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1 Title page

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Hunter-gatherers across the Great Adriatic-Po Region during the Last Glacial Maximum: environmental and cultural dynamics

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32 Abstract

33 During the Last Glacial Maximum (LGM, 30 to 16.5 ka ago), the Great Adriatic-Po Region (GAPR) was deeply affected by the spread of glaciers from the Alps to the southern foreland and by 34 the dropping of the sea level to ~-120 m amsl. The combination of these two events triggered the 35 aggradation of the Great Po Plain (GPP), a vast flat area between the Alpine chain, the Italian 36 37 Peninsula and the north-western Balkan Peninsula, physically and ecologically featured through a range of palaeogeographic and palaeocological conditions. The low-elevated Prealpine sectors and 38 the Alpine foothills supported more extensive forest stands, due to increased orographic rainfall. 39 These were open boreal forests which persisted throughout the LGM, while open woodlands, 40 steppes, semideserts and wetlands occupied the lowlands. A complex ecogradient, including both an 41 Alpine and a continental timberline, is documented by the fossil records at the NE Alpine border, 42 with a larch-pine forest-steppe belt, in contact with steppes and loess areas extending in the plain, 43 on the dry extreme of the gradient. Still, edaphic wetlands occupied the waterlogged silty soils in 44 the lowlands. Other areas, marked by active geodynamic processes, supported semideserts, i.e. 45 grooves of xerophytic herbs and shrubs. Enhanced aridity and the development of deflation areas, 46 prompted the accretion of loess cover at the northern and southern margins of the GPP. Fauna 47 recorded the gradual disappearance of mammoth, woolly rhino and giant deer, together with cave 48 bear. Gravettian and Epigravettian hunter-gatherer groups inhabited the GPP, although their 49 presence and settlement dynamics at the margins and across this region has long been questioned. 50 As a matter of fact, a handful of archaeological sites composes a patchy record of the peopling of 51 the plain itself. At the northern rim of the GAPR, characterized by a well-developed karst region, 52 several caves and rock shelters record the presence of hunters of bisons and horses at the margins of 53 the GPP and ibexes and cave bears in some hilly landscapes. Nonetheless, evidence of contacts 54 across this area is provided by the exploitation of chert sources and by stylistic and technical 55 similarities in the lithic industries. The work resumes the currently available multidisciplinary data 56 57 and adds new petroarchaeological evidence for reconstructing the settlement dynamics of the Gravettian - Epigravettian hunter-gatherers in this vast region up to the early Late Glacial, when the 58 Prealpine and the Apennine foothills, along with the Dinarids, were persistently settled. 59

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- Key words: Environmental reconstruction; Human mobility; Upper Palaeolithic; Last Glacial
 Maximum; Adriatic basin; Southern Europe
- 63

64 1. Introduction

Since the time of the Middle Pleistocene Revolution, the increased magnitude of glacial cycles and 65 66 unstable climatic conditions deeply influenced the human settlement dynamics. It is possible to 67 assume that Palaeolithic populations in Western Eurasia underwent the process defined as "Ebb and Flow" (Hublin and Roebroeks, 2009), which led to their disappearance across vast areas of 68 69 continental Europe during the maximum extension of the ice sheets. Therefore, despite their biological and cultural success with respect to the previous European "native" populations, Upper 70 71 Palaeolithic Homo sapiens hunter-gatherers experienced dramatic biological turnovers during the 72 Late Pleistocene as attested by discontinuous archaeological record (Djindjian et al., 1999, Bocquet-73 Appel et al., 2005). The timing and pattern of multiscalar shifts that occurred from the Last Glacial 74 Maximum (hereafter LGM; 30-16.5 ka sensu Lambeck et al., 2014) to the onset of the Late Glacial 75 (hereafter LG) interstadial (14.7 ka cal BP) are considered to be among the most important events. This period was characterized by large-scale climatic oscillations triggered by changes in insolation 76 that led to the build-up of boreal ice sheets (terminology of millennial climatic phases in the 77 following work is in accordance with Rasmussen et al., 2014). Their waxing drove sea level drop 78 79 and produced distinctive regional and global responses along the coasts of the North, Southwest and South of Europe sea level fell to -120 m amsl (Shackleton et al., 1984) leading to the emersion of 80 major continental shelves (Fig. 1). In the Alps, glaciers were already growing before 30 ka BP 81 (Martinez-Lamas et al., 2020) and reached their maximum extent around 25.0±1.7 ka cal BP 82 (Monegato et al., 2017). It is also known that forested area was very reduced in central Europe and 83 northern Europe was mostly treeless during the late MIS 3 (including GS-5) and MIS 2 (Willis et 84 85 al., 2000; Müller et al., 2003; Gerasimenko, 2011; Magyari et al., 2014; Rousseau et al., 2018) with limited resource availability for hunters-gatherers. Nevertheless, the impact of the LGM on human 86 ecosystems has been thoughtfully investigated in Northern and Eastern Europe (Maier et al., 2016; 87 Tallavaara et al., 2015; Burke et al., 2017; Sinitsyn, 2015). Despite the ecological implications of 88 huge geographic and climate changes (Antonioli and Vai, 2004), in Southern Europe several 89 regions experienced more favourable conditions supporting the development of open boreal forests 90 and highly productive wetlands (Willis, 2000; Monegato et al., 2015; Badino et al., submitted). This 91 offered favorable environmental conditions for several mammal species (Svenning et al., 2008), 92 93 which could here thrive, while large part of their former distribution areal, in Central and Northern 94 Europe, was covered by ice sheets. The presence of a rich mammal fauna in these southern glacial survival and refugial areas in turn gave subsistence to hunters-gatherers groups enhancing their 95 capability to maintain large-scale networks (Soffer and Gamble, 1990; Straus, 1991; Djindjian et 96 al., 1999; Roebroeks et al., 2000; Moreau, 2009). South of the Alps, these more favourable 97

98 conditions allowed the survival and delayed extinction of important consumers like cave bears

99 (Terlato et al., 2019a).

100 FIGURE 1 ABOUT HERE

Human groups reacted to the ecological turnovers by increasing their resilience, as shown by a large 101 array of evidence revealed by sites persisting at the middle latitudes. But also large migrations took 102 place through the corridors connecting the European regions, and pronounced changes in 103 104 demography and behaviour occurred, resulting in the synchronic and diachronic development of a variety of archaeological cultures in different regions at different times (some of which remain 105 poorly understood: Djindjian et al., 1999). Lastly, this deeply contributed to the shaping of our 106 present genetic ancestry (Fu et al., 2016; Posth et al., 2016). However, a full understanding of how 107 Upper Palaeolithic groups modulated their biological, cultural and social adaptation to the Late 108 Pleistocene climate change is still far from being achieved, especially in regions of strategic 109 importance for their geographic position, geomorphological setting and biodiversity. One of these 110 corridors was the vast continental shelf that emerged as consequence of the LGM sea level low 111

stand, extending from the Western Balkan Peninsula to peninsular Italy (Maselli et al., 2014).

113

114 Study area: geographic delimitation, subdivisions, terminology and abbreviations (see Fig. 2)

Previously known as the Great Adriatic Plain, this area is indeed part of the Great Po Plain 115 (hereafter GPP), a vast alluvial landscape composed by the Po Plain (the plain of the Po River and 116 its tributaries, hereafter PP), the Venetian-Friulian Plain (the plain where present-day Venetian and 117 Friulian rivers flow not joining the Po River, hereafter VFP) and the Adriatic Plain (the plain 118 emerged during the LGM lowstand, hereafter AP) (Fig. 2). The GPP was at the centre of the Great 119 Adriatic-Po Region (hereafter GAPR), circumscribed by the northern and central Apennines, the 120 southern side of the Alps, and the Dinarides. The term Alpine (upper case) is used geographically to 121 ecompass the Alps, whereas the term alpine (lower case) indicates the ecological zone above the 122 123 timberline ecotone (i.e. the alpine timberline, Holtmeier, 2009). Apart from the alpine timberline, a continental timberline (Holtmeier, 2009) is envisaged for the LGM in the Alpine foreland. The 124 external sector of the Alps facing the GPP plains is a full mountain range but reaching lower 125 elevations compared to the internal core sector of the Alps, not exceeding the 2,200-2,300 m amsl. 126 We named such an external sector Prealpi (Prealps). It does not correspond to a foothills belt. 127 Additional terms relate the Prealps indicating specific regions (Fig. 2). In this study we focus on the 128 129 main part of the GAPR, bounded by the Apennine watershed, the Alpine glacier catchments and the northern Adriatic coast, leaving out the central-southern belts of Italy and Croatia down to Albania. 130

132 Aims of the work

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133 This area is thus supposed to have represented a paradigmatic case, thanks to its peculiar geographic setting and climatic and ecological variability, which supported refugia for temperate species and 134 witnessed vast movements of populations. The human adaptive flexibility expressed by the 135 Gravettian-Epigravettian material culture, human mobility, subsistence and symbolic thinking from 136 137 this region has been the focus of multidisciplinary investigations. To boost our understanding of the settlement dynamics, in the last decade new data were obtained from a large set of sources 138 circumscribing the GAPR, including the Italian Prealps. The present work aims to resume the 139 current state of the art regarding the paleo-geographic, ecological and anthropogenetic 140 circumstances and the evidence of the Late Pleistocene southern European population. We also 141 present additional original data issued from a new petroarchaeological investigation aimed to 142 reconstruct large-scale circulation patterns in the GAPR. These data consolidate the view that this 143 region was settled and crossed by Gravettian-Epigravettian hunter-gatherers. 144

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2. The geomorphological and ecological setting of the Great Po Plain and Great Adriatic-Po Region during the Last Glacial Maximum

The distribution pattern of terrestrial and freshwater ecosystems at the culmination of the last 148 149 glaciation is not a simple function of climate, but instead can be conceived as the interplay between active geodynamic processes, the nature of available biodiversity, and active ecological processes 150 151 under the forcing of climatic conditions. In this section, we combine both physical and biotic site factors to characterize ecosystems, i.e. an ecological classification system, first proposed in Italy by 152 the CLIMEX Group (Antonioli and Vai, 2004). The CLIMEX approach provided a first attempt of 153 154 ecozonation over the GAPR in the LGM (Ravazzi et al., 2004), which is incorporated in the updated and simplified ecological zonation system shown in Tab. 1. 155

According to this system, it appears that the degree of geomorphic activity was the primary forcingover the vegetation patterns during the LGM, both in the Alps and the Apennines (glacial,

158 periglacial and slope processes) and in the plains (fans and megafans aggradation). Mature steps of

the ecological progressions, controlled by the climate state and changes, could be achieved on

upland stable surfaces only and in wetlands isolated from the main drainage system (see Figs. 2 and3).

