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# **An overview of Alpine and Mediterranean palaeogeography, terrestrial ecosystems and climate history during MIS 3 with focus on the Middle to Upper Palaeolithic transition**

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## 32 **Abstract**

33 This paper summarizes the current state of knowledge about the millennial scale climate  
34 variability characterizing Marine Isotope Stage 3 (MIS 3) in S-Europe and the  
35 Mediterranean area and its effects on terrestrial ecosystems. The sequence of Dansgaard-  
36 Oeschger events, as recorded by Greenland ice cores and recognizable in isotope profiles  
37 from speleothems and high-resolution palaeoecological records, led to dramatic variations  
38 in glacier extent and sea level configuration with major impacts on the physiography and  
39 vegetation patterns, both latitudinally and altitudinally. The recurrent succession of (open)  
40 woodlands, including temperate taxa, and grasslands with xerophytic elements, have been  
41 tentatively correlated to GIs in Greenland ice cores. Concerning colder phases, the  
42 Greenland Stadials (GSs) related to Heinrich events (HEs) appear to have a more  
43 pronounced effect than other GSs on woodland withdrawal and xerophytes expansion.  
44 Notably, GS 9-HE4 phase corresponds to the most severe reduction of tree cover in a  
45 number of Mediterranean records. On a long-term scale, a reduction/opening of forests  
46 throughout MIS 3 started from Greenland Interstadials (GIs) 14/ 13 (ca. 55-48 ka), showing  
47 a maximum in woodland density. At that time, natural environments were favourable for  
48 Anatomically Modern Humans (AMHs) to migrate from Africa into Europe as documented  
49 by industries associated with modern hominin remains in the Levant. Afterwards, a variety

of early Upper Palaeolithic cultures emerged (e.g., Uluzzian and Proto-Aurignacian). In this chronostratigraphic framework, attention is paid to the Campanian Ignimbrite tephra marker, as a pivotal tool for deciphering and correlating several temporal-spatial issues crucial for understanding the interaction between AMHs and Neandertals at the time of the Middle to Upper Palaeolithic transition.

**Keywords:** Middle Upper Palaeolithic, Palaeoecology, Palaeoclimate, Marine Isotope Stage 3, Terrestrial records

## 1 Introduction

Climate variability and landscape transformations underlie the complex interaction between natural resources and human dynamics. The understanding of these changes over time relies on palaeoclimate and palaeoecological information obtained from different natural archives (e.g. terrestrial and marine sediments, speleothems, ice cores, etc.), which are well known for their potential to record even abrupt and high frequencies events. The Marine Isotope Stage 3 (MIS 3) in the Last Glacial Period (Lisiecki and Raymo, 2005) is one of the most highly unstable phases, as far as climate is concerned, closely interwoven with the recent human evolution history. MIS 3 (ca. 60-30 ka) was characterized by major rapid climatic changes showing high variability, associated with abrupt atmospheric shifts over Greenland (Dansgaard-Oeschger [D-O] events) and episodes of massive iceberg discharge into the North Atlantic (Heinrich events [HEs]),

70 enhancing cold and dry conditions at mid-to-low latitudes (Fletcher and Sánchez Goñi,  
71 2008; Fleitmann et al., 2009; Naughton et al., 2009; Fletcher et al., 2010a).

72 Within this context, the Middle to Upper Palaeolithic transition (ca. 50-30 ka in Europe and  
73 western Asia, Higham et al. 2014; Benazzi et al., 2015; Hublin 2015; Douka and Higham,  
74 2017; Been et al., 2017; Margherita et al., 2017) represents one of the pivotal phases in  
75 human evolution documenting the demise of the autochthonous Neandertals and their  
76 replacement by Anatomically Modern Humans (AMHs). Many authors suggest that the  
77 eastern Mediterranean region and, in turn, the Italian Peninsula, served as gateways for  
78 the immigration and spread of AMHs from Africa to western Eurasia (van Andel et al.,  
79 2003; Müller et al., 2011; Moroni et al., 2013; 2018), where various transitional  
80 technocomplexes (eg., the Uluzzian in Italy and Greece, the Châtelperronian in central and  
81 south western France and northern Spain, the Neronian in south eastern France) replaced  
82 pre-existing Mousterian cultures (Mellars, 2006). Neandertals and AMHs societies  
83 developed in a context of continuous climatic fluctuations between cold-arid (Greenland  
84 Stadial, GS) and mild-humid (Greenland Interstadial, GI) conditions (Staubwasser et al.,  
85 2018). Surprisingly, despite the apparent body adaptations to live under rigid climates  
86 conditions (Steegmann et al., 2002), e.g., a wide and tall nasal aperture useful in  
87 humidifying and warming cold and dry air (Franciscus, 1999; Wroe et al., 2018),  
88 Neandertals did not survive into the coldest phases of MIS 3. Their extinction is statistically  
89 placed around 40 ka cal BP (Higham et al., 2014) and almost in coincidence with  
90 Greenland Stadial 9/HE 4, which is a noticeable cold phase recorded in both marine and  
91 terrestrial records (e.g. Fedele et al, 2003; Guellevic et al., 2014 and references therein).  
92 Several hypotheses have been proposed about Neandertal extinction and AMHs

93 replacement, and the debate is still unresolved (e.g., Mellars 2006; Hoffecker 2009;  
94 Benazzi et al., 2011; 2015; Villa and Roebroeks, 2014; Higham et al., 2014; Hublin, 2015;  
95 Rey-Rodríguez et al., 2016; Greenbaum et al., 2018).

96 To disentangle the role played by climate, ecosystem changes and physiography in such  
97 human processes, a palaeoclimate and palaeoecological perspective focusing on Europe  
98 and the Mediterranean area is essential. These efforts represent part of a wider interest in  
99 determining how abrupt climate changes modified past environments.

100 The aim of this paper is to present the state-of-the-art of palaeoclimate and  
101 palaeoecological researches relevant to the ERC Consolidator Grant 2016 "SUCCESS -  
102 *The earliest migration of Homo sapiens in southern Europe: understanding the biocultural*  
103 *processes that define our uniqueness*". To contribute to the discussion about the arrival of  
104 AMHs in Southern Europe, the pattern of their diffusion and their interactions with  
105 Neandertals, a review of the current knowledge about the climate context and the  
106 landscape structure is presented. A selection of high-resolution palaeoecological records  
107 covering the time span between HE 5 to 3, known for their strong impact in western  
108 Eurasia, are discussed to explore the effects of short-term climate variability on  
109 ecosystems and human interactions.

110

## 2 Reference climate records for the Last Glacial period and signal synchronicity between different realms

### 2.1 MIS 3 as recorded in Greenland ice cores

MIS 3, which lasted from 60 ka to 30 ka, was characterized by millennial-scale climate oscillations commonly referred to as Dansgaard-Oeschger (D-O) events. These events, particularly well-defined in Greenland ice cores, were first described by Dansgaard et al. (1993). Typically, D-O events are featured by an abrupt transition (within a few decades) from a cold phase (GS), into a warm phase (GI). NGRIP, GRIP and GISP2 ice cores provide master records for these rapid climatic changes throughout the Last Glacial cycle (MIS 5d to the end of MIS 2; ca. 116–11.7 ka) in the North Atlantic region (McManus et al., 1999). Boundaries between GS and GI periods were established based on both stable-oxygen isotope ratios of the ice ( $\delta^{18}\text{O}$ , reflecting mainly local temperature) and calcium ion concentrations ( $[\text{Ca}^{2+}]$  reflecting mainly atmospheric dust loading) measured in the ice (**Fig. 1, a-c**) (Rasmussen et al., 2014). The close timing of  $\delta^{18}\text{O}$  and  $[\text{Ca}^{2+}]$  abrupt shifts is also indicative of reorganizations in atmospheric circulation (Steffensen et al., 2008). Notably,  $[\text{Ca}^{2+}]$  data reflect primarily changes in dust concentration but also changes in dust source conditions and transport paths (Fischer et al., 2007a, 2007b). During D-O events North Atlantic region temperature and East Asian storminess were tightly coupled and changed synchronously with no systematic lead or lag (Ruth et al., 2007), thus providing instantaneous climatic feedback. This relationship was stable over the entire Last Glacial period.

According to Petersen et al. (2013), the driving mechanism of GI onset is linked to the rapid collapse of an ice-shelf fringing Greenland, potentially due to subsurface warming.



134 During GI, a gradual cooling controlled by the timing of ice-shelf regrowth leads to GS  
135 conditions that lasted for centuries up to millennia. NGRIP temperature reconstructions  
136 based on  $\delta^{15}\text{N}$  isotope measurements (**Fig. 1, b**) show T increase at the onset of each GI  
137 ranging from 6.5 °C (D-O 9) up to 16.5 °C (D-O 11), with an uncertainty of  $\pm 3$  °C (Kindler  
138 et al., 2014).

139 A recent important step forward is represented by the development of the ice-core GICC05  
140 chronology (Andersen et al., 2006; Rasmussen et al., 2006; Svensson et al., 2008;  
141 Seierstad et al., 2014) and its flow model-based extension (GICC05modelext) published in  
142 Rasmussen et al. (2014), which allowed to achieve a reference template for the pattern of  
143 climate variability during the Last Glacial cycle.

## 144 **2.2 Climate signals in mid- to low-latitude marine records**

145 A well-known feature in North Atlantic marine sediments is the presence of coarse  
146 sediment layers, i.e. the ice-rafted debris (IRD, Ruddiman, 1977). Such depositional  
147 episodes, known as Heinrich Events (HE), are related to massive discharge, rafting and  
148 melting of icebergs into the ocean and the consequent fall of detrital sediments trapped in  
149 the ice on the ocean floor (Heinrich, 1988) and unambiguously identified during GS phases  
150 of the Last Glacial period (e.g. Bond et al., 1992; 1993; Hemming 2004).

151 It is widely assumed that D-O events and HE are linked to reorganisations and/or  
152 variations in the strength of the Atlantic Meridional Overturning Circulation (AMOC)  
153 (Broecker et al., 1990). Specifically, Bagniewski et al. (2017) suggest a 30-50% weakening  
154 of the AMOC during GSs and a complete shutdown during HEs, also coinciding with large  
155 increases in the abundance of foraminifer polar species (e.g. *N. pachyderma*, **Fig. 1, h-g**).

156 The Iberian Margin (**Fig.1**) is a key area for the reconstruction of these dynamics thanks to  
157 its distal position, i.e. outside of the main belt of ice rafting, which limit disturbance of the  
158 sediments (Bard et al., 2000; Pailler and Bard, 2002). The recently obtained Sea Surface  
159 Temperature (SST) curve based on the biomarker  $\text{TEX}^{\text{H}}_{86}$  in MD95-2042 core (Darfeuill et  
160 al., 2016) highlights that the greater cooling peaks occurred during HEs (about 3-5 °C; **Fig.**  
161 **1, f**). This feature is in disagreement with the general pattern emerging over Greenland,  
162 where temperatures reconstructed during GS are roughly comparable and show more  
163 stable values to each other (**Fig. 1, b**). In addition, Martrat et al. (2007) argue that SST  
164 changes occur a few centuries before the subsequent generation of icebergs, which are  
165 traced by increases in IRD percentage. Regarding this issue, various studies state that  
166 HEs are shorter (Roche et al., 2004; Peters et al., 2008) than the corresponding GS and  
167 occur after the AMOC entered a weakening trend (Flückiger et al., 2006; Marcott et al.,  
168 2011). Thus, HEs seem to be a consequence rather than the cause of the AMOC  
169 weakening (e.g., Alvarez-Solas et al., 2010, 2013; Marcott et al., 2011; Barker et al.,  
170 2015).

171 Given the uncertainty across the North Atlantic in the ocean reservoir correction (e.g.,  
172 Stern and Lisiecki, 2013; Butzin et al., 2017), and the lack of a clear HE signature in the  
173  $\delta^{18}\text{O}$  Greenland isotopic record (Rasmussen et al., 2014), it is difficult to establish where  
174 HEs lie exactly within the D-O framework (Andrews and Voelker, 2018). Indeed,  
175 Rasmussen et al. (2014) did not designate the temporal positions of HEs. However, new  
176 Greenland ice cores proxy records (e.g.,  $^{17}\text{O}$ -excess; **Fig. 1, d**) are linked to a lower-  
177 latitude hydrological cycle signal (Guillevic et al., 2014). This might help in the future to

better constrain HE in the ice core series, allow exploring time leads and lags in between events happening at different latitudes.

