dunarobba.

1346 Figure 3 - Sedimentological/stratigraphic sections in the San Lazzaro area. Location of the  
1347 biostratigraphic (dots) and carpological (FU3-6) samples is also reported. *tDb*=*Discoaster broweri*  
1348 LO; *bmG*=medium-sized *Gephyrocapsa* sp. FO (sensu Raffi, 2002). CS = clay, silt; G = gravel.

1349 Figure 4 - Panoramic view of the San Lazzaro quarry. The richest fruit and seed bearing deposit  
1350 (FU5) was located at the transition from the grey to the yellowish sediments (1/3 above the bottom  
1351 of the image).

1352 Figure 5 - Detail of a lens of mixed shells and compressed phytodebris at ca. 8 m from the base of  
1353 the San Lazzaro section (see FU4 in Fig. 3).

1354 Figure 6 - Resumed geological setting, sedimentological interpretation, magnetostratigraphic and  
1355 biochronological calibration, and fossil record for the Cava Toppetti II site (redrawn after Abbazzi  
1356 et al., 1997). Original vertebrates taxonomy reported by Abbazzi et al. (1997) is not revised nor  
1357 further discussed herein.

1358 Figure 7 - Aspect of the deposits with compressed macroscopic plant remains in the Cava Toppetti  
1359 II section as they appeared in the year 1998. The sampled fruit and seed bearing sediment  
1360 (consolidated sandy mud, see NJ1 in Fig. 7) is shown in the detail below.

1361 Figure 8 - Histograms of the percentage of HUTEA species in some well-dated early Pliocene to  
1362 Early Pleistocene floras of Italy (dark grey bars). Records from San Lazzaro, Dunarobba and Cava  
1363 Toppetti II are also reported (pale grey bars). Numbers indicate the total of HUTEA species in each  
1364 assemblage. See label explanations and locality data in Table 2.

1365 Figure 9 - Scheme summarizing the chronological distribution of carpological records of selected  
1366 species in the Pliocene and early Pleistocene of northern-central Italy. The records from all the  
1367 localities accessed into the CENOFITA database (Martinetto and Vassio, 2010; Martinetto et al.,

1368 2015) are reported, according to data published by Basilici et al. (1997), Bertoldi and Martinetto  
1369 (1995), Ghiotto (2010), Gregor (1990), Martinetto (1994, 1995, 1999, 2001a, 2001b, 2003, 2009, in  
1370 press), Martinetto et al. (2015). Both the HUTEA and CTEA have been subdivided in groups  
1371 according to the chronostratigraphic distribution, in such a way that the numbers 1 to 4 corresponds  
1372 to the Groups 1 to 4 in Martinetto et al. (2015). All of the species referred to the HUTEA and  
1373 CTEA4 have been reported, whereas for the CTEA2 and CTEA3 only selected examples have been  
1374 shown. The age range for each species is indicated by black bars for the records originating from  
1375 reliably dated localities (Martinetto, 1999, 2001a, 2003; Martinetto et al., 2007, 2015): Lugagnano  
1376 (5.1-4.5 Ma), Canale (4.5-3.8 Ma), Cherasco (4.5-3.8 Ma), Pocapaglia (4.5-3.8 Ma), Breolungi (5.1-  
1377 3.8 Ma), Morozzo (5.1-3.8 Ma), Sento I (3.8-3.6 Ma), Candelo (4.5-3.6 Ma), Baldichieri-Fornace  
1378 (3.8-3.3), Roatto (3.3-3.2 Ma), RDB Quarry of Villafranca d'Asti (3.3 to 3.1 Ma), Stura di Lanzo  
1379 Fossil Forest (3.1-3.0 Ma), Marecchia (3.0-2.9 Ma), San Miniato (3.0-2.8 Ma), Castell'Arquato-  
1380 Monte Falcone (3.0-2.8 Ma), Meleto (2.9-2.8 Ma), Santa Barbara (2.9-2.7 Ma), Castell'Arquato-  
1381 Arda-AD3 (2.5-2.4 Ma), Casnigo (2.1-1.9 Ma), Poggio Rosso (ca. 1.9 Ma), Santerno-Codrignano  
1382 (1.8-1.7 Ma), Lefte 1st browncoal (1.6-1.4 Ma), Stirone-Laurano-LA1 (1.1-1.0 Ma), Enza-EZ38  
1383 (1.1-1.0 Ma), Ranica (1.1-1.0 Ma), Oriolo (1.0-0.8 Ma), Stirone-Laurano-LA3 (0.9-0.8 Ma),  
1384 Pianico-BVC lithostratigraphic unit (0.8-0.7 Ma). Hatched bars indicate records from the following  
1385 poorly dated localities (see Martinetto, 1999; Martinetto et al., 2015): Ca' Viettone (late Zanclean,  
1386 possibly 3.8 to 3.6 Ma); Fossano (late Zanclean, possibly 4.0 to 3.6 Ma); Sento II (possibly late  
1387 Zanclean, 3.8 to 3.6 Ma); Cossato (possibly late Zanclean-early Piacenzian, 3.8 to 3.2 Ma); Front  
1388 (possibly Piacenzian, 3.3 to 3.0 Ma); Momello-Lanzo (possibly Piacenzian, 3.6 to 3.0 Ma);  
1389 Castelletto Cervo I (possibly late Piacenzian, 2.8 to 2.6 Ma); Castelletto Cervo II (possibly  
1390 Gelasian, 2.6 to 2.0 Ma); San Pietro di Ragogna (Gelasian, 2.6 to 1.8 Ma); Buronzo (possibly  
1391 Gelasian, 2.2 to 1.8 Ma); Steggio (Calabrian, 1.8 to 0.8 Ma). Abbreviations: c = climber; h = herb;  
1392 MAT = Mean Annual Temperature; Mes = Messinian; MP = Middle Pleistocene; NLR = Nearest  
1393 Living Relative; s = shrub; t = tree.

1394  
1395 Table 1 - Mean Annual Temperature lower threshold values for modern plant genera or subgeneric  
1396 taxa extinct in Europe ("exotic"), according to the Paleoflora database (PFDB, Utescher and  
1397 Mosbrugger, 2015), the GrimClim database (CG, Grimm and Denk, 2012), and to different  
1398 literature sources listed in Appendix 1 (Alternative MATmin). The list is limited to taxa of the  
1399 HUTEA and CTEA categories with a proved occurrence in the late Cenozoic of Italy, selected as a  
1400 representative territory for the evaluation of the southern European floral change.

1401 Table 2 - List of the reference localities selected for the calculation of HUTEA species percentage  
1402 reported in Fig. 8.

1403 Table 3 - Occurrence of HUTEA and CTEA genera in the main Early Pleistocene carpofloras of  
1404 Europe.

1405 Table 4 - List of the carpological taxa identified in four sediment bulk samples from the San  
1406 Lazzaro section, see Fig. 3. In brackets the number of specimens for each species.