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163 **2.1. Physical setting**

For almost the whole Alps, wide portions of the Apennines and large sectors of the GPP, the LGM 164 represented a morphogenetic phase of paramount importance because of the erosion produced by 165 glacial and periglacial processes in the mountain catchments, and of the depositional phase, 166 sustained by the glaciofluvial and fluvial systems, in the plains. Thus, before the LGM the 167 168 landscape was dramatically different and this significantly limits the possibility to clearly reconstruct the paleolandscapes existing at the onset of the LGM itself. On the other hand, the 169 170 surfaces and landforms related to the last phase of the LGM are still largely cropping out over major portions of the GPP (Fontana et al., 2014a). Exceptions are the Apennine fringe, the Adriatic shelf 171 172 and the coastal plains, where the post-LGM marine transgression and the Holocene highstand sedimentary processes largely reworked and/or buried them (e.g., Amorosi et al., 2008, 2016). 173 New available data for the Dalmatian coast (Brunović et al., 2020) confirm that, since the end of 174 MIS 5, the relative sea level of the Adriatic basin lowered below -50 m amsl (c.f. Antonioli et al., 175 2009), leading to a significant increase of the alluvial plain areas in MIS 4. During MIS 3, the 176 marine level was probably between -60 and -90 m amsl (Benjamin et al., 2017), in agreement with 177 the available reconstruction for the Red Sea (Siddall et al., 2003, 2010). At that time, a complex 178 system of isolated lakes occupied part of the valleys exposed in the Kvarner Gulf and along the 179 Dalmatian coast because of the sea-level fall (Miko et al., 2016; Brunović et al., 2020). This area 180 was characterized by a karst landscape and by development of lacustrine environments, during the 181 marine lowstand (Fig. 2). Some valleys in the Prealpine hills were also occupied by lakes, as the 182 area of Fimon, in the Berici Hills (Monegato et al., 2011), and Palù di Livenza, in the Carnic 183 184 Prealps (cf. Bassetti and Cavulli, 1999; Peresani and Ravazzi, 2001).

Since MIS 4 and until the onset of the LGM, extensive swampy environments existed along the present coastal sector of the Friulian Plain and in the eastern portion of the Venetian Plain (Fontana et al., 2010). It is likely that in this period the PP and VFP experienced a prolonged phase of morphological stability over large sectors. During MIS 4 and MIS 3 a major unresolved problem in the geomorphological setting is the possible occurrence of large and deep incised fluvial valleys, which could have eventually characterized the landscape of the PP and VFP, as postulated by recent reviews (Fontana et al., 2014a; Amorosi et al., 2017).

The transition between MIS 3 and MIS 2 coincides in the southern side of the Alps with glaciers spread since HS3 at 30 ka BP and followed by the glacier culmination at 25.0±1.7 ka cal BP (Fig. 2). Glaciers maintained their front in the piedmont plain until 19 ka cal BP (Monegato et al., 2017; Braakhekke et al., 2020) and, thus, the Alpine ice-field acted as a physical and environmental

barrier for about 10 ka, making north-south migrations of warm temperate plants, animals and even 196 of human groups unlikely. During this cold phase, the GPP lowlands were characterized by highly 197 dynamic environments with semideserts and rocky deserts; open boreal forest occupied the moister 198 areas (see section 2.2). Such climate and environmental conditions are expected to have enhanced 199 200 the wind strength and allowed the production, transport, and accumulation of loess deposits along the margins of the whole GPP and especially on top of terraces, isolated hills, and pre-LGM 201 moraines (Cremaschi, 1987, 1990; Wacha et al., 2011a, 2011b; Cremaschi et al., 2015; Peresani and 202 Nicosia, 2015; Zerboni et al., 2015, 2018; Frigerio et al., 2017; Fontana and Ferrari, 2020; Badino 203 204 et al., 2020).

FIGURE 2 ABOUT HERE

Even if, in a global perspective, the onset of the LGM started already 30 ka cal BP, the fronts of the 206 major Alpine glaciers reached their first maximum advance at the outlet of the valleys only around 207 26-25 ka cal BP. This is evidenced by the up-building of terminal moraines in the southalpine 208 morainic amphitheatres (Monegato et al., 2007; 2017; Ivy-Ochs et al., 2018; Braakhekke et al., 209 2020) and the beginning of a consistent aggradation phase of the fluvial systems fed by the southern 210 Alps (Fontana et al., 2014a; Rossato and Mozzi, 2016). The glaciers produced a strong dismantling 211 action in the mountain catchments and supported the efficient transport of the eroded sediment to 212 their fronts in the piedmont belt. Most of the major Alpine rivers acted as glacial outwashes, with a 213 significant water and solid discharge that allowed the progradation and aggradation of alluvial 214 megafans over the plain (Fontana et al., 2008). Those Alpine rivers that were not directly supplied 215 by piedmont glaciers, together with the main Apennine fluvial systems, experienced a significant 216 activity and formed large alluvial fans from their valley outlet (Castiglioni et al., 1997; Fontana et 217 al., 2014a and reference therein). In the western PP, the general tectonic framework provided high 218 accommodation space in the Savigliano basin, leading to the trapping of most of the fluvial 219 sediment yield from the south-western Alps upstream of Torino (Piana et al., 2017). Just 220 downstream of Torino, fluvial sedimentation was confined between terraces of older fluvioglacial 221 222 fans emanating from the Ivrea glacial amphitheatre (Giraudi, 2017). Due to this local morphological constraint, the overall extent of the LGM glaciofluvial fans is, thus, significantly smaller when 223 compared with the megafans of the central PP and VFP (Fontana et al., 2014a). 224

In the proximal sector of the central PP and VFP megafans the rivers were gravelly braided, while about 15-20 km downstream of the glacial fronts they were rapidly shifting to sandy braided and further on to sandy wandering style, with formation of fluvial ridges along the active channels, interspersed by silty and clayey floodplains. This longitudinal variation along the rivers was

responsible of the important differentiation in permeability and hydrographic characteristics 229 between the proximal and distal sectors of the alluvial plain along the southern side of the Alps, 230 with consequent formation of the so-called piedmont plain and low plain. Thus, we should expect 231 that a kind of spring belt already existed since the first part of the LGM (Fig. 2), generating 232 important edaphic and environmental diversity from the proximal gravelly sector, where the 233 groundwater table was at some tens of meters of depth from the surface, to the distal silty plain, 234 where the water table was close to the ground. This setting allowed the occurrence in the distal plain 235 of soils in waterlogged conditions, even over rather large areas. 236

River channels had a very high lateral mobility and avulsion was a dominant process in the fluvial dynamics, so the hydrographic pattern was not stable, with frequent and rapid shifting of the river paths over fan and megafan surface (Rossato and Mozzi, 2016). As documented in the distal portion of the VFP megafans, the floodplain areas temporarily not affected by sedimentation could be characterized by marshy environments, lasting for some decades up to several centuries, before being buried by the reactivation of the overbank fluvial deposition on that portion of the plain (Miola et al., 2006).

In the western and piedmont PP the main fluvial systems were likely merging their alluvial 244 megafans with the plain of the Po River (Fig. 2). In the northern Apennines, where small glaciers 245 were sparse and limited to the highest catchments (Losacco, 1949, 1982; Mariani et al., 2018), the 246 alluvial sedimentation partly occurred within the mountains, as documented along the major rivers 247 of Emilia-Romagna and Marche regions, where fluvial terraces dating to LGM are found between 248 15 and 60 m above the present valley floor (Picotti and Pazzaglia, 2008; Wegmann and Pazzaglia, 249 2009; Nesci et al., 2012). Alluvial fans formed from the outlets of the major valleys of the northern 250 Apennines and expanded up to 10-20 km from the mountain front (cf. Bruno et al., 2015). 251 Generally, these fluvial depositional systems were considerably smaller and thinner than the ones 252 supplied by the Alps and they have been extensively covered by the post-LGM alluvial deposition 253 in the PP (cf. Cremaschi and Nicosia, 2012). The rivers of the Marche region did not form 254 important alluvial fans in the piedmont area (Nesci et al., 2012) and they were probably incised in 255 the AP and draining into the Po River. The Po represented the trunk river of the GPP, collecting the 256 contributions of the Apennine streams and forming its delta on the shelf scarp (Amorosi et al., 2016; 257 258 Pellegrini et al., 2017). Nevertheless, the connections between the hydrographic network fed by south-eastern Alps and the Po River are still unclear. 259

In the VFP, the megafans can be recognized for their diverging fluvial pattern and decreasing slope up to about 15-20 km from the present coastline (i.e. from -20 to -30 m amsl). It is worth noting that

in these megafans a clear evidence of meandering channels is missing, both in the present plain and 262 in the portion submerged by the Holocene transgression, where extensive and detailed geophysical 263 surveys have been carried out (Trincardi et al., 2011). The recognized paleochannels have a rather 264 small dimension, generally not comparable even to the Holocene ones, suggesting that significant 265 part of water and sedimentary discharge was probably dispersed on the surface of the megafans. 266 Moreover, in the northern sector of the AP, the LGM fluvial network was not incised but aggrading 267 over the plain (Fontana et al., 2014a). North of the present Po River delta only a single small incised 268 fluvial valley has been documented for the LGM, 30 km offshore of Chioggia, but this belonged to 269 270 a minor stream not connected to a mountain catchment (Ronchi et al., 2018).

These data allow hypothesizing that, during significant periods of the LGM, the hydrography of NEItaly was not merging together in a single large river and, eventually, not reaching the Po River.