### **2.3 Synchronicity between abrupt Greenland events and terrestrial responses in Southern Europe**

Over the last two decades, the INTIMATE project (INTEgrating Ice-core, MARine, and TERrestrial records; e.g., Blockley et al., 2012; Rasmussen et al., 2014) has proposed a series of event-stratigraphic templates based on the isotopic and dust concentration changes in Greenland ice cores. The alternating pattern of stadial and interstadial geologic-climatic units, due to their very high stratigraphic and temporal resolution and precise dating, constitute the most comprehensive and best resolved archive of high-frequency climate variability. The Northern-Hemisphere transmission of such millennial-scale signals (reflected in  $\delta^{18}\text{O}$  variations) depends on the extremely rapid atmospheric circulation changes (probable lag a couple of years only; Rasmussen et al., 2014). These changes are induced by migration of the Polar Front (PF) and shifts of the Intertropical Convergence Zone (ITCZ) at mid-to-low-latitudes (Europe and the Mediterranean areas) (e.g., Peterson and Haug, 2006), which in turn induce atmospheric circulation and local rainfall changes.

Problems in synchronization of MIS 3 records mainly arise from the uncertainties of the age models, based on different dating methods, the intrinsic difficulties in dating these events, in particular for those intervals at or beyond the limit of the radiocarbon technique (see section 7.1) and the scarcity of precisely dated and unambiguously synchronous

200 stratigraphic events, such as tephra layers, magnetic excursions and cosmogenic nuclide  
201 peaks. Speleothems are excellent archives for recording these abrupt isotopic changes  
202 (e.g., Fleitmann et al., 2009; Moseley et al. 2014; Weber et al., 2018), since they are  
203 among the most accurately datable archives, i.e., within the last ca 100 ka, two sigma  
204 (95%) errors can be below 1% of the U/Th age. Their deposition is predominantly  
205 influenced by either temperature (higher latitude) or precipitation (lower latitude), but both  
206 ultimately linked to Northern Hemisphere temperature fluctuations (e.g., McDermott, 2004;  
207 Genty et al., 2006). In general, speleothem records unambiguously show the signature of  
208 D-O cycles and HEs on European and Mediterranean climate, and a millennial to sub-  
209 millennial scale synchronicity in climatic shifts between European and Greenland isotopic  
210 records. Despite a generally continuous calcite deposition during the GI 14-GI 13 interval,  
211 even at the elevation of the modern snowline in the Alps (Spötl and Mangini, 2007;  
212 Moseley et al., 2014), their registration is often fragmentary and hiatuses may have  
213 occurred during cold/dry phases (i.e. HE 5 and HE 4; Spötl et al., 2002; Moseley et al.  
214 2014, **Fig. 1, e**; Weber et al., 2018). In fact, ITCZ variations may have also affected local  
215 rainfall patterns, triggering enhanced dryness notably in the Mediterranean (Fletcher and  
216 Sánchez Goñi et al., 2008; Fleitmann et al., 2009). However, precise determination of the  
217 durations of these hiatuses may provide valuable information about climatic thresholds that  
218 affect regional climatic conditions (Moreno et al., 2010; Zhornyak et al., 2011; Stoll et al.,  
219 2013). Overall, the climatic pattern underlying these  $\delta^{18}\text{O}$  profiles during MIS 3 strongly  
220 resembles that of Greenland ice cores at millennial scales, and in many cases  
221 corresponding to the detail of decadal-scale cooling events within interstadials (Moseley et  
222 al., 2014).

### 3 Reference mid-to-high resolution MIS 3 palaeoecological records in Southern Europe and in the Mediterranean region

Palaeoecological and palaeoclimate archives considered in this review paper (**Tab. 1**) are mostly located in Southern Europe and in the Mediterranean region between ca. 36° and 46.5° N throughout the Atlantic, Continental, Alpine, and Mediterranean biogeographical regions (**Fig. 2**; European Environment Agency, 2016). A few others dataset from central Europe accompany these sites. Selected records (i) cover a relevant interval during the ca. 30 – 60 ka time-frame, (ii) are mostly characterized by a sub-millennial/multi-decadal time resolution (see **Tab. 1**), and (iii) include quantitative or semi-quantitative geochemical (i.e., stable isotopes) and/or vegetation (i.e. palynological data) climate proxy variables. Most of them are placed in the Mediterranean region, which borders the Atlantic region in the west and the western Eurasian sub-continental region including both the Black Sea and the Anatolian regions (**Fig. 2**). The latter area is of particular interest because it possibly served as a gateway for the spread of AMHs into Europe (Müller et al., 2011). Thus, palaeoclimatic and palaeoecological information from these sites are of great importance and serve as background for the archaeological work in the Levant.

Site	Archive type	Latitude (decimal degrees)	Longitude (decimal degrees)	Elevation (m asl)	Interval/Time period (ka)	Palaeoenvironmental /climate proxies	Mean temporal resolution for MIS 3 (yrs/sample)	References
<b>TERRESTRIAL</b>								
<b>Abric Romani (Spain)</b>	Carbonate sediments/ travertine deposits	41.53	1.68	310	41-70 ka	Palynological data	200 yrs	<i>Burjachs et al., 2012</i>
<b>Azzano Decimo (Italy)</b>	Lake sediments	45.85	12.9	10	0-215 ka (discontinuous)	Palynological data	1150 yrs	<i>Pini et al., 2009</i>
<b>Lac du Bouchet (France)</b>	Lake sediments	44.83	3.82	1200	ca. 8-120 ka	Palynological data	ca. 1000 yrs	<i>Reille and Beaulieu, 1990</i>
<b>Eifel maar (Germany)</b>	Lake sediments	50.16	6.85	420	0-60 ka	Palynological data	Decadal/centennial	<i>Sirocko et al., 2016</i>
<b>Fimon (Italy)</b>	Lake sediments	45.46	11.53	23	27-138 ka	Palynological data	960 yrs	<i>Pini et al., 2010</i>
<b>Füramoos (Germany)</b>	Peat deposits	47.98	9.88	662	0-14 ka, 40-140 ka	Palynological data	ca. 900-1200 yrs	<i>Müller et al., 2003</i>
<b>Ioannina 284 (Greece)</b>	Lake sediments	39.75	20.85	470	0-132 ka	Palynological data	325 yrs	<i>Tzedakis et al., 2002</i>
<b>La Grand Pile (France)</b>	Lake sediments	47.73	6.50	330	0-140 ka	Palynological data	ca. 250 yrs	<i>Woillard 1978; Guiot et al., 1992</i>

<b>Lagaccione (Italy)</b>	Lake sediments	42.57	11.8	355	4-100 ka	Palynological data	420 yrs	<i>Magri, 1999</i>
<b>Les Echets (France)</b>	Lake sediments	45.9	4.93	267	ca. 10-75 ka	Palynological data	ca. 500 yrs	<i>Beaulieu and Reille, 1984</i>
<b>Kopais K-93 (Greece)</b>	Lake sediments	38.43	23.05	95	10-130 ka	Palynological data	830 yrs	<i>Tzedakis, 1999</i>
<b>Megali Limni (Greece)</b>	Lake sediments	39.1	26.32	323	22-62 ka	Palynological data	150 yrs	<i>Margari et al., 2009</i>
<b>Lago Grande di Monticchio (Italy)</b>	Lake sediments	40.93	15.62	656	0-132 ka	Palynological data	210 yrs	<i>Allen et al. 1999; Wutke et al., 2015</i>
<b>Ohrid (Republic of Macedonia and Albania)</b>	Lake sediments	40.91	20.67	693	0-500 ka	Palynological data	ca. 850 yrs	<i>Sadori et al. 2016</i>
<b>Prespa (Republic of Macedonia, Albania and Greece)</b>	Lake sediments	40.95	20.96	849	0-92 ka	Palynological data	ca. 1070 yrs	<i>Panagiotopoulos et al. 2014</i>
<b>Ribains (France)</b>	Lake sediments	44.83	3.82	1075	10-150 ka	Palynological data	ca. 1500 yrs	<i>Beaulieu and Reille, 1992b</i>
<b>Tenaghi Phillippon (TF II) (Greece)</b>	Peat-dominated succession	41.17	24.33	40	0-130 ka	Palynological data	120 yrs	<i>Wijmstra 1969; Müller et al., 2011; Wulf et al., 2018</i>

<b>Valle di Castiglione (Italy)</b>	Lake sediments	41.88	12.77	44	0-250 ka	Palynological data	440 yrs	<i>Follieri et al., 1988-1998</i>
<b>Lago di Vico (Italy)</b>	Lake sediments	42.32	12.28	507	0-90 ka	Palynological data	ca. 500 yrs	<i>Leroy et al., 1996; Magri and Sadori, 1999.</i>
<b>Bunker cave - Bu2 (Germany)</b>	Speleothems	51.36	7.6	184	From 52 to 50.9 ka and from 47.3 to 42.8 ka	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$	decadal/ multidecadal-scale	<i>Weber et al., 2018</i>
<b>Hölloch cave (Höl-7, Höl-16, Höl-17, and Höl-18) - NALSP (Germany)</b>	Speleothems	47.38	10.15	1240–1438	35-65 ka (discontinuous)	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$	decadal/ multidecadal-scale	<i>Mosely et al., 2014</i>
<b>Klee gruben cave - SPA 49 (Austria)</b>	Speleothems	47.09	11.67	2165	46-58 ka	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$	decadal/ multidecadal-scale	<i>Spötl et al., 2002</i>
<b>Soreq cave (Israel)</b>	Speleothems	31.7	35	400	0-60 ka	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$	40 yrs	<i>Bar-Matthews et al., 1999-2000</i>
<b>Villars cave - Vil 27 (France)</b>	Speleothems	45.3	0.5	175	30-55 ka	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$ )	53 yrs (between 48.5 and 40.5 ka) and 203 yrs (between 40.5 and 30 ka)	<i>Genty et al., 2010</i>



<b>Villars cave - Vil 9 (France)</b>	Speleothems	45.3	0.5	175	32-83 ka (discontinuous)	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$	91 yrs (between 51.8 and 40.4 ka) and 195 yrs (between 40.4 and 31.8 ka)	<i>Genty et al., 2003</i>
<b>Villars cave - Vil 14 (France)</b>	Speleothems	45.3	0.5	175	29-52 ka	Calcite $\delta^{18}\text{O}$ , $\delta^{13}\text{C}$	81 yrs (between 52.2 and 41.7 ka) and 1066 yrs (between 41.7 and 28.9 ka)	<i>Wainer et al., 2009</i>
<b>NGRIP (Greenland)</b>	Ice core	75.1	42.32	2917	8-120 ka	$\delta^{18}\text{O}$ ; calcium ion concentration data ([Ca <sup>2+</sup> ])	re-sampled to 20-year resolution	<i>Seierstad et al., 2014; Rasmussen et al., 2014</i>
<b>MARINE MD04-2845 (Western France)</b>	Marine sediments	45.35	-5.22	-4100	30-140 ka	Palynological data; Foraminiferal $\delta^{18}\text{O}$ ; Ice-rafted debris record	540 yrs	<i>Sánchez Goñi et al., 2008</i>
<b>MD95-2042 (Iberian margin)</b>	Marine sediments	37.8	-10.17	-3148	27-138 ka	Palynological data; Foraminiferal $\delta^{18}\text{O}$ ; Ice-rafted debris record; $\text{U}^{k}_{37}$ and $\text{TEX}_{86}$ biomarkers (SST)	ca. 370 yrs	<i>Sánchez Goñi et al., 1999-2000-2008-2009</i>

<b>MD95-2043 (Alboran sea)</b>	Marine sediments	36.13	-2.62	-1841	0-50 ka	Palynological data; Foraminiferal $\delta^{18}\text{O}$ ; $\text{C}_{37}$ Alkenones (SST)	260 yrs	<i>Cacho et al., 1999; Sánchez Goñi et al., 1999; Fletcher and Sánchez Goñi, 2008</i>
<b>LC21 (Aegean sea)</b>	Marine sediments	35.66	26.58	-1522	0-160 ka	Foraminiferal $\delta^{18}\text{O}$	ca. 200 yrs	<i>Grant et al., 2012</i>
<b>ODP 976 (Alboran sea)</b>	Marine sediments	36.20	-4.30	-1108	>1Ma	Palynological data; Foraminiferal $\delta^{18}\text{O}$	Ranging between 50 and 200 yrs	<i>Combourieu- Nebout et al., 2002; Combourieu- Nebout et al., 2009; Genty et al., 2010</i>

**Tab. 1** List of selected sites from S-Europe and the Mediterranean area that entirely or partially cover the MIS 3 chronological framework, specifying location, available vegetation-climate proxy variables and time resolution. References to published data are also indicated

243

### 244 **3.1 Vegetation response to D-O events and HEs in Southern Europe and** 245 **Mediterranean region**

246 The history of vegetation during MIS 3 in Southern Europe and in the Mediterranean area  
247 relies on several palaeoecological studies carried out in lake and peat stratigraphic  
248 sequences. In **Fig. 3** we consider the evidence for millennial-scale variability and long-term  
249 vegetation trends from selected records covering the period between ca. 60 - 30 ka (i.e.,  
250 GI 17 to GI 5). The records are presented on the most recent chronology available for  
251 each one. On the whole, this data shows a high sensitivity of vegetation response to D-O  
252 events, making South Eastern Europe and the Italian Peninsula a key geographical area  
253 for high-resolution palaeoenvironmental researches during the last glacial period.