A rather different situation characterized the eastern side of the AP, along Istria and Dalmatia, 273 where most of the rivers had a limited water and sedimentary discharge because of their karst 274 catchments (Pikelj and Juračić, 2013; Felja et al., 2015; Furlani et al., 2016, Novak et al., 2020). 275 Small ice-caps developed in the highest mountains but outwash fans were confined to polje areas 276 (Žebre and Stepišnik, 2015; Žebre et al., 2016; Sarıkaya et al., 2020). It is likely that the related 277 fluvial network was incised in the AP but, for a complete reconstruction of the LGM 278 palaeogeography, a major obstacle is represented by the lack of information from the offshore 279 sector of Croatia. 280

The idea of an AP with a well-formed and interconnected hydrographic network, as proposed in the 281 first reconstruction by De Marchi (1922) and also described in recent papers (e.g. Amorosi et al., 282 2016), is hardly applicable to the unstable fluvial systems characterizing the LGM. 283 284 Notwithstanding, the role of the Po River as the main fluvial system collecting most of the sediment produced in the GAPR during the LGM is well testified by the formation of its delta in the Mid 285 Adriatic Depression. Between 31.8 and 14.4 ka cal BP the delta aggraded for about 350 m of 286 thickness over the scarp of the continental shelf but, because of the steep slope of the scarp, the 287 coastline shifting was rather limited, in the range of about 30 km during the LGM (cf. Pellegrini et 288 al., 2017, 2018). 289

Approximately between 24 and 23 ka cal BP the glaciers of the southern Alps experienced a limited recessional phase, which led them to temporary withdraw for some kilometers from the most external moraines, as shown in the Tagliamento and Garda end-moraine systems (Monegato et al., 2007, 2017). This setting induced also a reduction in the fluvial activity over fans and megafans (Rossato and Mozzi, 2016; Hippe et al., 2018). The recession phase broadly encompasses the so-

called Greenland Interstadial 2 (GI2), a phase of important cultural turnover among huntersgatherers societies of Europe (Djindjian et al., 1999; Ducasse, 2012).

A second peak of glacial advance occurred between 23 and 22 ka cal BP (Monegato et al., 2017), leading to a renewed expansion of the glacial fronts in the piedmont area. During this phase, the fluvial activity had the same characteristics described above for the first LGM glacial expansion (i.e. 27-25 ka cal BP).

Since about 22 ka cal BP, the Garda glacier started its recessional phase, anyhow it occupied part of the morainic amphitheatre until 17.7 ka cal BP, when it collapsed (Ravazzi et al., 2014; Monegato et al., 2017). A similar chronology is suggested for the Tagliamento end-moraine system, where the glacier abandoned the plain already 19.0 ka cal BP (Fontana et al., 2014b). The same time intervals are documented also for the last activity of the alluvial megafans of the VFP, where the Brenta megafan was the last one to switch from aggradation to incision at around 17.5 ka cal BP (Rossato and Mozzi, 2016).

Between 18 and 17.5 ka cal BP, the glaciers were collapsing (Wirsig et al., 2016) and they rapidly 308 withdrew towards the upland catchments, leading to dramatic changes both in the Alpine valleys 309 and in the alluvial plains. Between 22 and 17.5 ka cal BP part of the fans and megafans did already 310 experience an erosive phase, which led the active channel to entrench in their apical portion. The 311 northern sector of PP experienced the entrenchment of the Alpine rivers up to their junction with the 312 Po River (Marchetti, 2001). The VFP major incised valleys formed in the alluvial megafans of the 313 Tagliamento and Piave Rivers (Carton et al., 2009; Fontana et al., 2014a) between 19 and 15 ka cal 314 BP, while in the Brenta megafan they started after 17.5 ka cal BP (Mozzi et al., 2013). Thus, 315 between 19 and 16 ka cal BP, the GAPR experienced a dramatic change in the geomorphic 316 317 processes, especially in the Alpine sector, where the glacial withdrawal allowed the progressive opening of valley corridors, while in the northern PP and VFP large surfaces became stable. Since 318 about 16.5 ka cal BP also the rapid sea-level rise begun (Lambeck et al., 2014), but the position of 319 the Adriatic coastline started to change considerably only after 15 ka cal BP, when the sea stepped 320 over the edge of the continental scarp and could transgress over the AP. 321

During the LG, a short cooling occurred at about 16.4-16.2 ka cal BP, which is marked by the Ragogna oscillation (Monegato et al., 2007; Ravazzi et al., 2012; Schmidt et al., 2012). This may be correlated to a short glacier readvance, known as Gschnitz stadial, which is documented from the Maritime Alps (Federici et al., 2017) to the Central Alps (Ivy-Ochs et al., 2009; Ghinoi and Soldati, 2017). 327

328 2.2. Ecozones of the Great Adriatic-Po Region in the Last Glacial Maximum, their vegetation 329 and climatic patterns

In this section, we combine both physical and biotic site factors to characterize ecosystems, i.e. an ecological classification system, first proposed in Italy by the CLIMEX Group (Antonioli and Vai, 2004). The CLIMEX approach provided a first attempt of ecozonation over the GAPR in the LGM (Ravazzi et al., 2004), which is incorporated in the updated and simplified ecological zonation system shown in Tab. 1.

According to this system, it appears that the degree of geomorphic activity was the primary forcing over the vegetation patterns during the LGM, both in the Alps and the Apennines (glacial, periglacial and slope processes) and in the plains (fans and megafans aggradation). Mature steps of the ecological progressions, controlled by the climate state and changes, could be achieved on upland stable surfaces only and in wetlands isolated from the main drainage system (see Figs. 2 and 3).

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The vegetation of the plain ecozones. Active megafans were pioneered by edaphic semideserts, 342 343 dominated by xerophytic herbs and shrubs (Artemisia, Hippophäe, Juniperus, Ephedra, Berberis) on bars and abandoned riverbeds, especially on coarse (gravelly) sediments (see Tab. 1 and Fig. 3 344 345 for fossil sites documenting this ecozone; see Fig. 4 for a modern analogue). Downstream, these semideserts probably connected with climatic semideserts and deserts (annual rainfall below 300 346 mm; see Badino et al., submitted) that developed in the depressed Adriatic plain. Here we also 347 envisage riverside vegetation relevant both for the mammal fauna and the humans, but the 348 palaeoecological documentation is scarce (Tab. 1). Extensive wetlands developed in the lower 349 350 megafan belts, in the water-saturated silty soils in the lowland areas, especially in the VFP (Miola et al., 2003; Serandrei Barbero et al., 2005). A birch swamp has been recently described in the lower 351 Adda megafan (Ravazzi et al., 2018, 2020). 352

353 TABLE 1, FIGURES 3 AND 4 ABOUT HERE

The forest ecozone and its double timberline ecogradient. The continental timberline and the elevational timberline. The concept of double timberline, elaborated in the modern analogues of the high mountain ranges emerging from semiarid steppe of Asia and North-America (Walter and Breckle, 1986; Chytrý et al., 2008; Holtmeier, 2009) may apply to the southern border of the Alps and their foothills during late MIS 3-MIS 2 and it is visualized in the sketch of Fig. 4. The fossil

sites of Azzano Decimo, Renče and Fimon (Pini et al., 2009; Monegato et al., 2015; Badino et al., 359 submitted) document the continental boundary of the forested region at the NE Alpine border (Fig. 360 3). The modern pollen analogues lie in the forest-steppe ecogradient in the Altaj mountains at the 361 Russian-Mongolian border (Chytrý et al., 2008; Magyari et al., 2014; Badino et al., submitted), with 362 a larch-pine forest-steppe belt at the continental timberline limit (300 mm annual rainfall and boreal 363 continental climate; Zhambazhamts and Bat, 1985; Makunina, 2016), in contact with steppes and 364 loess areas on the dry extreme of the gradient. The structure and position of the elevational 365 timberline in the LGM is hardly documented by fossil elevational sites, so far available for the early 366 Late Glacial only (Vescovi et al., 2007; Ravazzi et al., 2012). Based on modern Asian pollen 367 analogues, an ecoclimatic elevational model based on temperature lapse rate (Gorbunov, 1978; 368 Matthews, 1992) allowed estimating the elevation of the Alpine timberline at around 700 m in the 369 NE Prealps (Ravazzi et al., 2004). It is envisaged that *Pinus mugo* dwarf forests played an important 370 role at timberline elevations on areas characterized by carbonate bedrock in the Eastern Prealps 371 (Ravazzi and Vescovi, 2009), especially on south-facing slopes with periglacial activity. According 372 373 to ecological analogues, and to palaeoglaciological and climate modelling (Barron and Pollard, 2002; Luetscher et al., 2015; Becker et al., 2016), the forest ecozone experienced orographic 374 375 precipitation due to the windward forced advection of southern airmasses. Simulations of winter snowfall at the southern Alpine fringe provide a net increment of winter snow height moving from 376 MIS 3 stadials (Berici Hills = 10 cm winter snow height) to an advanced phase of the LGM, 21 ka 377 cal BP (Berici Hills = 138 cm winter snow height) (see Barron and Pollard, 2002; Pini et al. 2010, 378 379 their tab. 4).

The alpine vegetation ecozones. A wide ecotone of alpine grasslands, steppe-grasslands and 380 petrophytic semideserts is predicted to have withstood the LGM on stable unglaciated areas beyond 381 the elevational timberline (Tab. 1). Unfortunately, this figure is still poorly documented by fossil 382 sites and only at low elevation (Fig. 3; Ravazzi et al., 2012). This ecozone supported rich 383 populations of ungulates and preserves hotspots of endemic herbs and invertebrate herbivore 384 communities. The biodiversity in this ecozone experienced great success downhill of its interglacial 385 range, following late MIS 3 forest withdrawal (e.g. Pini et al., 2010). The alpine ecozone is 386 predicted to have expanded downhill over the sunny slopes. Still, these communities were able to 387 settle areas over the valley glaciers (Antonioli and Vai, 2004). The range of many species shifted 388 389 down, prompting vehiculation by wind, organisms, runoff, waterscapes, or by the glaciers themselves (Pelfini et al., 2012) towards adjacent regions that acted as survival or refugial areas, 390 391 and back at the Late Glacial climate reversal. Consequently, the LGM refugial areas of mobile 392 species mismatched the modern range of modern biodiversity hotspots, a fact readily overlooked by

fenetic biogeography and by phylogeography in the Alps (Merxmüller, 1952, 1953, 1954;

- Schönswetter et al., 2005). Indeed, and contrary to recent statements (Cheddadi and Bennett, 2020),
- 395 yet there is no fossil record supporting the location of LGM microrefugia in the Prealps based on

modern ecogeography. For other elevational ecozones see Tab. 1.

397

398 2.3. Zoogeographic setting

The distribution of the continental fauna in the GAPR has a transitional character, given the position 399 of this area between two zoogeographic regions, south-western and central-eastern Europe. During 400 the Middle and Late Pleistocene, continental and peninsular Italy was divided into a temperate 401 Ligurian-Tyrrhenian-Ionic bioprovince and a Padano-Adriatic bioprovince with fauna of harsher 402 climatic conditions, in particular during the LGM (Sala, 2004). The path in central Slovenia served 403 as a passage from the Pannonian basin and the Balkans for many mammals. This was the case for 404 large pachyderms as the mammoth (Mammuthus primigenius), and woolly rhino (Coelodonta 405 antiquitatis), and large ruminants as the giant deer (Megaloceros giganteus), the moose (Alces 406 alces), and the steppe bison (Bison priscus). Apart from the woolly rhino, which entered Italy only 407 during the Last Glaciation, the other large ungulates had already reached the Po Plain through the 408 northern Adriatic route during the previous glaciation (MIS 6 - Sala and Marchetti, 2006) together 409 with the alpine ibex (*Capra ibex*), the chamois (*Rupicapra rupicapra*), and the marmot (*Marmota* 410 *marmota*). However, during the last interglacial warm phase, ibex, chamois and marmot retired to 411 higher elevation to find their climatic optimum. This was due to the particular geographic situation 412 of Italy, closed at the north by the Alpine chain which created a barrier to the latitudinal migration 413 of megafaunas which otherwise interested most of Europe, during the glacial-interglacial episodes 414 415 of the Middle and Late Pleistocene. Thus, while the warm stages were trapping into the Italian Peninsula cold adapted species, leading to their altitudinal shift or local demise, cold episodes 416 417 opened the northern AP as an easy access route from the Pannonian Basin and the Balkans through central Slovenia. 418

During the last glacial period (Monegato and Ravazzi, 2018), this same route into Italy was
followed also by several cold-adapted rodents and lagomorphs now retired in north-eastern Europe
or central Asia, such as the tundra vole (*Microtus oeconomus*), the northern birch mouse (*Sicista betulina*), the European hamster (*Cricetus cricetus*) and the steppe pika (*Ochotona pusilla*). These
have been recorded from different layers of Riparo Tagliente (n°30 in Fig. 3 - Berto et al., 2018)
and Fumane Cave (n°29 in Fig. 3 - López-García et al., 2015). Some of these small mammals
colonised only the Po Plain and the lower hills of the Prealpine and pre-Apennine zones, as, among

large ungulates, the cold-adapted moose, which never crossed the Apennine barrier to reach the 426 Tyrrhenian side of Italy (Breda, 2002) and which retired in north-eastern Europe as well. This 427 distribution of some elements of the fauna, supports the idea of the existence of two distinct 428 bioprovinces (Sala and Marchetti, 2006). On the contrary, animals such as mammoth, wholly rhino, 429 giant deer and bison dispersed through the entire peninsula, reaching the Tyrrhenian side but also as 430 far south as the Salento (Puglia region, Petronio et al., 1996). However, during the LGM, further 431 immigration from the nearby Pannonian basin did not take place probably because the north-east 432 passage through Slovenia was inaccessible due to the high snow cover (Sala, 2004). So, when 433 434 mammoth, woolly rhino and giant deer gradually disappeared from Italy between 33 and 24 ka, together with pre-existing elements, such as the fallow deer (Dama dama), the leopard (Panthera 435 pardus), the cave bear (Ursus spelaeus), and the hyena (Crocuta crocuta), toward the end of the 436 LGM, they left a much-impoverished fauna (Sala 2007). Particularly, the radiocarbon dating of cave 437 438 bear remains from the Berici Hills in the subalpine area ($n^{\circ}11$ in Fig. 3), to 24.2 - 23.5 ka cal BP, makes them the latest known record of this species in Europe (Terlato et al., 2019a). The latter 439 440 evidence testifies that the Berici Hills – thanks to the availability of trophic resources and caves – were the last refugium for the large plantigrade in Europe. Despite the long trend of negative human 441 442 and climate effects, increased at around 30 ka cal BP, had fragmented the cave bear population into various subpopulations inhabiting small refugial habitats, the broad range of plant types available 443 along the meltwater rivers and wetlands at the edge of the VFP and favourable winter temperatures 444 on low elevation karstic hills allowed their survival here for few additional thousand years. Isotopic 445 446 values from the bones suggest that the dietary preferences of cave bears remained unchanged until their disappearance (Terlato et al., 2019a) and that interaction with the Palaeolithic hunters, who 447 settled the same district, were (probably) the forcing factors leading to their final extinction. A 448 similar trend could be envisaged also for Ursus ingressus, an intrusive species in this region and 449 representative of the genetically impoverished relict of a larger East European population, as 450 revealed from the sequencing of mitochondrial DNA (Gretzinger et al., 2019). 451

Thus, during the LGM and up to the LG interstadial, the iconic herbivorous species in the plain and in the lower hilly landscapes of the Apennines was the steppe bison (*B. priscus*). Remains have been found in the Karst, at Grotta Tilde (Trieste – $n^{\circ}26$ in Fig. 3), associated with horse (Riedel, 1980), at Manerba in the glacial amphitheatre surrounding the Garda lake ($n^{\circ}12$ in Fig. 3 - Ravazzi et al., 2014), at Settepolesini quarry at the centre of the Po Plain ($n^{\circ}25$ in Fig. 3 - Sala, 2001), at

457 Cava a Filo quarry at 225 m of elevation in the nothern slope of the Apennine ($n^{\circ}27$ in Fig. 3), and

- in minor sites scattered at several locations in the rim of the GAPR (Fig. 3). The Cava a Filo faunal
- assemblages, dated between 24.5 and 17.5 ka cal BP (Paronuzzi et al., 2018a), are dominated by

bison in association with Canis lupus and Capreolus capreolus in an environment with poorly 460 differentiated fauna. Three chronological intervals have been recognised through radiocarbon 461 dating, representing two cold intervals of the LGM and the beginning of the LG (Paronuzzi et al., 462 2018a). Megaloceros giganteus appears in the Cava a Filo 1 association with Meles meles, Lepus 463 timidus and Marmota marmota, which in Cava a Filo 2 association, are joined by Vulpes vulpes. 464 Cava a Filo 3 dates to 18.6-17.4 ka cal BP and records an increased diversity with Sus scrofa and 465 Mustela erminea, in addition to the large mammals already present in the older levels, consistent 466 with a more forested environment and with the climatic amelioration of the beginning of the LG 467 468 (Paronuzzi et al., 2018a). Roughly correlated with the Cava a Filo 3 fauna, but recording a drier environment, are the Late Glacial levels of Settepolesini (n°25 in Fig. 3) where Bison priscus 469 persists beyond 16.4 ka cal BP in virtue of its reduced nutritional requirements that allowed it to 470 thrive also in arid steppes where more demanding herbivores could not survive (Sala and Gallini, 471 472 2002).

In the foothills and subalpine area of southeastern Alps, the ibex is the most common species during 473 the LGM. The deer and the roe deer are very rare like the Equidae (Bartolomei et al., 1977). As 474 noted by Sala (2007), in the sites dated to the earliest LG period on the Berici hills and at the foot of 475 the Venetian Prealps, the ibex is still very abundant, together with the chamois where steep slopes 476 are present (e.g. lower levels of Riparo Tagliente; n°30 in Fig. 3 - Fontana et al., 2009). 477 Archaeofaunas from cave deposits also record the presence of carnivores like Vulpes vulpes, Felis 478 silvestris and Canis lupus in addition to the cave bear (Romandini and Nannini, 2012). The moose 479 is recorded and relatively abundant both in the plains along with the bison (e.g. Settepolesini). 480 481 Bison also reached the moraine amphitheatres (e.g. Manerba; Ravazzi et al., 2014) and low Prealps (e.g. Riparo Tagliente, Grotta Paina, Grotta Trene and Grotta Tilde) because, moving along riparian 482 habitats, it can span a wide variety of environments and climates (Breda, 2001; 2002). Conifer or 483 mixed open forests with grasslands, slow-flowing water bodies and mountain meadows with rocky 484 outcrops are are the habitat predicted by bird assemblages from sites in the Carnic Prealps (Grotta 485 Rio Secco: n°31 in Fig. 3 - Carrera et al., 2018a) and the Berici Hills (Buso Doppio Broion: n°6 in 486 Fig. 3 - Carrera et al., 2018b) alongside with sparse cyprinid and salmonid remains (Romandini et 487 al., 2015). Furthermore, the presence at the onset of LGM of Bubo scandiacus and Surnia ulula, 488 two cold-adapted species currently distributed at high latitude in the Boreal hemisphere, is a clear 489 490 marker of cold ecozones with herb and low shrub vegetation and of boreal forest (Carrera et al., 2018b). Still on the Adriatic side, as well as in Apulia, the most widespread species is the ibex, 491 along with the horse, and frequently Equus hydruntinus as well. In the southern sector of the GAPR 492 (not included in this work), the bison is replaced by the aurochs, which are numerous there, while 493

red deer and wild boar are rare (Sala, 2004). The horse (*Equus ferus*; *Equus hydruntinus*) is also
part of the faunal assemblages in Istria along with auroch, ibex, red deer and roe deer (Janković et al., 2017; Mauch-Lenardić et al., 2018; Weinstock, 2017). Marmot and hare are recorded with
variable incidence across the whole GAPR.