254 In southern Europe, the recurrent succession of (open) woodlands, including temperate  
255 taxa, and grasslands with xerophytic elements (**Fig. 3**), have been tentatively correlated to  
256 GIs in Greenland ice cores (Fletcher et al., 2010b). This assumption is reasonable for this  
257 geographic area as thermophilous trees persisted in refugia and appeared to have  
258 expanded rapidly during each interstadial without substantial migration lags (Harrison and  
259 Sánchez Goñi, 2010).

260 Investigations at Lago Grande di Monticchio (Allen et al., 1999, 2000) were the first to  
261 provide an independently dated Late Pleistocene palaeoenvironmental record, due to its  
262 varved sequence. Furthermore, the identification of known tephra layers, one of which is  
263 the Campanian Ignimbrite (CI), has also been used to improve the age-depth model  
264 (Wutke et al., 2015). The high-resolution pollen record (ca. 200 yrs/sample) obtained from

the Monticchio core reveals millennial-scale changes in woody/open environments throughout MIS 3. Palaeoecological data indicate an alternation between cold/dry steppic vegetation, referred to GS periods, and an increased range of woody taxa including deciduous *Quercus*, *Abies* and *Fagus* (up to 30–60% AP), referred to GI periods (Allen et al., 1999; Fletcher et al., 2010b). Similarly, other long pollen records from volcanic lakes in central and southern Italy, i.e., Lagaccione and Valle di Castiglione (**Fig. 3**; Follieri et al., 1988, 1998; Magri, 1999), show remarkable changes of vegetation composition, structure and biomass including millennial-scale fluctuations in forest development with deciduous and evergreen *Quercus*, *Corylus*, *Fagus*, *Betula* and *Picea* (Fletcher et al., 2010b). The lower temporal resolution of these latter records (ca. 400 yr/sample) in turn reduced the chances to precisely identify each GI (**Fig. 3**).

In northern Italy, pollen records from Lake Fimon (**Fig. 3**) and Azzano Decimo (Pini et al., 2009; Pini et al., 2010) indicate phases of conifer-dominated forest expansion (*Pinus sylvestris-mugo* and *Picea*), rich in cool broad-leaved trees (*Alnus* cf. *incana* and tree *Betula*) and accompanied by a reduced warm-temperate component (*Tilia*). In both records, individual D–O events cannot be identified due to the low temporal resolution (ca. 800–1000 yr/sample), nevertheless the well-documented long vegetation trend is indicative of a persistent afforestation. In fact, only moderate forest withdrawals occurred and some temperate trees (e.g., *Tilia* and *Abies*) persisted up to ca. 40 ka BP (Pini et al., 2010). Interestingly, peaks of *Tilia* pollen were found (Cattani and Renault-Miskowski, 1983–84) in layers preserving Mousterian artefacts and dated to 40.6–46.4 <sup>14</sup>C ka in the cave sediments at the Broion shelter (Leonardi and Broglio, 1966), and also in Paina cave interpleni-glacial deposits (Bartolomei et al., 1987–88; Cattani 1990).

288 At southern latitudes, high-resolution pollen records from Ioannina, Tenaghi Philippon and  
289 Megali Limni (Greece, **Fig. 2** and **Fig. 3**; Wijmstra, 1969; Tzedakis et al., 2006; Margari et  
290 al., 2009; Müller et al., 2011; Wulf et al., 2018,) show exceptional series of millennial and  
291 sub-millennial vegetation changes correlated to a number of GI/GS (Fletcher et al. 2010b;  
292 Pross et al. 2015). Concerning colder phases, the GSs related to HEs appear to have a  
293 more pronounced effect than other GSs on woodland withdrawal and xerophytes  
294 expansion. Notably, GS 9-HE 4 phase corresponds to the most severe reduction of tree  
295 cover in a number of records (e.g., Megali Limni, Tenaghi Philippon, Valle di Castiglione  
296 and Ioannina; **Fig. 3**). Interestingly, pollen records from different bioclimatic areas seem to  
297 show differences in terms of magnitude of the response to cold events due to local  
298 ecosystem structures. In sites where moisture availability was not a limiting factor,  
299 differences in the magnitude of climate forcing during HEs seem to be well expressed in  
300 terms of major vegetation changes (e.g., Ioannina, Monticchio) (**Fig. 3**). However, where  
301 temperate tree populations were near their tolerance limit, the environmental stress  
302 associated with HEs probably crossed a critical threshold resulting in large population  
303 contraction with an almost complete drop in forest cover (i.e., Tenaghi Philippon, Megali  
304 Limni) (Tzedakis et al., 2004) (**Fig. 3**).

305 On a long-term scale, a reduction/opening of forests throughout MIS 3 (see **Fig. 3**) took  
306 place from GI 14, showing a maximum in woodland density, to the following GI 12 and GI  
307 8. During GI 14/ 13 interval, conditions were notably humid and mild in the eastern  
308 Mediterranean as indicated by the Soreq cave isotopic record (Bar-Matthews et al., 2000)  
309 and also over Europe (Allen et al., 1999; Sánchez Goñi et al., 2002; Fletcher et al., 2010b).

310 Despite the relatively high amount of palaeoecological information for southern Europe,  
311 the spatial distribution of records in this heterogeneous geographic sector remains uneven.  
312 Such differences in the expression of millennial-scale events suggest that site  
313 characteristics need to be taken into account when mapping the spatial patterns of  
314 changes and trying to elucidate the mechanisms involved. New records are needed (e.g.,  
315 from northern and southern Italy, Turkey, the Levant), in order to refine the knowledge of  
316 eco-climatic gradients across the continent and to better understand regional vegetation  
317 patterns.

### 318 **3.2 Fire dynamics in Southern Europe and Mediterranean region**

319 High-resolution microcharcoal records can provide new insights to understand fire-  
320 vegetation dynamics in relation to climate variability (e.g. D-O cyclicity/HE events) and/or  
321 human activities (e.g., Whitlock and Larsen, 2001; Iglesias et al., 2015). As for the Last  
322 Glacial period, few microcharcoal records are available from terrestrial (e.g., Magri, 2008;  
323 Margari et al., 2009; Pini et al., 2009, 2010) and marine records (e.g., Danian et al., 2007,  
324 2009). **Fig. 3** shows microcharcoal data for some Southern East European terrestrial sites:  
325 Lake Fimon, Valle di Castiglione, Lagaccione and Megali Limni (MIS 3 partially  
326 documented).

327 Overall, a fire regime variability mainly associated with fluctuations in forest cover occurred  
328 between GS (lower fire activity) and GI (higher fire activity). Higher microcharcoal  
329 concentration during periods of afforestation suggests enhanced fire activity favoured by  
330 increasing woody fuel and biomass accumulation during GI (Magri, 1994), as observed  
331 also by Danian et al. (2007; 2009) for southwestern Iberia (MD95-2042 and MD04-2845  
332 cores, **Fig. 2**). Contrary to this pattern, NE-Italy experienced isolated major fire episodes

over a generally low-intensity fire regime; at Lake Fimon (Pini et al., 2010; **Fig. 2**) the strongest fire episode of the whole Late Pleistocene record is coeval to a drop in forest cover mirrored by steppe expansion, possibly correlated to HE4 (**Fig. 3**). Since the palaeoecological data from this site suggest relatively high moisture availability during MIS 3 (Pini et al., 2010), such climatic context may have prevented long-term fire activity south of the Alps, despite biomass availability. This evidence indicates that the incidence of fires is not always directly correlated with the degree of afforestation. This framework supports a regional climatic influence on fire regimes over SE-Europe with a direct climatic control on fuel availability during the Last Glacial period.

#### **4 Snapshots of European palaeogeography and ecoclimatic zones during GI 12 and the LGM**

With the aim of setting Palaeolithic humans in a palaeoenvironmental scenario, we chose two MIS 3-2 key intervals relevant for the human evolution and marking paleoclimate extreme conditions: the GI 12 and LGM. We plotted the main European palaeogeography and palaeoecology landscape features on geographical snapshots (**Figure 4A and B**). In detail, GI 12 snapshot (ca. 46.8 to 44.2 ka according to Rasmussen et al., 2014) represents a phase of major forest expansion during MIS 3 also coincident with the AMHs arrival in Europe (Grotta del Cavallo, ca. 45.5 ka; Benazzi et al., 2011; Zanchetta et al., 2018) (**Figure 4A**). The second one spans the time interval of both the SIS (Scandinavian Ice Sheet) and the European mountain glacier culminations during the LGM (26 to 21 ka cal BP in Europe, see Hughes et al., 2016; Monegato et al., 2017), which was characterized by one of the most pronounced forest contractions of MIS 3-2 time span

(**Figure 4B**). From GI 12 to LGM, climate changes led to dramatic variations in glacier extent and sea level with major impacts on the physiography of mountain areas, coastal regions and the hydrologic systems. The latter two are also known for their important role in AMHs dispersal into Europe (Mellars, 2006; Hublin, 2014).

#### 4.1 Palaeoenvironmental setting during Greenland Interstadial 12 (MIS 3)

##### 4.1.1. Reconstructed gradients ecogeography within eco-climatic zones

We reconstructed terrestrial ecosystems for a time frame corresponding to GI 12 (**Fig. 4A**) by combining palaeobotanical records (for Central Europe: see Van Meerbeeck et al., 2011 and references therein; Follieri et al., 1988; Beaulieu and Reille, 1992a-b; Drescher-Schneider et al., 2007; for Mediterranean Europe: Magri, 1999; Sánchez Goñi et al., 2002 and 2009; Pini et al., 2009, 2010; Müller et al., 2011) and ecoclimatic gradients. These gradients rely both on large scale latitudinal zones (i.e., Tundra zone and Forest-tundra zone, and related positions of polar timberline, see Holtmeier, 1985; Archibold, 2012), spanning the northern half of European subcontinent and on regional elevational mountain belts in southern Europe (see Fig. 4A). We assumed GI 12 and GI 14 vegetation peaks to have been similar at the same site, although GI 12 was shorter, and used both GI 14 and GI 12 data to implement our reference dataset. Fossil data was improved by (a) elevational ecoclimatic relationships and (b) vegetation models (Alfano et al., 2003). However, available gridded vegetation models do not account for vegetation distribution in complex mountain regions that actually represent 75% (total areas above 500 m altitude obtained from GIS elaboration) of the southern European landscape. Indeed, elevation gradients can be very steep and, within a 1-km<sup>2</sup> grid cell, elevation can vary up to, or even more than, 500 m. In these contexts, forests display a characteristic discontinuity in their



379 distribution with a main boundary representing the upper limit of forest canopies  
380 associated with temperature decrease along elevational gradients. Thus, some  
381 inaccuracies in the vegetation distribution can be expected in global models due to the  
382 coarse spatial resolution of climate datasets that can be affected by errors in the local  
383 temperature estimation (i.e., more than 1°C for a lapse rate of about -0.5°C/100 m).