498

499 3. Hunther-gatherers around the Great Adriatic-Po Region

The GAPR is suggested to have played a major role in promoting large-scale migratory fluxes, a phenomenon also hypothesised for much older periods across the whole Pleistocene (Palombo and Mussi, 2006; Muttoni et al., 2010). Due to its geographic position and ecological variability, this area can provide evidence for reconstructing the evolution of the present-day amphi-Adriatic biogeographical connections displayed by several floral and invertebrate taxa (Frajman and Schöwnswetter, 2017), together with human settling and exploitation of mountain refugial habitats at both sides of the GPP during the LGM (Peresani, 2019) (Fig. 3).

507

508 **3.1. Cultural background**

509 Given its geographic position at the interface between two main domains regions of southern Europe, the GPP represented a crossing-area along the route of human groups starting from around 510 the Danube basin to the Mediterranean regions (Montet-White, 1996). Evidence of this is the spread 511 of the Gravettian and Epigravettian cultures, which are recorded with detail up to the southern 512 Adriatic coast (Palma di Cesnola, 2004). Gravettian-Epigravettian societies adapted in response to 513 environment, resources and exploitation strategies; technical hunting behaviour turns out to be a key 514 element in the identification of these phenomena (Wierer, 2013). Backed tools are the most 515 diagnostic trait of the Gravettian and their typological features were used for its tripartite 516 subdivision into early, middle (evolved) and late (final), being the first phase characterized both by 517 invasive backed points and the occurrence of marginally backed points. Among these latter, the 518 specific type *fléchette*, a leaf-shaped point characterized by marginal semi-abrupt retouch 519 sometimes inverse at one or both ends of the blade blank, is rather typical for the early Gravettian as 520 confirmed at Grotta Paglicci, layer 22 (Palma di Cesnola, 2004). This technocultural facies (also 521 522 known as "Undifferentiated" or "Gravettian with backed points"; Palma di Cesnola, 2006) is present in the whole Italian Peninsula (Palma di Cesnola, 1993; Gambassini, 2007). The Gravettian 523 524 is also typified from the invasive Gravette-type backed points and the Vachon points (Simonet, 2011). End-scrapers are also a basic component of the common domestic Gravettian tool-sets, in 525

addition to scrapers made on flake and to splintered pieces. The Gravettian is also known for the 526 vast array of burin types, considered as diagnostic elements of specific cultural facies diffused in a 527 short time-span at the regional or supraregional scale after the early Gravettian. This is the case of 528 the *Noailles* type, a burin spread from Western Europe to the Tyrrhenian coast of Italy (Palma di 529 Cesnola, 2001) and inland until the western slope of the Central Apennine at 28.6-28.0 ka cal BP 530 (Aranguren and Revedin, 2008), but which is completely absent in Adriatic Italy (Gambassini, 531 2007), the Balkan region (Mihailović and Mihailović, 2007) and Greece (Adam, 2007). Partition of 532 the middle phase of the Gravettian along the Italian Peninsula in two facies based on the presence or 533 534 absence of burins correlates to the biogeographic zonation described above.

535 Typological indications for industries of the oldest phase corroborate the hypothesis of the broad expansion of the Swabian Gravettian and Pavlovian techno-complexes from Central Europe along 536 537 eastern routes, possibly supported by high mobility of hunter-gatherers. Large-scale movements of people might have enhanced culturally mediated migrations and facilitated the diffusion and 538 assimilation of innovations in the technical behaviours of neighbouring regions (Moreau, 2009). 539 This could also have been the main factor leading to the first appearance of the techno-complex 540 with shouldered points (Fig. 5), the iconic tool of the third phase of the early Epigravettian, in 541 western Balkans and the GAPR refugia, settled by late Gravettians coming from the middle Danube 542 region. Kozłowski (1999; 2008) suggested to trace the occupation of this region by the early 543 Epigravettians on a morpho-stylistic comparative analysis with similar eastern types, like the 544 Kostienky and Willendorf ones. To this lane, Broglio (1997) revealed a delayed trend in the 545 appearance of shouldered points according to the latitude position of the sites towards the south of 546 547 the Italian Peninsula based on the distribution of the dates which record the oldest at 25.8-24.8 ka cal BP at Grotta Arene Candide (layers P9 and P8; Bietti and Molari, 1994), Grotta Paina, Ovčja 548 Jama and Šandalja II cave (although challenged from the date of layer 17E – 23.9-23 ka cal BP - at 549 Grotta Paglicci; Palma di Cesnola, 1993). More recently, alternative points of view have been 550 offered. After Borić and Cristiani (2016), it is possible that the design, manufacture and use of 551 shouldered points were transferred as a cultural package along networks developed between 552 populations, rather than these tools were directly spread in consequence of the movement of human 553 groups. Further on, the shouldered point as cultural marker has been challenged by the extension of 554 its chronological range. New dates from Kastritsa cave in Greece and Vrbička cave in Montenegro 555 556 shift the appearance of these points back to 28-26.7 ka cal BP, so much earlier than expected, with persistence in their use until the end of the LGM and beyond it for a lapse of time in the late 557 558 Epigravettian. If this is the case, such a large chronological dispersion, which encompasses a variability of ecological changes, does not reinforce the usefulness of this implement in the 559

identification of a specific cultural facies (Vukosavljević and Karavanić, 2017), and claims for
renewed analyses.

562 FIGURE 5 ABOUT HERE

According to the Laplace's model (1964; 1966; but see also Palma di Cesnola 1993; Bietti, 1997; 563 Broglio, 1997 for discussion), the early Epigravettian splits into three phases defined on a 564 typological ground: unifacial points, bifacial points and shouldered points, the first two interpreted 565 like the result of a cultural influence from the Solutrean spread in western Europe. Given the 566 sparseness of bifacial points, only the first and the third horizons show consistency, having been 567 recorded at several sites also on the Tyrrhenian side (Peresani, 2006). However, chronological 568 boundaries are still far from being positioned. Unifacial points are present in the final Gravettian as 569 much as in the earliest Epigravettian, leaving uncertainty for the cultural attribution of assemblages 570 to one or another techno-complex. Indeed, the Epigravettian is characterized by the persistence of 571 Gravettian traditions, as it has been presumed in the technology of lithic industries, despite the main 572 reference role assumed by the typology of tools and lithic insets. It has been claimed that 573 typological assets do not help to clarify the cultural consistency of the early Epigravettian, so its 574 chronological frame needs to be strengthened as much as information on the procedures of lithic 575 technology (Tomasso, 2017). Large uncertainty also concerns the upper boundary of the early 576 Epigravettian, being its latest appearances recorded at 21.8 ka cal BP at the top of the Arene 577 Candide sequence layer P1 (Bietti and Molari, 1994), at 20.9 ka cal BP at Trene, layer BI (Broglio 578 and Improta, 1995), and at a later range of 19-18.7 ka cal BP southward at Grotta Paglicci layers 579 13d, 13b and 12a (Palma di Cesnola, 2001) and Riparo Taurisano, spits 22-6 (Bietti, 1979). 580

Correspondingly, the chronological position of the lower boundary of the late Epigravettian is still 581 582 far from being secured. This second part of the Epigravettian is punctuated by increasing innovations in lithic production especially in the time span between 15 and 11.5 ka cal BP which is 583 584 better investigated than others (Bertola et al., 2007; Montoya and Peresani, 2005; Fontana et al., 2015; Montoya et al., 2018). Currently, lithic assemblages record the lack of shouldered points at 585 Baracche (Marche area) and Campo delle Piane (central Apennines) at 18.4-17.9 ka cal BP. Both 586 these open-air sites were extensively excavated (Olive, 2017; Peresani et al., 2005), thus yielding a 587 large amount of lithic artifacts with common tools and hunting implements. A later chronology is 588 provided by Tagliente rock-shelter in the Venetian Prealps, where the lowermost lavers of the 589 590 Epigravettian series dating back between 17 and 16 ka cal BP, attest the presence of sporadic items 591 of this typology (Bartolomei et al., 1982; Fontana et al., 2012, 2015, 2018).

592 Trends driving responsive technology in tool making might have been encouraged by the possibility
593 to exploit Alpine territories previously inaccessible offered by the LG climatic and environmental

changes (Bertola et al., 2018). However, it is still unclear when changes in the technological know-

bow occurred during the beginning of the late Epigravettian in the GAPR. Although there are traces

- referring to the presence of hunter-gatherers on both edges of this vast region, the currently
- 597 available evidence remains too sparse yet.
- 598

3.2. The Gravettian-Epigravettian settlement landscape: geographic coverage, chronology and behavioural evidence

601 Including sparse surface findings and open-air sites, most of the Gravettian – Epigravettian record

in the GAPR ranges from very close to the present-day coastline (Vlakno cave, 30 m amsl) up to

close to the Northern Apennine watershed (Piovesello, 870 m amsl), with the highest frequency

604 between 135 and 350 m amsl (Tab. 2, Figs. 3 and 9).

605 TABLE 2 ABOUT HERE

606

607 **3.2.1. Factors of bias**

Speculating about the organization of a settlement system extended in a now submerged geographic 608 zone like the Adriatic Plain could be meaningless due to weakened reliability of any proposed 609 scenario. The loss of a large continental land extent due to the rise of the sea-level during 610 Termination I was the most relevant change in the geographic setting of the GPP, leading to the 611 submersion of the Adriatic Plain. The incision of the Alpine alluvial megafans led to the 612 downstream formation of LG fans (Fontana et al., 2014a) alongside with the Apennine alluvial fans, 613 which also grew over the LGM plain (Amorosi et al., 2016). Wetlands and lowlands patterns on 614 marine coasts or around lakes and marshes, riverside forests, desert landscape were all potentially 615 settled environments, the exploration of which is prevented to us. Furthermore, also the paucity of 616 617 sites older than 14 ka cal BP, as it has been revealed in many traits of the GAPR and especially along the foot of the Northern Apennines or in caves in the Dinarides (Vukosavljević and 618 619 Karavanić, 2017), could be interpreted in a contrasting way: should it be viewed as an expression of sparseness human population compared to the later periods or as a lost of evidence determined by 620 621 intensive erosion and submersion? These factors contributed to set up an incomplete picture of a far broader land-use, although the archaeological evidence provides a basis to infer coherent patterns of 622 623 local settlement systems.

A representative case is the northern Apennines, on the southern margin of the Po Plain, where 624 despite extensive surveying along the low terraces, no comparable archaeological evidence has been 625 documented. This makes the record extremely patchy and should suggest that this belt was 626 characterised by a dearth of settlements through all the Upper Palaeolithic (Lenzi and Nenzioni, 627 1996). However, land surface processes have been invoked in the above chapter as a bias factor 628 responsible for the absence of human traces in large areas, like this sector of the Apennines. The 629 landscape is shaped on mainly poorly lithified claystones, sandstones and marlstones, while caves 630 and shelters are limited to the karst complex of the Gypsum Ridge with fillings producing the only 631 Upper Palaeolithic record currently dated (ex. Cava a Filo; Paronuzzi et al., 2018b). In the more 632 external low hills and foothills huge colluvial and alluvial deposits deeply sealed the archaeological 633 sites. Surface findings are extremely sporadic in the numerous clay and sand quarries in the area. 634 One example is the Fornace San Damiano site in the Savio Valley, where a late Gravettian -635 636 Epigravettian site was found, in a quarry, several meters below the ground surface and was partly excavated. Among the artefacts found at this site, there are blades made of Umbria-Marche Scaglia 637 638 Rossa chert. This site attests human shifts along the Apennines slope between Marche and Romagna (Guerreschi and Veggiani, 1983). 639

An additional factor of bias relates to the inhomogeneity of the resolution of archaeological investigations carried out since the 50's of past century, when sites have been discovered in intensively surveyed zones along the eastern Alpine range and foreland, on the Apennines foothills range, in the Karst, in Istria and Dalmatia. Starting from the 80's, new Gravettian and Epigravettian sites have been added to this heritage, only a part of which has been indeed investigated using modern standards and multidisciplinary practices. As a consequence, archaeological evidence at the northern and middle rim of the Adriatic basin is affected by variability in the density of

archaeological and osteoarchaeological materials as recorded at a number of sites.

The sites excavated until the 70's provided a lot of evidence and sometimes resulted in an

abundance of findings (see Malez, 1987; Palma di Cesnola, 2001, Bertola et al., 2007,

650 Vukosavljević and Karavanić, 2017 for lists and critical refinements). However, some uncertainties,

due to diversity in the documentation of the archaeological record, arose regarding the exact

provenance and stratigraphic position of the finds, and the lack of dating or of selective data

653 collection. Moreover, some of these sites have been studied with major detail with respect to others,

thus creating a bias in the comparison with contemporary sites. Part of these still requires in-depth

analyses, new sampling for geochronological data and re-assessment of faunal assemblages to avoid

underestimation in the accuracy of typo-technological contextualisation (Mussi and Peresani, 2004).

As an example, new chronometric data are needed in order to assess the consistency of the ¹⁴C 657 chronological gap between the northern and the southern early Epigravettian sites previously 658 claimed by Broglio (1997) to support this technocomplex spread in later times to southern latitudes. 659 Another concern is the reliability of the cultural assemblages coming from the stratigraphy of 660 Šandalja II, a cavity in the Karst situated about 4 km north-east of downtown Pula in Istria. The 661 sedimentary succession was divided into eight units from layer H to layer A, with units C and B 662 divided into three subunits respectively, in addition to interface units (Malez excavations 1962-663 1989; Malez, 1979; Miracle, 1994-1995; Karavanić 2003; et al., 2013). According to old ¹⁴C dates 664 and cultural content, layer C/d at the base of unit C should belong to early Epigravettian (Karavanić 665 et al., 2013), while new but unpublished dates place layer C/d and the entire unit C into the late 666 Epigravettian (Miracle and Brajković, 2013). Lithic material from Layer D results from mixing of 667 both Aurignacian and Epigravettian elements (Karavanić et al., 2013). Furthermore, one of the two 668 dated samples from Aurignacian levels, is consistent with the Epigravettian and also suggests that 669 some mixing of material between different units took place (Richards et al., 2015). 670

671

672 **3.2.2. Distribution of the radiocarbon dates**

Except for some sparse surface findings and very few open-air sites, most Gravettian -673 Epigravettian sites in the GAPR were radiocarbon dated to the LGM chronological range (Tab. 2 674 and Fig. 6). Aside Piovesello, Riparo Broion, Stria, Rio Secco, Ponte di Pietra, Paina, Trene, Riparo 675 Tagliente, Romualdova Pećina and Campo delle Piane, only one date is available for each site or 676 layer from multilayered archaeological sites. Charred wood is the most dated material, followed by 677 animal bone, human bone (Tagliente), and organic silt associated with charcoal (Fonte delle 678 679 Mattinate). When additional dates were produced on bulk samples from palaeosoils (Fonte delle Mattinate), we excluded the date from the list. Primary reference literature does not report any 680 information neither about the xilotomic determination for charred wood samples (with the exception 681 of Büs dei Lader: Larix), nor about the taphonomy of animal bones (natural or anthropogenic 682 origin?). For most contexts, dispersed charcoal fragments were collected from archaeological 683 layers, with only few cases documenting sampling from fire-places (Riparo Broion, Campo delle 684 685 Piane) or from primary anthropogenic structures next to fire-places (Piovesello). Most dates were made using AMS technique, some using conventional technique, producing large deviation ranges. 686 The dates cover with discontinuity the LGM range, being the Pećina kod Rovinjskog Sela 1 (Pećina 687 Cave near Rovinjskog Selo 1), Piovesello, Grotta Broion and Riparo Broion, Rio Secco and Fonte 688 delle Mattinate positioned in the 33-29 ka cal BP interval. Radiocarbon chronology at Grotta 689

Fumane in the Lessini Mountains marks one of the oldest range ever recorded in Europe for an 690 early Gravettian industry and it is currently under discussion. Sporadic lithic artefacts, backed 691 bladelets and one Vachons point were discovered in association with an extended accumulation of 692 charcoal in layer D1d, embedded in the detrital macro unit D, whose deposition filled-up the main 693 entrance of the cave (Falcucci and Peresani, in press). Following this first group of sites after a gap 694 of few thousands years, human presence is testified on the Berici Hills, the foot of the Marche 695 Apennine and in the Karst, starting from 25 ka cal BP in the late/final Gravettian and all along the 696 early Epigravettian until 21 ka cal BP. Dated sites are very sparse in the three following millennia, 697 provided by only one site in the Berici Hills (Stria) and in Northern Dalmatia (Vlakno) and by the 698 exception of Büs dei Lader, a small cavity in the Prealpine foothills west of the Garda glacier front. 699 Although the charcoal fragment from Büs dei Lader was determined as *Larix*, its association with 700 the only artifact found in 1956 during a survey remains uncertain (Biagi, 2000). Starting from 18 ka 701 cal BP, late Epigravettian groups settled at the foot of the Marche Apennine and then in Istria and 702 inland. Interestingly, after the collapse of the Garda glacier, human groups frequented persistently 703 the foothills of the Veneto Prealps (Tagliente) and inland in Western Mountain Croatia (Zala). 704 Given this distribution of the archaeological dated evidence across the LGM, the peopling of the 705 706 GAPR will be examined basing our assumptions on the currently available and original information about the use of the ecological and petrological resources by the Gravettian – Epigravettian hunter-707 708 gatheres. Four main cultural-temporal ranges will be considered to facilitate our view on how the use of this vast land evolved: 32-29, 26-23, 23-19, 18-16 ka cal BP, corresponding approximately to 709 710 the early Gravettian, the middle (evolved) and late (final) Gravettian, the early Epigravettian and the earliest part of the late Epigravettian. The lack of dates between 29 and 26 ka cal BP does not 711 support a complete scenario of settlement dynamics during the Gravettian. 712

- 713 FIGURE 6 ABOUT HERE
- 714

715 **3.2.3. Early Gravettian**

A paucity of sites features the Gravettian since its oldest phase (Tab. 2, Figs. 6 and 9a) leaving the
middle (evolved) phase ephemerally recorded by archeological evidence. Data currently available
are from Piovesello and Fonte delle Mattinate on the Apennine watershed, Grotta Broion and
Riparo Broion in the Berici Hills, Rio Secco in the Carnic Prealps and Pećina kod Rovinjskog Sela
1 in Istria. All together, these sites record human presence at the edge of the settled landscape.
Piovesello dates to 30 ka cal BP and is an open-air site located at 870 m amsl on the edge of a
shallow wet basin, in an arid cold environment slightly above the timberline, climatically correlated

to GS-5 (Peresani et al., 2018). The site attests short-term frequentations of a small group mostly
equipped with raw blocks of red radiolarite collected a few kilometres away (Peresani et al., 2018).
By contrast, a handful of finished artefacts have further provenance, suggesting long-range mobility
from south-eastern France. Multiple refittings are ascribable to complete reduction sequences on
local raw material, with prevalence of maintenance flakes and blades and maintenance products,
underrepresentation of end-products and very few retouched tools (Peresani et al., 2018; Zangrossi
et al., 2019).