384 A number of ecoclimatic zones are featured by distinct regional climates (i.e. coniferous  
385 and broad-leaved woodlands along the northern coast of Portugal and Spain; map of the  
386 European Environment Agency, 2015). Within each zone, local climates (i.e. mountain  
387 areas) have been qualified by elevational gradients of orographic precipitation. The main  
388 features of these altitudinal gradients are the upper timberline limit and the glacier  
389 Equilibrium Line Altitude. Given the determinants of the warmest month temperature  
390 (TJuly) on the upper timberline, caused by heat deficiency (Tranquillini, 1979; Jobbagy and  
391 Jackson, 2000; Körner and Paulsen, 2004), we used TJuly reconstructions for GI 12 to  
392 estimate the altitude of montane timberline. In order to moderate the effects of CO<sub>2</sub>  
393 changes on plant fertilization (Farquhar, 1997), we included past timberlines as calibration  
394 test of our estimations. The timberline position in the Italian Central Alps during the  
395 Bølling-Allerød (1700-1800 m asl: Tinner et al., 1999; Ravazzi et al., 2007) is a good test  
396 as the GI 1 is the only D-O interstadial which occurred under moderately low CO<sub>2</sub>  
397 concentration; furthermore, relevant fossil records are relatively common as they were not  
398 erased by LGM glacier activity. Given the position of the alpine timberline during the  
399 Bølling-Allerød and the associated pollen-based mean TJuly (18,5-19°C; Vallè et al.,  
400 unpublished data), we infer the timberline position during GI12 using the difference  
401 between TJuly for GI12 (ca. 18°C) and the Bølling-Allerød. This difference was projected

over an elevational gradient using an average environmental lapse rate of about -  
0,67°C/100 m (Furlanetto et al., 2019), to obtain an historical timberline for GI 12 (ca. 1600  
m in the Italian Central Alps). The method was also tentatively applied to estimate  
timberlines in the Mediterranean region. Here, however, many boreal tree species were  
missing during MIS 3, thus ecophysiological requirements of Mediterranean timberline  
species were considered.

#### **4.1.2. Estimating Equilibrium Line Altitudes of mountain glaciers**

By using elevational lapse rates we also estimated the Equilibrium Line Altitude (ELA)  
position during GI12 in the Central Alps (Vallé et al., unpublished data). Again,  
temperature differences between the LGM ELA positions (e.g. Kuhlemann et al. 2008;  
Hughes and Woodward, 2016) and GI 12 were projected over elevational gradients and  
tested against the temperatures and ELA related to the Egesen stage, Younger Dryas  
(Kelly et al., 2004; Ivy-Ochs et al., 2008; Delmas, 2015; Ruszkiczay-Rüdiger et al., 2016;  
Popescu et al., 2017; Gromig et al., 2018). The results of a recent Parallel Ice Sheet Model  
(PISM) with climate forcing deriving from WorldClim and the ERA-Interim reanalysis  
(Seguinot et al., 2018) proved to fit our results for the Central Alps (GI 12 ELA 2100 m,  
626 m higher than the LGM ELA). As a best approximation, the same value was added to  
the LGM ELA position for the Pyrenees, Balkans and Carpathians, providing a GI12  
reconstructed ELA of ca. 2400 m, ca. 2100 m and 2000 m, respectively.

#### **4.1.3. The GI 12 palaeoenvironmental map**

European vegetation gradients were particularly strong during the major interstadial  
phases (i.e., spanning about 2000-2500 years), characterized by large arboreal excursions

both latitudinally and altitudinally, north and south of the Alps. The GI 12 is one of these key representative warm intervals. In **Figure 4A**, we depict the palaeoenvironmental setting of mid and southern Europe (between 52° and 35° latitude N) during GI 12. It is also shown a reconstruction of the coastline: -74 m a.s.l. (Waelbroeck et al., 2002; Antonioli, 2012). A substantial seashore enlargement over Europe led to increased connectivity, especially between the Italian peninsula and the Western Balkans region, between Mediterranean islands, and also the emergence of large areas north of the Black Sea and in the North Sea (**Fig. 4A**). The Scandinavian Ice Sheet (SIS), which grew during MIS 4, had almost entirely melted at mid MIS 3 (60–45 ka) (Lambeck et al., 2010; Wohlfarth, 2010).

We summarize hereafter the main constrains of the featured ecoclimatic zones.

**Forest tundra ecozone.** The northern timberline was given as the northern limit of the forest tundra mosaic (*sensu* Walter and Breckle, 1986; Holtmeier, 2009; Van Meerbeeck et al., 2011). The abundance of gleysols with charred wood dated to around 45 ka at the base of loess-luvisol sequences in Central and Eastern Europe (Haesaerts et al., 2009; Moine et al., 2017) supports locating the zonoecotone of forest tundra for wetter interstadial phases of MIS 3 between 47° and 52° - 54° N, i.e. north of the Alps (Fig. 2A). The geography of northern timberline in Central and Eastern Europe was drawn according to modelling results by Alfano et al. (2003). In the forest tundra zonoecotone, the forest is found mainly in warmer and drier places, with stunted individuals at the waterlogging edaphic ecotone.

445 **Atlantic zone.** This biogeographical region closely interacts with the northeast Atlantic  
446 Ocean margin. Expansion of Atlantic forests with *Betula*, *Pinus* and deciduous *Quercus* is  
447 recorded during GI 12 and 14, probably reflecting obliquity forcing at higher latitudes  
448 (Sánchez Goñi et al., 2008). Vegetation in Western Iberia also responded immediately  
449 (within the resolution of the record) to SST changes on millennial time scales during MIS 3.  
450 Increases in temperatures offshore translated to increased tree cover on land and vice  
451 versa. This rapid response to interstadials warming supports the idea that thermophilous  
452 taxa persisted in NW-Iberian refugia throughout the last glacial period (Roucoux et al.,  
453 2005).

454 **Iberian region.** Average annual precipitation map for the Iberian peninsula (years 1901-  
455 2009; Schneider et al., 2014) depicts a strong gradient from the north-western to northern  
456 Atlantic coasts (1100 - 1500 mm/year) to central Spain and Mediterranean areas (250 -  
457 700 mm/year). During GI 12, humid Atlantic air masses promoted higher moisture  
458 availability on the northern coasts of Portugal and Spain, which could support the  
459 occurrence of open temperate woodlands. In the inner Iberian areas, grasslands occupied  
460 drier lowlands; increasing afforestation was visible along altitudinal gradients.

461 **Adriatic and Tyrrhenian Basins.** Lowering of the sea led to the emergence of a wide  
462 area north of the 44° parallel in the Adriatic sea. The area hosted terrestrial vegetation,  
463 from mixed conifer and broad-leaved woodlands in the inner Friulian-Venetian Plain to  
464 more open communities and then grasslands, the latter building a wide belt along the  
465 coastal margins. Differences in the humidity regimes between the eastern Adriatic and the  
466 western Tyrrhenian Basins bordering Italy are responsible for the asymmetry of

ecosystems represented in Fig. 2A. Palaeoecological records from the Tyrrhenian coast suggest almost persistent moisture availability during MIS 3. Similar to the current situation, it can be assumed that precipitation was mainly generated by the orographic uplift of air charged with moisture from the Tyrrhenian Sea.

**Balkans and Aegean regions:** During GI 12, terrestrial ecosystems were dominated by open temperate woodland and/or temperate forest-steppe south of 40°N, with increasing amount of trees north of this latitude. At lower altitudes, in wider belts bordering the eastern Adriatic, Ionian and eastern Mediterranean Seas, grasslands developed.

**Central Anatolian plateau.** In the Anatolian region the reconstructed historical GI 12 timberline is located at 1500 m asl. Areas down to 500-800 m could support open forest vegetation, especially along the Turkish coasts of the Black Sea, characterized by a temperate oceanic climate with the greatest amount of precipitation of the whole region (Turkish State Meteorological Service, 2006). Moisture does not reach inland areas; inner plateau bordered by the Pontic Mountains to the north and the Taurus to the south is characterized by a continental climate with strongly contrasting seasons. During GI12, in these inner areas open grasslands expanded.

A reconstruction of European vegetation patterns during a warm/moist phase of MIS3 was proposed by van Andel and Tzedakis (1998). The vegetation subdivisions provided in this early reconstruction largely overlap with the picture of terrestrial ecosystems provided in our Fig. 2A, with some differences **(i)** the reconstruction of van Andel and Tzedakis (1998) is plotted on a simplified sketch map of Europe not taking into account the altitudinal gradients, indeed represented on our GIS topographic base. This is important as far as

489 temperature and moisture gradients play an important role in determining both latitudinally  
490 and altitudinally extents of vegetation belts; **(ii)** minor differences between the two  
491 reconstructions are visible in the shape of the limit of the northern timberline (between 53-  
492 55°N in Fig. 2A - based on Alfano et al., 2003; around 50°N according to van Andel and  
493 Tzedakis, 1998); **(iii)** Fig. 2A provides indication on ELA and timberline positions during an  
494 interstadial, thanks to data from papers published in recent years and quantitative climate  
495 reconstructions for the last glacial cycle.

## 496 **4.2 Palaeogeography of Southern and Central Europe during LGM**

497 We attempted a LGM palaeogeographical reconstruction of mid-southern Europe in order  
498 to allow direct comparison of physical patterns between GI 12 (i.e. a major interstadial  
499 within MIS 3) and the subsequent LGM (i.e. 30 to 16.5 ka cal BP, Lambeck et al., 2014)  
500 cold phase. For this map, we chose to represent the physical geography of Europe during  
501 the time interval spanning both the SIS and the European mountain glacier culminations  
502 (26 to 21 ka cal BP in Europe, see Hughes et al., 2016; Monegato et al., 2017). At this  
503 time, main climatic patterns can be displayed though different climate zones according to  
504 Köppen-Geiger classification (Becker et al., 2015).

505 The SIS passed the coast of western Norway at the time of the Laschamp palaeomagnetic  
506 excursion (ca. 41 ka) (Valen et al., 1995; Mangerud et al., 2010). At ca. 21 ka the ice-sheet  
507 attained its maximum extent (**Fig. 4 B**; Hughes et al., 2016). During this period the  
508 European Alps were extensively covered by an ice-dome which generated valley glaciers.  
509 In the Alps, the maximum ice extent was reached during the LGM around 25 ka, when  
510 large piedmont glaciers advanced onto the Alpine foreland. This is well constrained by the  
511 end-moraine systems, in which the LGM moraines were dated (radiocarbon, OSL and

512 cosmogenic nuclide surface exposure dating methods) and point to large ice lobes at the  
513 outlet of major valleys (e.g., Monegato et al., 2007, 2017; Ivy-Ochs et al., 2008, 2018;  
514 Ravazzi et al., 2012; Reber et al., 2014; Salcher et al., 2015). In the south-western and in  
515 the eastern sectors many valley glaciers remained confined within the valley (e.g., Jorda et  
516 al., 2000; Bavec and Verbic, 2011; Rossato et al., 2013, 2018; Federici et al., 2016), as  
517 testified by the reconstruction of LGM moraines. In the fringe area of the Alpine chain  
518 many isolated small ice caps or mountain glaciers developed without merging with the  
519 major trunk glaciers (e.g., Carraro and Sauro, 1979; Forno et al., 2010; Monegato, 2012).  
520 Large outwash megafans developed from the front of the Alpine glaciers or from the  
521 funnelling of outwash streams in the lower reach of the valleys (Fontana et al., 2014). By  
522 this time, large glaciers developed in the Pyrenees and many frontal moraines were dated  
523 (Delmas, 2015 and references therein); here glaciers mostly remained confined within the  
524 valleys and several small and isolated glaciers occurred (e.g., Pallas et al., 2010). Other  
525 small glacier systems were present in the Iberian mountains; these advances had different  
526 age development, from 31 to 20 ka, according to Oliva et al. (2019) compilation.  
527 Documented ice-caps in the French Massif Central (de Gôer, 1972) and in the Vosges  
528 (Seret et al., 1990), but chronology on glacial landforms needs to be improved  
529 (Buoncristiani and Campy, 2004).

530 Valley glaciers spread in the Carpathians and Tatra ranges (e.g., Ehlers et al., 2011;  
531 Makos et al., 2018). Their size were reconstructed on the basis of remote sensing and field  
532 analyses (Zasadni and Klapysa, 2014) and the age of their maximum spread is constrained  
533 with exposure dating at about 25 ka (Engel et al., 2015; Makos et al., 2018).

534 The Balkan Peninsula was deeply studied in the last decay (see Hughes and Woodward,  
535 2016 for a review). Therein, mountain glaciers developed in a karstic environment with  
536 specific characteristics (Adamson et al., 2014; Zebre and Stepisnik, 2015; Zebre et al.,  
537 2016). Most of the outwash system into the karstic network and the outwash fans were  
538 very confined and limited to the basins where glaciers flowed (Zebre et al., 2016, 2019).  
539 Also small glaciers formed on the highest mountain chains of the Apennines (e.g., Giraudi  
540 and Giaccio, 2016; Baroni et al., 2018; Mariani et al., 2018).

541 The region surrounding the Adriatic lowstand plain collected the drainage from Alpine  
542 outwash systems and from the surrounding Apennine and Balkan rivers, which had  
543 important karst underground flows. The large Adriatic lowstand delta (**Fig. 4B**; Maselli et  
544 al., 2014; Pellegrini et al., 2015) accreted as sea level fell down to -120 m or -149 m  
545 (Antonioli and Vai, 2004).