Grotta Broion yielded a handful of blades, bladelet waste products and a few retouched tools from 730 layers C, D and E in the main cavern (Sala Grande) and in a small lateral cavity (Grottina delle 731 Marmotte) (Leonardi and Broglio, 1951, 1954). Riparo Broion was settled before and in the same 732 chronological range as Grotta Broion. Typological features of the backed points and backed 733 734 bladelets found in layer 1c suggest their attribution to the Gravettian (De Stefani et al., 2005). Typological imbalance in assemblages in layers 1a, 1b and correlate, plays in favour of gravettes 735 and *microgravettes* and backed bladelets and, in addition to the presence of impact fractures on 736 these artifacts, points to interpreting this settlement as strictly related to hunting parties (De Stefani 737 et al., 2005). The previous attribution (De Stefani et al., 2005) of these layers to the early 738 Epigravettian was based on the presence of fragmented shouldered points, unifacial leaf pieces and 739 740 one radiocarbon date (UtC-10506). This was challenged by the same authors (De Stefani, pers. comm), who marked out typological similarities and differences respectively for gravettes at 741 742 Paglicci cave (Palma di Cesnola, 2004) and shouldered points at Paina, Trene and Buso Doppio caves. Further dissimilarity raised from noting that the chert used for should ered points at Riparo 743 744 Broion is of local provenance in contrast with the exotic material used at Paina, Trene and Buso Doppio. Grotta Rio Secco attests ephemeral frequentations, represented by few common tools (one 745 end-scraper, burin-cores), backed points and bladelets recovered sparse in layers 4 and 6 where 746 remnants of fire-places were also brought to light (Peresani et al., 2014). 747

The early Gravettian record appears too ephemeral also in Western Dalmatia and Istria to estimate
the nature of human presence. However, systematic excavations carried out between 2014 and 2018
at rockshelter Abri Kontija 002 on the northern side of the Lim channel in the western part of Istria,
yielded consistent archaeological evidence (Janković et al., 2015). This is represented by traces of
fire and burnt bones, faunal remains, ochre and several thousand of lithic artifacts and small chips.
Most common retouched types are backed bladelets and marginally retouched bladelets.
Radiometric dates (unpublished, I. Janković) confirm this was one of the earliest sites with backed

tools in the eastern Adriatic. Pećina kod Rovinjskog Sela 1 is located in the close proximity of

Romualdova pećina and Abri Kontija 002. Evidence of Gravettian frequentation represented bylithics, faunal bones and marine shells was produced from a survey in 2007.

758 A context partly comparable to Piovesello has been reconstructed from geoarchaeological 759 investigation on the Marche Apennines watershed at Fonte delle Mattinate on the Colfiorito plateau, where evidence of early Gravettian frequentation has been related to the interval between GI-5 -760 761 HE3. Archaeological data point for a camp, where the acquisition and processing of cherts were aimed to accomplish immediate tasks. Worked or semi-worked products were introduced by 762 763 hunther-gatherers that inhabited this plateau for short term, recurrent, frequentations. Further later traces of frequentation date to HE3 and relate to harsher physical and ecological conditions 764 765 constraining human mobility in the innermost zone of the central Apennine (Giaccio et al., 2004; Silvestrini et al., 2005a). 766

767

768 3.2.4. Middle (evolved) and late (final) Gravettian

769 The middle (evolved) and late (final) Gravettian record is ephemeral in the north Adriatic rim (Fig.

9b). In the Berici Hills, similarly to the Gravettian at Riparo Broion, typological imbalances are

dominated by backed points at Paina (layer 7), Trene and Stria caves, settled probably later. At

Cava a Filo, in the central section of the Northern Apennines (n. 27 in Fig. 3), of the

palaeontological amount of large artiodactyls, few *Bison priscus* bones grooved by cut-marks

associated with a few lithic implements point for human frequentation of this low altitude hilly

175 landscape not later than 24.2 ka cal BP (Paronuzzi et al., 2018b).

776 More to the south, in proximity of the western margin of the AP, the late Gravettian is recorded in the low hills of the external belts of the Apennines (Broglio et al., 2005). Archaeological evidence 777 points to an exclusive presence of open-air sites, close to streams and major rivers, at the lower end 778 779 of gorges. Such sites were devoted to extractive and productive activities undertaken during shortterm visits. The set of available radiocarbon dates, for instance, constrains the occupation of Ponte 780 di Pietra and Fosso Mergaoni sites between 25.2 and 20.9 ka cal BP and between 22.5 and 21.4 ka 781 cal BP. Ponte di Pietra is situated along the river Misa, in a district plenty of excellent lithic 782 resources (Lollini et al., 2005). Fosso Mergaoni is mainly featured by two groups of lithic 783 workshops scattered on the alluvial ground. The spatial pattern with intra and inter-workshop 784 refittings, the paucity in retouched implements, the technological composition of the lithic artifacts 785 concentrations, the low incidence of use-wear related to the acquisition of alimentary resources and 786 to the processing of animal resources observed on a sample of artifacts, prove that the site was 787 788 functionally aimed to lithic production. Presumably, it was an area nearby a camp or part of a

settlement system related to the fluvial basin and its lithic resources (Cancellieri, 2015; Silvestrini et
al., 2005b; Ziggiotti, 2007). At both sites, lithic sets define the existence of lithic workshops in
proximity of possible dwelling areas. These include core shaping flakes, cores, laminar products
and different by-products resulting from the production of large blades, blades and bladelets from
chert nodules collected very close to the site. Technological composition, rare retouched
implements and spatial patterns, are indicative of specialized tasks consisting of the extraction and
knapping of fine-grained chert nodules (Cancellieri, 2015).

796

797 **3.2.5. Early Epigravettian**

798 Additional data are available for the early Epigravettian along both the Adriatic sides (Fig. 9c). In the Berici hills, the lithic industries consistently include a number of end-products like blades and 799 bladelets, shouldered points and *microgravettes* backed points. Minimal archaeological remains 800 801 have been recovered in the same string of caves and rockshelters previously settled during the Gravettian: Trene, Paina, Stria and Buso Doppio. Typological assemblages are dominated by 802 weapons for huntings (backed points and backed bladelets) together with unretouched blade and 803 bladelet blanks. Shouldered projectile points found at Paina and Trene bear impact scars, which 804 consistently provide hints for interpreting these contexts like short-lived campsites and hunting 805 stands (Broglio et al., 1993; 2009). At Buso Doppio Broion, recent excavations brought to light a 806 sequence where the uppermost layer 1tt.1I and reworked sediments yielded backed and shouldered 807 points (Romandini et al., 2015). According to the radiocarbon date, the presence of fragmented 808 shouldered points and of unifacial leaf pieces mentioned above, Riparo Broion was settled during 809 the early Epigravettian (De Stefani et al., 2005). A marginally retouched point is the only 810 811 archaeological find recovered at Büs dei Lader (Biagi, 1976). No data on the early Epigravettian settlement at Stria Cave have been produced yet. 812

The site Madonna dell'Ospedale lies on a fluvial terrace along the Rudielle stream valley, one of the 813 incisions which dissects the Cingoli Mountain ridge (Marche Apennines). Chert in this zone, 814 especially from Maiolica and Scaglia, is of the most excellent in the Marche Apennines. The site 815 has been culturally attributed on a tecnological and typological basis (shouldered points) and 816 interpreted as specialized for the production of blanks and the manufacture of hunting weapons 817 (Silvestrini et al., 2008; Cancellieri, 2015). In the north-western Balkans, the earliest spread of the 818 early Epigravettian comes from Šandalja II. In the Slovenian karst, reference sites for the early 819 Epigravettian are Zakajeni Spodmol, Ovčja Jama, Županov Spodmol and Jama V Lozi (with one 820 shouldered point) (Montet-White, 1996). A shouldered point was found at Romualdova pećina, 821

another site on the Lim channel in Istria also known for cave paintings likely attributed to the 822 Aurignacian (Ruiz-Redondo et al., 2019). Similarly to the Berici area, cave and sheltered sites are 823 generally interpreted as temporary encampments located along mobility routes used by small groups 824 of hunters, which is suggested by the limited amount of tools and the ephemeral indications of 825 knapping activity. In some cases, like at Županov Spodmol, Epigravettian groups reached the cave 826 equipped with finished tool kits as well as some cores that were further exploited on site. In the case 827 of Ovčja Jama, a more intensive use of the site is documented, along with a possible longer-term 828 occupation (Montet-White, 1996). 829

More to the south, Vlakno cave locates on the northwestern side of Dugi Otok Island, the biggest and longest of the Zadar archipelago. The sedimentary sequence has produced evidence of human frequentations dated from the late LGM until the end of the Holocene (Vujević and Parica, 2009; Vukosavljević et al., 2014; Cvitkušić et al. 2018), and embeds the Neapolitan Yellow Tuff in its central part. The composition of the lithic and faunal assemblages from layers 27-33, sealed by the tuff, points to an intensive use of the cave. Backed bladelets and blades, and backed points largely prevail on the other tool types, despite excavated in a limited survey (Malnar, 2017).

837

838 **3.2.6. Late Epigravettian >16ka BP** (Fig. 9d)

The evidence from Riparo Tagliente is more consistent than the sites described above. This site 839 attests the first re-occupation of the south-eastern Alps at the end of the LGM, starting from 17 ka 840 841 cal BP, in a steppe-forest environment with increased density in conifers at 16.5 ka cal BP (Ravazzi et al., 2014). The favourable position of the site at the crossway between different ecotones and its 842 location along the corridor of Valpantena giving access to the Lessini plateau and the inner Alps 843 have enhanced its intense occupation along time (Fontana et al., 2009). All late Epigravettian layers 844 document an intense activity of exploitation of the Lessini abundant chert outcrops and ochre 845 deposits (Fontana et al., 2015; Cavallo et al., 2017), while in the area protected by the over-hang of 846 the shelter several dwelling structures were uncovered (Fontana et al., 2018). Tagliente has also 847 vielded one of the most important Epigravettian collections of tools made of animal hard materials 848 and ornamental objects, as well as a series of mobile art objects and a burial dated to 16.6-15.5 ka 849 cal BP (Guerreschi and Veronese, 2002; Gazzoni et al., 2013). 850

In southeastern Istria, Ljubićeva pećina cave is a multistratified site with lithic artifacts represented
by blades, bladelets, backed blades, bone tools and other finds (Percan et al., 2008; Simonet, 2013;

Janković et al., 2015). More inland, ca. 50 km acf from the present-day coast, Zala cave locates

between the eastern Peri-Pannonian and western mountainous Croatia, where the Pannonian Plain is

- closest to the Adriatic Sea. Short-term human frequentations are recorded by a small amount of
- 856 lithic artefacts. Blades are produced off site, backed bladelets are the most frequent tool type,
- 857 endscrapers and other domestic tools are also present, suggesting that different activities were
- carried out during short stays (Vukosavljević et al., 2015). Aside the radiocarbon date, no detail on
- human frequentation at Romualdova are currently known.
- Baracche lies on a Late Glacial gravelly alluvial terrace along the same incised valley of Madonna
 dell'Ospedale at the foot of the Cingoli Ridge. This open-air site includes lithic workshops aimed to
 the exploitation of local chert nodules, as it has been inferred from the litho-technological features,
- the structures and the refittings (Peresani et al., 2005).