546 Late Pleistocene aeolian sediments are widespread in Europe (e.g. Haase et al., 2007;  
547 **Fig. 4B**) and they represent further indicators of past environmental changes. Loess is  
548 commonly distributed in Central, Eastern, and Southern Europe (e.g., Kukla, 1975;  
549 Smalley and Leach, 1978; Frechen et al., 1997; Haase et al., 2007; Cremaschi et al.,  
550 2015; Marković et al., 2015; Terhorst et al., 2015; Zerboni et al., 2018); in the  
551 Mediterranean region loess bodies formed also along the present day coastline (Chiesa et  
552 al., 1990; Cremaschi, 1990; Wacha et al., 2011a,b; Boretto et al., 2017). Loess is generally  
553 associated with glacial environmental conditions, with dry and cool climate and increased  
554 wind strength (Pye, 1995). In continental Europe and in the Mediterranean basin  
555 Pleistocene loess accumulated in mid-continental plains free of ice sheets, at the margins  
556 of mountain ranges, along the shorelines of the Mediterranean and at the semi-arid



557 margins of the Sahara and Levantine deserts (Obruchev, 1914; Cremaschi, 1990; Haase  
558 et al., 2007; Crouvi et al., 2010; Lindner et al., 2017; Lehmkuhl et al., 2018 a,b; Zerboni et  
559 al., 2018). In Mediterranean Europe, as in the Po Plain, major loess sources are the  
560 outwash plains fed by glaciers flowing from mountains (Alps and Apennines)  
561 (Cremaschi, 1990). Loess deposition occurred during most of the Quaternary glacials and  
562 was related to a general decrease in forest cover and expansion of semideserts, steppe,  
563 and treeless environments (Rousseau et al., 2018). Notwithstanding many efforts in  
564 establishing fine MIS 4 to 2 loess chronology with luminescence methods and stratigraphic  
565 correlations (e.g., Timar et al., 2010; Timar-Gabor et al., 2011; Thiel et al., 2014) due to  
566 intrinsic properties of loess and to the possible occurrence of sedimentary gaps (Thiel et  
567 al., 2014), the resolution of loess studies is still lower than those of other continental  
568 archives. Likely, Late Pleistocene loess sedimentation occurred, at least, since the end of  
569 MIS4 and during MIS 3 and 2 (Marković et al., 2015; Terhorst et al., 2015). In Italy, loess  
570 sedimentation is recorded along the margins of the Po Plain and discontinuously along the  
571 shorelines of the Mediterranean, where loess is better preserved within rockshelters  
572 (Cremaschi, 2004; Peresani et al., 2008). Italian loess dates back to the Late Pleistocene  
573 and mostly formed since the end of MIS 4 (Cremaschi, 1990, 2004); but loess deposits  
574 occur as well in sections that contain Mousterian artifacts dating to MIS 3 (e.g., Cremaschi,  
575 1990; Cremaschi et al., 2015; Zerboni et al., 2015; Delpiano et al., 2019). More recently, a  
576 few loess bodies have been dated also to MIS 2 (Ferraro, 2009; Zerboni et al., 2015),  
577 showing a good continuity in wind sedimentation in the Late Pleistocene, at least at the  
578 northern margin of the Po Plain. Italian loess is often interlayered by paleosols, allowing  
579 the identification of less arid phases. For instance, at the Val Sorda section a chernozem-  
580 like palaeosoil, has been dated at ca. 27 ka BP (Ferraro et al., 2009); whereas at Monte

581 Netto site moderate pedogenesis (including clay illuviation) compatible with forest cover  
582 occurred at times between 44 and 25 ka BP (Zerboni et al., 2015).

## 583 **5 Focus on spatial vegetation response in Italy during MIS 3**

584 The pie charts presented in **Fig. 5** show long-term vegetation dynamics and geographic  
585 patterns in Italy between ca. 30 and 60 ka cal BP using data from privileged sites (North to  
586 South): Lake Fimon, Lagaccione, Valle di Castiglione and Monticchio. For each record,  
587 selected pollen taxa are consistently grouped according to their ecology and climate  
588 preferences in order to facilitate their comparison (for further information see caption and  
589 legend in **Fig. 5**).

590 A higher forest cover in Northern Italy compared to Mediterranean sites is an unchanged  
591 background feature during MIS 3. Indeed, the glaciated Alps must have represented a very  
592 sharp rainfall boundary leading to more humid conditions in south-eastern alpine foreland  
593 persistently forested and a northern treeless boreal and continental landscape, as shown  
594 by La Grande Pile, Les Echets and Fùramoos pollen records (**Fig. 2**; Woillard, 1978;  
595 Beaulieu and Reille, 1984; Guiot et al., 1992; Müller et al., 2003). The palaeoecological  
596 record from Lake Fimon documents a mosaic of boreal forests dominated by *Pinus*  
597 *sylvestris/mugo* over the 60 to 30 ka cal BP time period. However, a continuous xerophytic  
598 steppe expansion (e.g. *Artemisia* and *Chenopodiaceae*), coupled with the reduction of  
599 temperate elements (deciduous *Quercus* and other thermophilous taxa) in favour of pine  
600 woodlands, notably since 40-45 ka, suggests a shift towards drier/colder conditions  
601 possibly enhanced by GS 9-HE 4 phase.

602 The contraction of temperate forests is also recorded throughout MIS 3 in central Italy  
603 (Lagaccione and Valle di Castiglione) and southern Italy at Lago Grande di Monticchio. In  
604 these sites, open forests dominated by deciduous *Quercus*, *Corylus*, *Fagus*, *Tilia*, *Ulmus*  
605 and *Carpinus betulus* experienced their maximum expansion between ca. 60-45 ka.  
606 Afterwards, open environments (*Artemisia*-dominated steppe/ wooded steppe) expanded  
607 between 45-30 ka (**Fig. 5**).

608 This general overview suggests latitudinal (and also altitudinal) climatic patterns and  
609 rainfall gradients along the Italian peninsula due to its complex physiographic structure (i.e.  
610 the presence of two high mountain ranges, Alps and Apennines), to be taken into account  
611 when reconstructing past vegetation dynamics as it has already been shown for Greece  
612 (Tzedakis et al., 2004).

613

## 614 **6 Archaeological framework**

615 During the first half of MIS 3, and particularly during GIs 14/13 ca. 55-48 ka, natural  
616 environments were favourable for AMHs to migrate from Africa into Europe (Müller et al.,  
617 2011). The scenario of an initial AMHs movement into Europe is supported by industries  
618 associated with modern hominin remains found in few excavated localities: Üçağızlı cave  
619 (Turkey) (Güleç et al., 2002; Kuhn et al., 2009); Ksar Akil (Lebanon) (Copeland and  
620 Yazbeck, 2002; Yazbeck, 2004; Douka et al., 2013); Manot cave (Israel) (Hershkovitz et  
621 al., 2015). Around 45 to 39 ka, Neandertals were replaced by AMHs (Higham et al., 2014),  
622 and a variety of early Upper Palaeolithic cultures emerged (e.g., Uluzzian and Proto-

623 Aurignacian in the central-eastern Mediterranean regions; see Arrighi et al. and Marciani et  
624 al., this issue).

625 The cultural complex known as Uluzzian has been attested in the Italian Peninsula and  
626 southern Balkans around 45-40 ka (**Fig. 6**; Palma di Cesnola, 1989; Ronchitelli et al.,  
627 2009; Moroni et al., 2013; Peresani, 2014; Zanchetta et al., 2018). This techno-complex  
628 was coeval with the arrival of AMHs in Europe as evidenced by the anatomical features of  
629 two deciduous teeth discovered in Grotta del Cavallo in Apulia (Benazzi et al., 2011,  
630 although challenged by Zilhão et al., 2015, and further discussed in Moroni et al., 2018).  
631 Along the Italian Peninsula, the Uluzzian is currently best known in cave sedimentary  
632 successions by its stratigraphic position above the Mousterian and under the Proto-  
633 Aurignacian, when the latter is present, and also in several open-air sites (**Fig. 6**).  
634 Recently, the Uluzzian has also been observed in northern Italian cave sites, expanding its  
635 cultural borders from what was thought to be exclusively central-southern after the  
636 discovery of assemblages at Grotta Fumane and at the Riparo Broion shelter (Peresani,  
637 2008; Peresani et al., 2016, 2018). Other sites in the Adriatic-Ionian region exhibit  
638 Uluzzian elements (Crvena Stijena; Mihailović et al., 2017; Klissoura Cave; Starkovich,  
639 2017; Kephalaria; Darlas and Psathi, 2016), opening new perspectives in looking at the  
640 appearance and spread of the Uluzzian over the entire area of the Adriatic basin.

641 In several sites from the Middle to Upper Palaeolithic transition is documented by the  
642 Proto-Aurignacian technocomplex. The available chronological framework indicates a  
643 Proto-Aurignacian occupation ending with the Campanian Ignimbrite eruption in Southern  
644 Italian Castelvita (Gambassini, 1997) and Serino sites (Lowe et al., 2012; Wood et al.,  
645 2012). However, this tephrostratigraphic marker also constrains the end of the Uluzzian

646 techno-complexes at Grotta del Cavallo on the Ionic coast of Salento (Lecce) (Zanchetta  
647 et al., 2018; section 7.2). In N-W Italy, the earliest Proto-Aurignacian is that of the Balzi  
648 Rossi sites complex in the region of Liguria (NW Italy), where it has been identified at  
649 Riparo Mochi and Riparo Bombrini sites (Douka et al., 2012; Riel-Salvatore and Negrino,  
650 2018). At these sites, the main outlines of the industry remain stable beyond the end of  
651 GS9/HE4 (Riel-Salvatore and Negrino, 2018), comparably to Grotta Fumane in the north  
652 of Italy (Falcucci et al., 2017; Falcucci and Peresani, 2018). The assessment of these  
653 temporal-spatial issues and new chronological information are fundamental for  
654 understanding the dynamics of the cultural and ecological-anthropological changes that  
655 occurred in S-Europe at the Middle to Upper Palaeolithic transition.

656 Already before 43 ka, very early Aurignacian assemblages, reflecting an initial AMHs  
657 advance into central Europe, have also been found along the Danube (Willendorf II, Lower  
658 Austria; Nigst et al., 2014), suggesting the Danube's role as a spatial corridor for human  
659 dispersal in the Early Upper Palaeolithic (e.g., Floss, 2003; Hussain and Floss, 2016). A  
660 similar role is hypothesized for the Don River system near the Black Sea (Anikovich et al.,  
661 2007). Beside large river systems, also coastal plains played a relevant role channelling  
662 AMHs dispersal into Europe (Mellars, 2006; Hublin, 2014). The close similarity between  
663 the available dates for the early AMH arrival in the Mediterranean and in Germany on the  
664 Danube, might suggest a rapid access in Europe via two routes, along both the Danube  
665 corridor and the Mediterranean coasts (Douka et al., 2012).

## **7 Chronological issues**

### **7.1 Difficulties in dating the Middle to Upper Palaeolithic transition**

Building reliable radiocarbon chronologies for sequences covering time intervals beyond and/or close to the limit of the radiocarbon technique (i.e., ca. 50 ka) remain challenging. Indeed, the low levels of residual  $^{14}\text{C}$  activity induces lower precision (higher uncertainty) and accuracy (higher offset of the measured isotope ratio with respect to the actual one) of AMS measurements and makes samples much more vulnerable to contamination (e.g., Bird et al., 1999; Higham, 2011; Wood, 2015). In old samples, due to the low  $^{14}\text{C}$  content, even very negligible percentages of modern carbon give very high contamination levels leading to wholly distorted chronologies, with resulting ages that can be younger of several millennia (Higham et al., 2009; Higham, 2011). Indeed, this makes the dating of small amounts of ancient carbon, i.e., more prone to contamination, even more challenging (e.g., Bird et al., 2014). Such problems can be partially overcome in long, continuous sedimentary succession that are biostratigraphically well-constrained using indirect approaches based on record alignment strategies, i.e., one record on a depth-scale is aligned onto a “dated reference” record (Govin et al., 2015); provided that the underlying assumptions, i.e., recognition of the events and their one-to-one correlation, are reasonably demonstrated. Yet, whenever possible, tephra markers and/or relative chronologies based on varved sediments can also be used to refine or validate age-models.

### **7.2 The Campanian Ignimbrite (CI) marker**

The Campanian Ignimbrite (CI) super-eruption (southern Italy,  $^{40}\text{Ar}/^{39}\text{Ar}$  age:  $39.85 \pm 0.14$  ka,  $2\sigma$ ;  $^{14}\text{C}$  age:  $34.29 \pm 0.09$   $^{14}\text{C}$  ka BP,  $1\sigma$ ; Giaccio et al., 2017) produced the most

widespread tephra of western Eurasia, extending from the Tyrrhenian Sea to the Russian Plain (e.g., Costa et al., 2012; Marti et al., 2016; **Fig. 7**). Its relevance as a key chronological and stratigraphic marker for addressing a series of issues concerning the European MIS 3 period – including the tempo and the palaeoecological factors involved in the human bio-cultural evolution at the Middle-Upper Palaeolithic transition – has been recognised long ago (e.g., Fedele et al., 2003) and eventually consolidated by a number of papers: e.g., Giaccio et al., 2006 (see Higham et al., 2009 for the updated chronology of Grotta Fumane); Pyle et al., 2006; Fedele et al., 2008; Giaccio et al., 2008; Hoffecker et al., 2008; Lowe et al., 2012; Satow et al., 2015; Wutke et al., 2015; Wulf et al., 2018; Zanchetta et al., 2018.

At several archaeological sites of the central Mediterranean, Balkans and Russian Plain the CI tephra acts as a marker for the end of either final Mousterian with Uluzzian elements (Crvena Stijena, Montenegro, Morley and Woodward, 2011; Mihajlovic and Whallon, 2017), Uluzzian (Apulia region in southern-eastern Italy and Greece; e.g., Douka et al., 2014; Zanchetta et al., 2018) or Proto-Aurignacian techocomplexes (e.g., Serino open-air site and Castelcivita Cave in southern-western Italy and Kostenki site complex in Russia; e.g., Giaccio et al., 2008 and references therein). However, although falling in its dispersal area, the CI has not been detected at the Adriatic site of Grotta Paglicci (Apulia, Southern Italy) and on the opposite Tyrrhenian side, at Grotta della Cala. In both caves the Protoaurignacian seems to stretch beyond the CI event based on  $^{14}\text{C}$  chronology (Paglicci) and the studied materials (Marciani et al., this issue).

710 The CI tephra occurs in all the above-mentioned sites either as a relatively proximal, thick  
711 primary pyroclastic succession (e.g., Serino open-air site; Accorsi et al., 1978; Giaccio et  
712 al., 2006) or as a discrete layer, with a sharp lower contact with underlying sediments,  
713 made of purely volcanic material (i.e., glass shards or pumice fragments with mineral  
714 accessories) with no or negligible contamination by clastic sediments. These features are  
715 consistent with a sub-primary (re)deposition of ash layers by the wind or run-off shortly  
716 after its emplacement as primary fallout along landforms nearby sheltered or open-air  
717 archaeological sites (e.g., Brunis et al., 2019). Specifically, at Castelcivita site, both Plinian  
718 pumice and co-ignimbritic ash layers are recorded in their eruptive stratigraphic order,  
719 suggesting that the two eruptive units were transported and redeposited in the cave  
720 immediately after their fall (fall and rolling process) (Giaccio et al., 2008; Giaccio et al.,  
721 2016). The sub-primary nature of the CI tephra, i.e., no appreciable time elapsed between  
722 CI tephra deposition and the eruption, is also supported by the available radiocarbon  
723 chronology of the archaeological layers immediately below CI tephra strata, which are  
724 statistically indistinguishable from the CI eruption age (Benazzi et al., 2011; Wood et al.,  
725 2012; Douka et al., 2014; Giaccio et al., 2017). On the whole, both radiocarbon chronology  
726 and CI tephra marker suggest that around 40 ka the central Mediterranean region was a  
727 cultural, and possibly biological, mosaic, suggesting the possible coeval occurrence of the  
728 final Mousterian (Crvena Stijena), Uluzzian (Apulia and Greece) and Protaurignacian lithic  
729 technocomplexes (Campania).

730 Particularly significant is also the climatostratigraphic position of the CI tephra as revealed  
731 by a number of marine and terrestrial palaeoclimatic records spread in the wide region of  
732 its dispersal area (**Fig. 7**). In this framework, the palaeoecological and tepthrostratigraphic



high-resolution (120 yr/sample) record of Tenaghi Philippon (Greece, Wulf et al., 2018) offers the unique opportunity to compare the chronostratigraphic position of CI in relation to the palaeoenvironmental context at a centennial scale during the Middle to Upper Palaeolithic transition. In detail, CI deposition occurred ca. 1000 years after the onset of a phase of marked arboreal pollen drop corresponding to the GS 9 (ca. 40.58 cal ka BP) and 3280 years before the onset of GI8 (ca. 36.3 cal ka BP) (**Fig. 7**; Wulf et al., 2018). Similarly, at Monticchio site, the CI was deposited ca. 820 years after the onset of GS 9 (**Fig. 3**). However, at Tenaghi Philippon the resulting total duration of ca. 4280 years for GS 9 strongly deviates from the ca. 2000 years obtained at Lago Grande di Monticchio (Wutke et al., 2015) and from the 1680 years in the NGRIP record (i.e. from 39.90 to 38.22 ka GICC05; Rasmussen et al., 2014). A similar position is verified in number of other terrestrial and marine palaeoenvironmental records (e.g., Mediterranean and Black Sea marine records and Lake Ohrid, and Lesvos Island pollen profiles; see Giaccio et al., 2017 and references therein). Despite the general agreement in placing the CI well after the beginning of GS 9 (ca. 400 years, according to the alignment of records proposed in Giaccio et al., 2017), which is marked by a drop in arboreal pollen and temperate taxa (**Fig. 7**), it seems that further investigations are needed to fully disentangle temporal discrepancies between records and to convincingly correlate the interval encompassing GI 8-10 to the D-O events. This is also challenging due to the inadequate resolution of most of the available pollen records if compared to the short GI 9 duration (i.e., 250-yr-long GICC05; Rasmussen et al., 2014), which only briefly interrupts the GS 10 to GS 9 interval representing over 4 millennia of cold stadial conditions.

755 With specific regards to these chronological issues, it is worth noting that the paired, high-  
756 precision, multiple  $^{40}\text{Ar}/^{39}\text{Ar}$  and  $^{14}\text{C}$ , ages for the CI revealed an offset of ca. 1 ka between  
757 the calendar age of the CI as determined by its direct  $^{40}\text{Ar}/^{39}\text{Ar}$  dating and the calibrated  
758  $^{14}\text{C}$  age of the CI using IntCal13 calibration curve (Giaccio et al., 2017), thus highlighting  
759 the occurrence of a further source of uncertainty when comparing records whose age  
760 models are based on calibrated  $^{14}\text{C}$  ages with others anchored to different time-scales  
761 (e.g., U/Th or Greenland ice chronology). This offset is now confirmed by a recent study,  
762 which reports a record of paired U/Th and  $^{14}\text{C}$  ages from the Chinese Hulu Cave  
763 stalagmite, continuously spanning the last 54 ka (Cheng et al., 2018). This new record also  
764 reveals a radiocarbon plateau between ca. 37.5 ka and ca. 39.1 ka at ca. 33.5  $^{14}\text{C}$  ka BP  
765 that could have affected the age model of records based on  $^{14}\text{C}$  chronology and thus be  
766 responsible for the above-mentioned notable age discrepancy in the length of the GS9 as  
767 recorded in different Mediterranean records. A distortion of the IntCal13 calibration curve  
768 at this time interval is also suggested by the recently published continuous record of the  
769  $\Delta^{14}\text{C}$  spanning between ca. 47.3 and 39.6 ka cal. BP from the Tenaghi Philippon lake  
770 succession (Staff et al., 2019).

771 All this information strictly related to this stratigraphic marker consolidate the notion of the  
772 CI as a pivotal tool for deciphering and evaluating the potential interconnection between  
773 climate, environmental, and human biological-cultural dynamics at the Middle to Upper  
774 Palaeolithic transition, as well as in disentangling several temporal-spatial issues, crucial  
775 for understanding the mechanisms underlying the interaction between AMHs and  
776 Neandertals.

## 777 8 Concluding remarks and future developments

778 In this review, we summarized the current state of knowledge, also contributing with new  
779 elaborations of available data, on climate history, terrestrial ecosystems and  
780 palaeogeography, with the main aim to place Neanderthals and AMHs in the context of  
781 MIS 3 European landscape. Neanderthals lived in Eurasia alongside anatomically modern  
782 humans until ca. 40 ka. This overlap suggests direct or indirect contacts between the two  
783 species on a European sub-continental scale, potentially leading to interbreeding and  
784 cultural exchanges (Higham et al., 2014). To decipher the possible implications of climate  
785 variability and palaeoenvironmental transformation in such human processes, including  
786 Neanderthals extinction, two main aspects must be kept in mind: (i) the millennial/sub-  
787 millennial terrestrial response to high-frequency climate variability resulted in a  
788 pronounced and rapid alternation between forested and more open environments.  
789 Interestingly, the most relevant tree cover reductions in southern Europe are correlated to  
790 HEs, notably GS9-HE4; (ii) a long-term climatic trend (i.e., between ca. 50 and 25 ka) that  
791 led to dramatic increasing of the glaciers extent and lowering of the sea level, with major  
792 impacts on the coast landscape and on physiography and vegetation patterns. This  
793 implied the progressive development of effective ecological and physiographic barriers (i.e.  
794 the Alpine ice-dome) that limited connections between continental and Mediterranean  
795 Europe. In contrast, the gradual enlargement of coastlines and reorganization of European  
796 river systems may have played a key role in the migration processes.

797 To better understand and integrate these aspects, within the ERC - SUCCESS project, a  
798 Work Package is specifically dedicated. Studies will concentrate on the time span between  
799 Heinrich Event 5 to 3, known for their strong impact in Mediterranean Europe, the Balkans

800 and Italy (Follieri et al., 1988; Allen et al., 2000; Lézine et al., 2010; Pini et al., 2010; Müller  
801 et al., 2011, Panagiotopoulos et al., 2014).

802 Attention will be paid to the reference record of Lake Fimon (Venetian Alpine foothills,  
803 north-eastern Italy). This area is indeed well-known as it provides both a Late Pleistocene  
804 palaeoecological record (Pini et al., 2010) and several Middle to Late Palaeolithic sites  
805 yielding evidence of Neandertal and AMH occupation (Grotta Fumane and Riparo Broion  
806 shelter; Peresani, 2011; **Fig. 3**). High-resolution palynostratigraphic researches are  
807 currently in progress on the Lake Fimon core will be matched with archaeological  
808 information from cave deposits in the same region to answer specific questions relevant to  
809 the ERC Project, i.e. the effects of climate variability on the environments of last  
810 Neandertals - early AMH, the role of fire, etc. Finally, to better comprehend regional  
811 vegetation patterns and eco-climatic gradients across the Italian peninsula,  
812 palaeoenvironmental proxies from Lake Fimon will be profitably compared to Central and  
813 Southern Italian records, through the elaboration of available series and the investigation  
814 of new sites.

815

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823

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## 1775 **Figure captions**

1776

1777 **Fig. 1** Comparison of Northern Hemisphere terrestrial and marine paleoclimate proxies: (a)  
 1778 NGRIP  $\delta^{18}\text{O}$  record (Rasmussen et al., 2014), (b) temperature reconstruction based on  
 1779  $\delta^{15}\text{N}$  (Kindler et al., 2014) and (c) calcium ion concentration ( $[\text{Ca}^{2+}]$ ) record (Rasmussen et  
 1780 al 2014), plotted all on the GICC05modelext chronology (Rasmussen et al., 2014); (d)  
 1781 NEEM  $^{17}\text{O}$ -excess permeg (Guillemin et al., 2014); (e)  $\delta^{18}\text{O}$  record from Northern Alps  
 1782 (NALPS) speleothems (Moseley et al., 2014) plotted on its timescale; (f) MD95-2042 Sea  
 1783 Surface Temperature record (Darfeuil et al., 2016), (g) *Neogloboquadrina pachyderma*

abundance and (h) Ice-Radfted Debris record (Sánchez Goñi et al., 2008), plotted each on their own timescale. Vertical grey bars indicate Greenland Stadial (GS). Heinrich events (HEs) are indicated according to MD95-2042 chronology (Sánchez Goñi et al., 2008).

**Fig. 2** European biogeographical map. Overview of mid- to high-resolution marine and terrestrial records entirely or partially covering MIS 3.

**Fig. 3** Vegetation changes throughout MIS 3 in several high- to mid-resolution terrestrial pollen records from S-Europe and Mediterranean region. Pollen curves: % of woody taxa (sum of trees and shrubs) (light green); % of arboreal pollen (dark green); % of xerophytic elements (sum of *Artemisia* and *Chenopodiaceae*) (grey). Black histograms show pollen-slide microcharcoal concentrations. All records are plotted using the latest available chronology for each individual site. NGRIP  $\delta^{18}\text{O}$  record is also shown (NGRIP members, 2004; Rasmussen et al., 2014). Red numbers indicate Greenland Interstadials (GI), modified from Fletcher et al., 2010. Heinrich events (HEs) are indicated according to MD95-2042 chronology (Sánchez Goñi et al., 2008).

**Fig. 4 - A)** Ecogeography of Greenland Interstadial 12 (GI 12; ca. 46.8 to 44.2 ka according to Rasmussen et al., 2014), showing reconstructed gradients within European eco-climatic zones. Digital Elevation Model (base topography – ETOPO 2011; ETRS\_1989\_LAEA\_152 projected coordinate system). Sea surface lowered to -74 m asl (Waelbroeck et al., 2002; Antonioli, 2012). Baltic lake drawn after Lambeck et al., 2010. The mountain glaciers (pale blue) and the main Alpine valley glaciers (cyan triangles) are inferred both from simulations (Seguinot et al., 2018) and ELA calculations, for more information see section 4.1.2. Colour scale bars depict eco-climatic zones gradients. Sharp limits mark reconstructed elevational timberlines position and mountain glaciers extent in different mountain systems within each eco-climatic zone, see sections 4.1 and 4.2. **B)** Palaeogeographic map of Europe during the Last Glacial Maximum. Digital

1812 Elevation Model (base topography – ETOPO 2011; ETRS\_1989\_LAEA\_152 projected  
 1813 coordinate system). Sea level drop at – 120 m (Pellegrini et al., 2015; Maselli et al. 2014).  
 1814 Scandinavian and British Islands ice sheets (pale blue) after Hughes et al. (2016) at 22 ka.  
 1815 The mountain glaciers (pale blue) from Ehlers et al. (2011) with updated reconstructions in  
 1816 the Tatra Mountains (Zasadni and Klapysa, 2014), Dinarides (Kuhlemann et al., 2009;  
 1817 Žebre and Stepišnik, 2014, 2015; Temovski et al., 2018), Pyrenees (Delmas, 2015),  
 1818 Cantabrian range (Serrano et al., 2015). Alpine glaciers downloaded from  
 1819 <https://booksite.elsevier.com/9780444534477/> and modified in the Italian side using  
 1820 updated reconstructions (Ravazzi et al., 2012; Monegato et al., 2017; Gianotti et al., 2015;  
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 1822 and rivers after Toucanne et al. (2015) and Verheul et al. (2015), Adriatic lakes (Miko et  
 1823 al., 2017) and rivers simplified from Maselli et al. (2014). Italian rivers draining major ice  
 1824 lobes at the outlet of alpine valleys are indicated with solid blue lines, outlined lines are  
 1825 used for lower-order rivers. Aeolian sediments (yellow polygons) based on data from  
 1826 compilations by Haase et al. (2007); Italian loess from Zerboni et al. (2018).

1827

1828 **Fig. 5** Spatial vegetation changes at fixed 5 ka yrs long time slices between 60 and 30 ka  
 1829 yrs cal BP. The selected taxa are grouped according to their ecology and climatic  
 1830 preferences. Eurythermic conifers (orange): sum of *Pinus* and *Juniperus*; Temperate forest  
 1831 (red): sum of deciduous *Quercus*, *Alnus*, *Fagus*, *Acer*, *Corylus*, *Carpinus*, *Fraxinus*, *Ulmus*,  
 1832 *Tilia* and *Salix*; Xerophytic taxa (dark blue): sum of *Artemisia* and *Chenopodiaceae*. Italian  
 1833 Peninsula sketch map shows sea level 70 m below the present-day coastline (courtesy by  
 1834 S. Ricci, University of Siena), based on the global sea-level curve by Waelbroeck et al.  
 1835 (2002), but lacking estimation of post-MIS3 sedimentary thickness and eustatic magnitude.

1836

1837 **Fig. 6** Sketch map showing the position of the Palaeolithic sites documenting the Uluzzian  
 1838 culture: 1) Klissoura Cave (Stiner et al., 2007); 2) Kephalaria Cave (Darlas and Psathi,  
 1839 2016); 3) Crvena Stijena (Morley and Woodward, 2011); 4) Grotta del Cavallo (Moroni et  
 1840 al., 2018); 5) Grotta di Serra Cicora (Spennato 1981); 6) Grotta Mario Bernardini (Borzatti

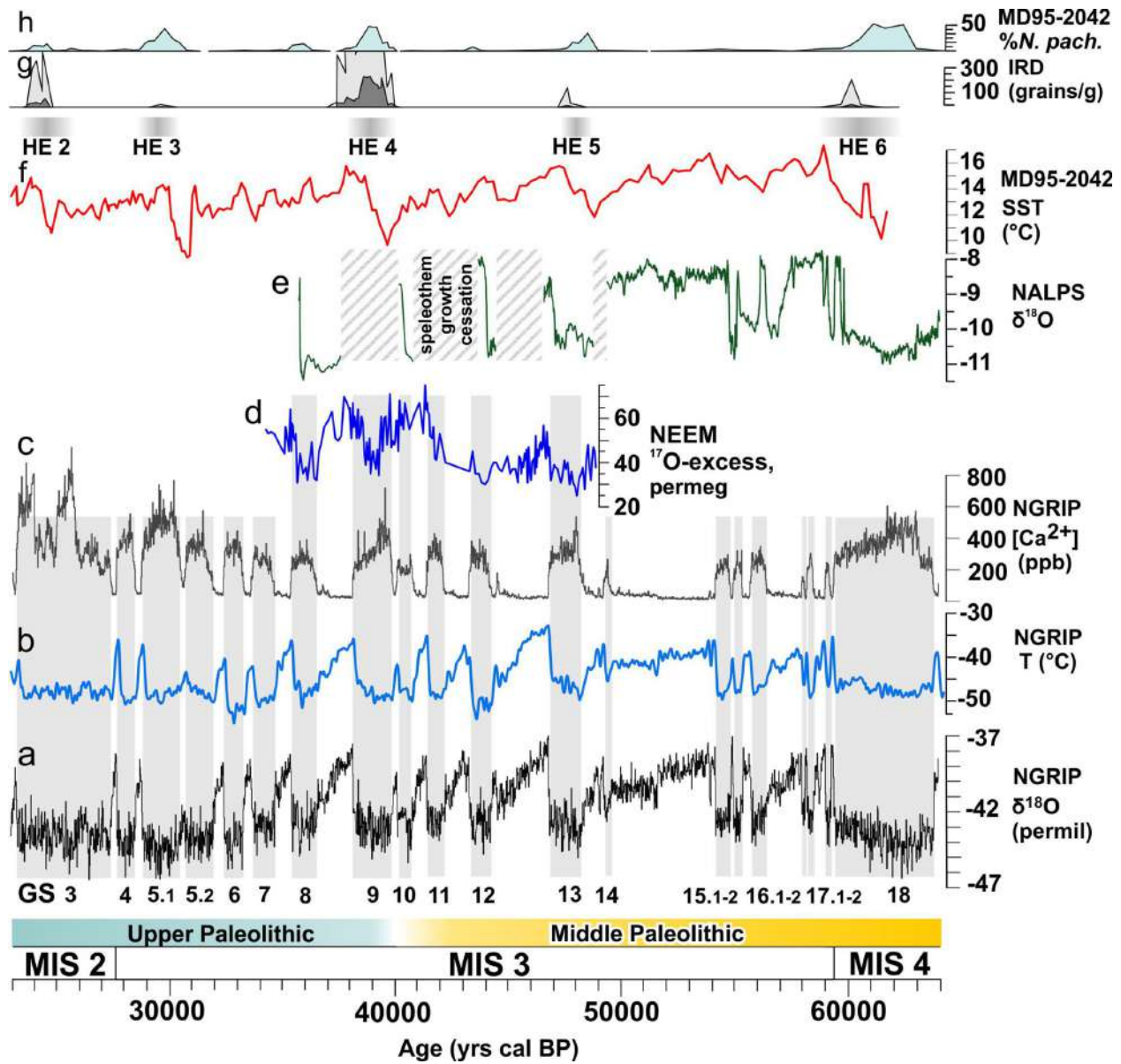
1841 von Löwenstern 1970); 7) Grotta di Uluzzo (Borzatti von Löwenstern 1965); 8) Grotta di  
 1842 Uluzzo C (Borzatti von Löwenstern 1966); 9) Grotta delle Veneri (Cremonesi, 1987); 10)  
 1843 Torre Testa (Moroni et al., 2018); 11) Falce del Viaggio (Moroni et al., 2018); 12) Foresta  
 1844 Umbra (Moroni et al., 2018); 13) Atella Basin (Moroni et al., 2018); 14) Castelvita  
 1845 (Gambassini, 1997); 15) Grotta della Cala (Benini et al., 1997); 16) S. Pietro a Maida  
 1846 (Moroni et al., 2018); 17) Tornola (Moroni et al., 2018); 18) Colle Rotondo (Moroni et al.,  
 1847 2018); 19) Grotta della Fabbrica (Dini 2012); 20) Val Berretta (Moroni et al., 2018); 21)  
 1848 Poggio Calvello (Moroni et al., 2018); 22) S. Lucia I (Moroni et al., 2018); 23) Indicatore  
 1849 (Moroni et al., 2018); 24) Villa Ladronaia (Moroni et al., 2018); 25) Maroccone (Moroni et  
 1850 al., 2018); 26) Salviano (Moroni et al., 2018); 27) Podere Collina (Moroni et al., 2018); 28)  
 1851 Val di Cava (Moroni et al., 2018); 29) Casa ai Pini (Moroni et al., 2018); 30) San Romano  
 1852 (Moroni et al., 2018); 31) San Leonardo (Moroni et al., 2018); 32) Porcari (Moroni et al.,  
 1853 2018); 33) Riparo del Broion (Peresani et al., 2019); 34) Grotta Fumane (Peresani et al.,  
 1854 2016).

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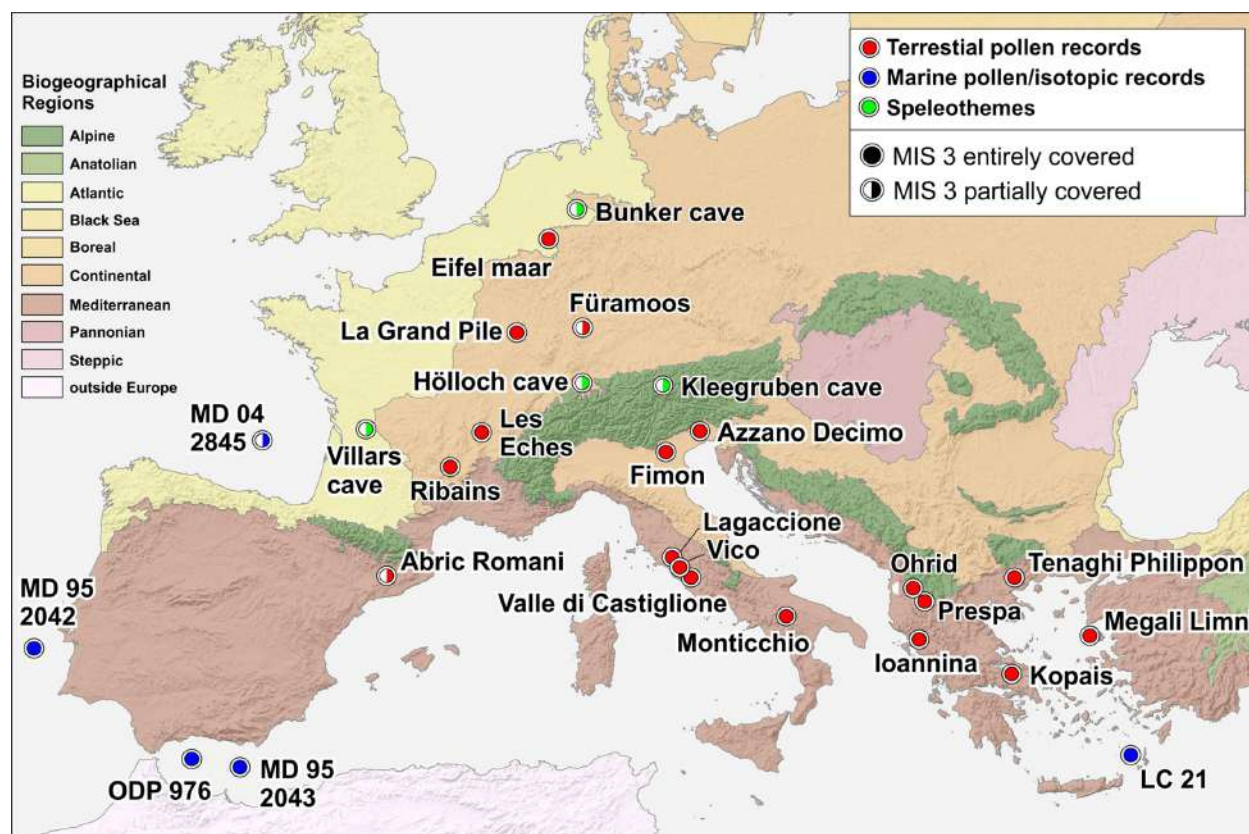
1856 **Fig. 7** Geographic distribution of the Campanian Ignimbrite (CI) distal tephra layer in  
 1857 terrestrial and marine records (red dots) and archaeological sites (yellow squares). On the  
 1858 right: Tenaghi Philippon paleoecological record showing the CI chronostratigraphic  
 1859 position. Selected pollen curves of % arboreal pollen (green) and temperate taxa (orange)  
 1860 between 30 and 60 ka are shown.

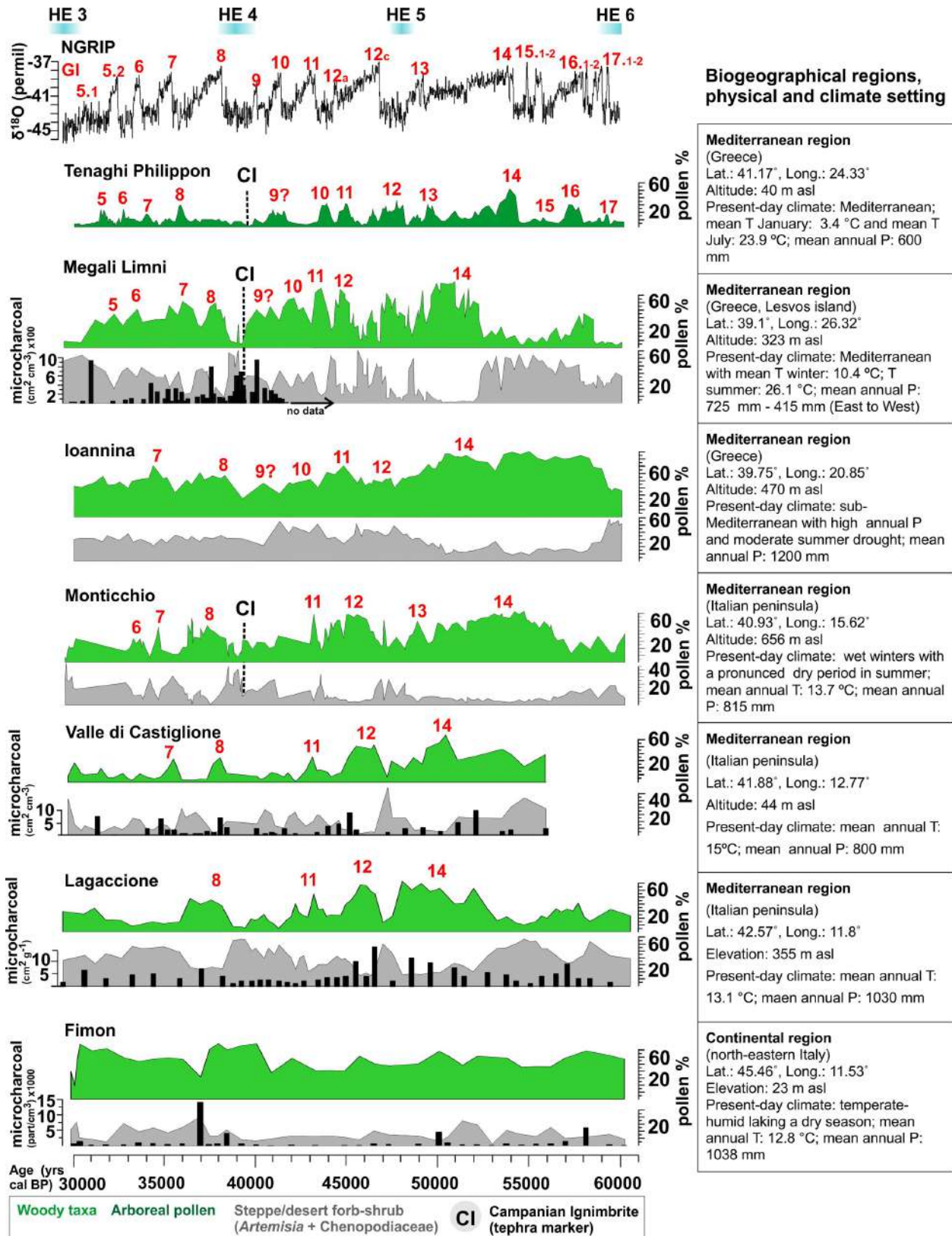
1861





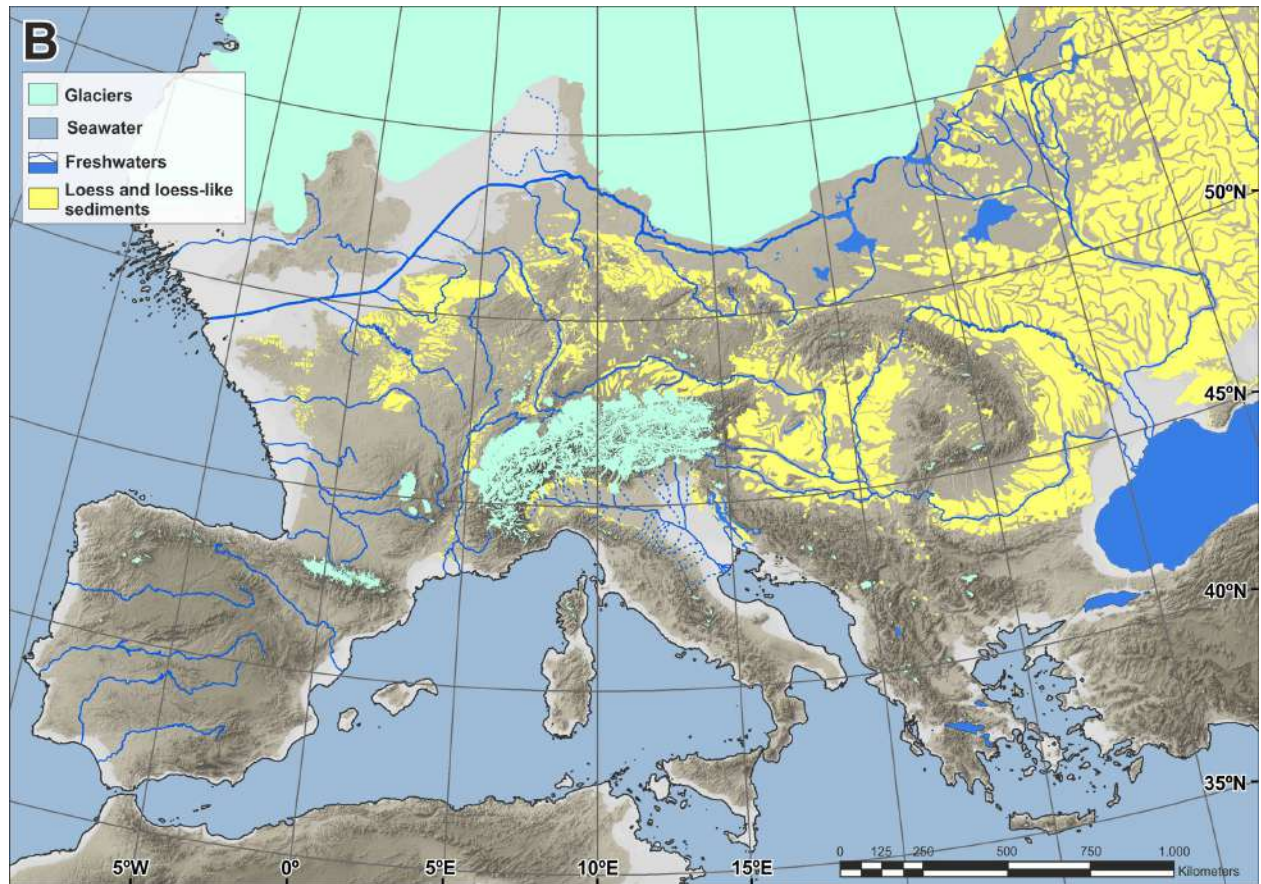


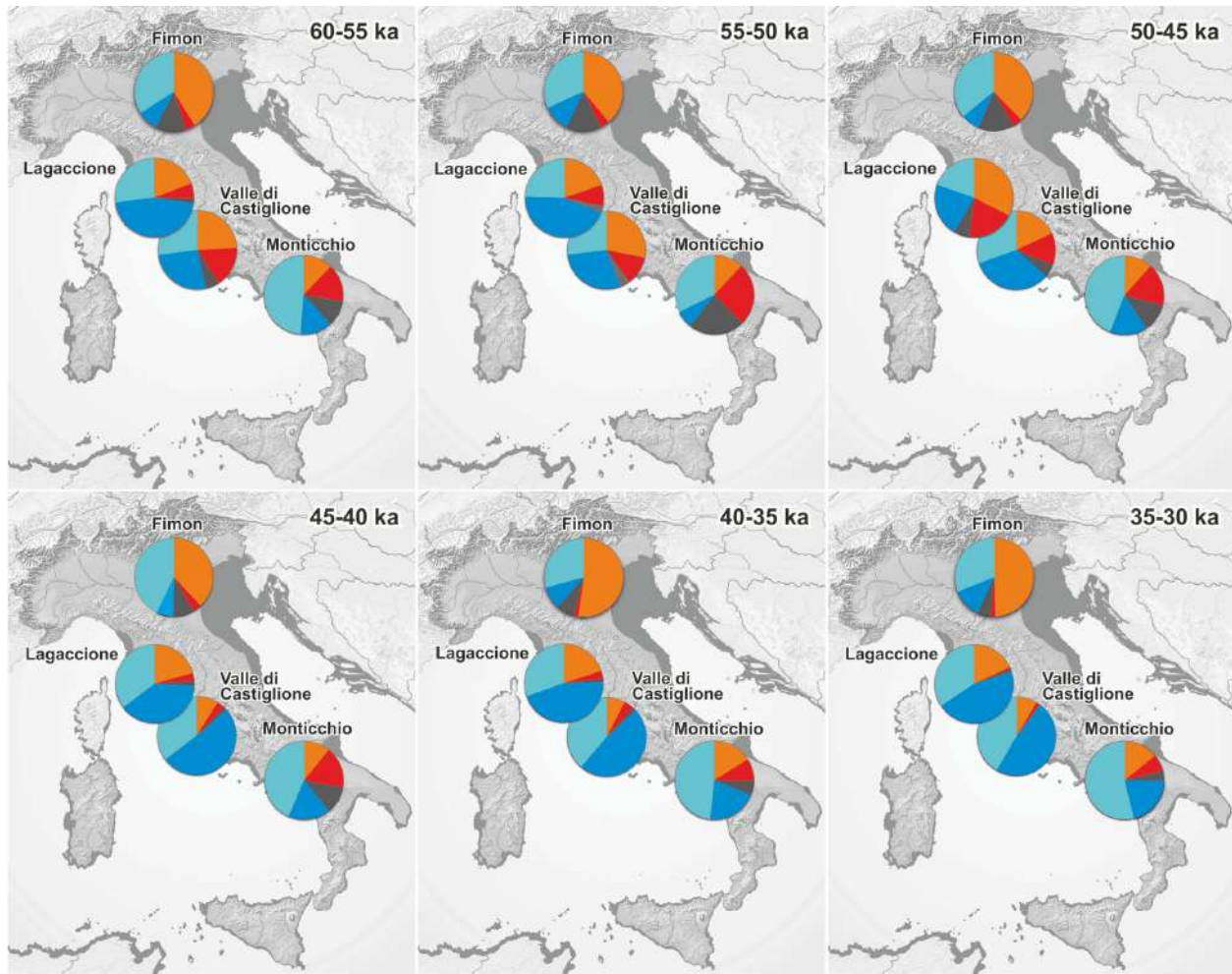










**Legend:**

■ Eurythermic conifers   
 ■ Temperate forest   
 ■ Other woody taxa   
 ■ Xerophytic steppe   
 ■ Other herbaceous taxa