864 Campo delle Piane CDP 7 lies on a Late Glacial alluvial terrace of the Gallero creek, a tributary of 865 the Tavo River, in a hilly landscape of the Abruzzo fore-Apennine. These terraces were extensively 866 settled, and human occupation in CDP 7 correlates to a pedogenetic phase developed during the 867 Greenland Stade 2b in an open landscape with sparse pine trees. Interpretation of different sources 868 of archaeological evidence points to an open-air site organised around fire-places associated to 869 lithic workshops (Olive, 2017).

870

871 **3.3. Exploitation of faunal resources**

Only a handful of sites has produced zooarchaeological data testifying for game hunting. This is the 872 873 case of caves in the Berici Hills, where bone remains attributed to ungulates and carnivores record the exploitation of resources available in the surroundings. Traces of human modification have been 874 observed on cervids (Cervus elaphus and Alces alces), caprids and wild boar as well as on cave 875 bears (Ursus spelaeus, sensu lato) at Paina, Trene and Buso doppio Broion (Romandini and 876 877 Nannini, 2012; Romandini et al., 2015). Cut-marks on several bear remains enable a reconstruction 878 of the main steps of fur recovery and the butchering process (Romandini and Nannini, 2012). In Istria and western mountanious Croatia, Šandalja II and Zala caves are the only source of 879 zooarchaeological evidence. At Zala, hunters targeted red deer and moose more than auroch (Bos 880 primigenius). Similarly to the Berici Hills caves, carnivores like brown bear (Ursus arctos) and 881

wolf (*Canis lupus*) were processed, as attested from butchery marks (Radović, 2015).

- 883 At Šandalja II, layer C/d gave evidence of human exploitation of horse, large bovids (more aurochs
- than bisons), large cervids and small carnivores like fox (*Vulpes vulpes*) and badger (*Meles meles*).
- 885 The top of layer C records continuity in the exploitation of this game, the moose being included
- among large herbivores and wild cat among the small carnivores (Miracle, 2007). Furthermore,

isotopic analysis of carbon and nitrogen bone collagen of faunal and human remains from late 887 Epigravettian layers, identifies freshwater fish in human diet as the main protein sources, although 888 large herbivores are represented at the site (Richards et al., 2015). A red deer dominated faunal 889 assemblage with chamois, ibex and few horse, hare, and fox was the exploited game around Vela 890 špilja cave (Lošinj Island), similarly to Pupićina and Nugljanska caves in the Kvarner region, in the 891 lower layers, undated, but preceding the interstadial warming. In addition to these sites, ephemeral 892 evidence is reported from Vešanska cave with assemblage consisting of red deer and marmot 893 (Miracle, 2007). 894

895

4. Human mobility across the Great Adriatic-Po Region inferred from petroarchaeological evidence

One of the clearest evidences of a large scale network of contacts between hunting bands and/or of 898 their high mobility across the GAPR is given by petrographic data on the provenance of lithic raw 899 materials, complemented by similarities in lithic industries from sites in north-eastern Italy, 900 Slovenia and Istria (Broglio, 1994). However, our knowledge on the use and circulation of cherts 901 from the GAPR is sparse and biased by differences in the development of investigations. Some 902 information is available in the literature for most of the sites taken into account in this work and 903 additional data are provided from new studies presented here. For the purpose of this investigation 904 aimed to achieve indicators of chert provenance, petroarchaeological data are presented only at 905 qualitative level. For access to computations of each lithic assemblage see references in tables 2 and 906 4. 907

908

909 4.1. A view on the distribution of chert bearing rocks along the GAPR

910 In the Southern and Eastern Alps, the Dinarides and the Apennines, the knappable lithic resources are represented mainly by cherts and radiolarites which differ in lateral and stratigraphic 911 distribution according to the regional palaeogeographic domains. Southern Alps, Dinarides and 912 Eastern Alps share a common paleogeographic and tectonic evolution since late Triassic and each 913 domain was composed of different sub-domains such as shallow-water platforms, submarine 914 915 plateaus and deep basins. Detailed regional studies, mainly aimed to recognize in the field the palaeogeographic borders of the major structural elements, the main depositional features of the 916 917 basins were reconstructed both in time and space (e.g., Auboin, 1963; Bosellini, 1965, 1973; Winterer and Bosellini, 1981; Bertotti et al., 1993; Santantonio and Carminati, 2011; Schettino and 918

Turco, 2011). This approach allowed identifying certain regional lithic raw materials markers or
"guide-fossils" such as, for example, the Eocene Scaglia Rossa chert of the Umbria-Marche
Apennines.

In the Neotethys basinal domains of the Southern Alps, there are thick Jurassic-Eocene cherty series 922 (Calcari Grigi, Rosso Ammonitico, Maiolica, Scaglia Variegata Alpina, Scaglia Rossa, Scaglia 923 Cinerea) with abundant chert nodules and beds, some of them with exceptional rheological 924 properties due to their fine texture and homogeneity. Over the submarine plateaus, the series are 925 much more condensed and with different features both in sedimentary sequences and chert 926 properties. In adjacent areas such as the Karst or Dalmatia, where sea depths were shallower during 927 928 the Jurassic and Cretaceous (Friuli shelf), cherts are scarce and confined to few epicontinental basins. The Umbria-Marche area (easternmost Northern Apennines) was a different sector of the 929 930 epicontinental (Adria microplate) basinal domain of the Neothetys, where very thick cherty sequences developed, with some differences with respect to the ones of the Southern Alps (Fig. 7 931 and Tab. 3); this basin was delimited to the south by the Ancona-Anzio line, separating from the 932

933 Lazio-Abruzzi shallow shelves.

934 FIGURE 7 AND TABLE 3 ABOUT HERE

Since the Oligo-Miocene, at the foot of the Alps, the Venetian-Friulian foreland basin developed 935 (Massari et al., 1986; Stefani et al., 2007) and the cherts, eroded from the Southern Alps, were 936 redistributed in the clastic wedge; the coarser are preserved in the Montello, and other 937 conglomerates (Massari et al., 1974). At the same time, at the front of the Apennine chain, very 938 deep foreland basins formed, and the distribution of the Oligo-Miocene cherts in the northern 939 Apennines is mainly linked to the evolution of these basins NW-SE or even N-S oriented. In this 940 941 case, most of the cherts are of Oligo-Miocene age and formed in very deep foreland basins. Each of the quoted paleo domains was influenced by specific sedimentary processes and dynamics and 942 developed at different times, thus giving distinct features to each group of cherts. 943

Cherts in these regions crop out in the sedimentary rocks as nodules or layers, different in size, and 944 colour, texture, structure, paleontological content, silicification degrees and tectonic integrity 945 (Bertola, 2012, 2016). In the less deformed areas, chert layers or nodules are easily collectable near 946 primary outcrops but also as cobbles or blocks transported in the valleys bottom, along stream-beds 947 and alluvial deposits. Blocks and pebbles have different utility in function of the average size, 948 which is quite big and suitable for a range of sized blade and bladelet production (Cancellieri, 949 2015). Small sharp edged blocks, suitable for bladelet making could be collected in slope waste 950 deposits and soils. 951

In the Karst and Dalmatia, cherts are scarce and confined to few epicontinental basins. 952 Allochthonous siliceous clastic deposits of the Triassic, devitrified tuff and siliceous claystone 953 (green stone), and only a minor degree radiolarite and chert, occur on the northern side of the 954 Velebit Mountain (Sokač, 2009) and in primary exposures in the hinterland of Dalmatia in the 955 vicinity of Muć (Šćavničar et al., 1984), as well as on the Island of Palagruža (Korbar et al., 2009). 956 Upper Jurassic chert of poor quality to knapping are documented on islands in Dalmatia (Velić and 957 Vlahović, 2009). Conversely, upper Cretaceous (Cenomanian – Maastrichtian) chert of markedly 958 different quality is provisionable on limited outcrops scattered throughout Dalmatia and on the 959 Dalmatian islands of Korčula, Brač, Dugi Otok and in the subregion Zagora (Fuček, 2009; Perhoč, 960 2009, 2020). Chert is largely more frequent in the Lower to Middle Eocene Foraminifera limestones 961 and in the Middle to Upper Eocene Flysch exposures than in the upper Cretaceous one (Sikošek, 962 1971; Perhoč 2020). Also, in Istria chert is embedded in Cretaceous limestone (Šikić and Pleničar, 963 1975; Polšak, 1970; Šikić and Polšak, 1973), exceptionally in Jurassic deposits of plate limestone 964 (Polšak and Šikić, 1973). Small outcrops are scattered through the region, with highest 965 966 concentration in the southern part on the Premantura Peninsula near Medulin and Bay. Primary chert outcrops also distributes in central Istria and on mountains Učka in western and Ćićarija in 967 968 northern Istria.

There are no primary radiolarite sources in Dalmatia and Istria. Allochthonous sources have been 969 recorded in gravel alluvial deposits of Reka River in the Primorska-Notranjska regions of Slovenia 970 (Šikić and Pleničar, 1975; Perhoč, 2020) and in glacial-fluvial sediments near Ozalj in Croatia, 971 reworked from Kupa River (Perhoč, 2020; Vukosavljević et al., 2015). Pebbles of radiolarite, 972 together with chert and quartz sandstone are a fraction of Eocene conglomerates in the Ravni kotari 973 area in Dalmatia (Vlahović and Velić, 2009). Extensive primary and secondary sources of 974 radiolarite are part of the Ophiolite complex of Central Dinarides, in the Banovina region (Šikić et 975 al., 2009) and in Bosnia and Herzegovina (Šegvić et al. 2014; Perhoč, 2020). Because during the 976 LG it could transport radiolarite pebbles at least down to the islands of Hvar and Korčula, the 977 Neretva River is of particular interest among the Bosnian rivers (Sikora et. al., 2014; Perhoč, 2020). 978 979

980 4.2. Petroarchaeological evidence from Gravettian-Epigravettian sites: materials and methods

981 Investigating human mobility across the GAPR requires detailed determinations on the knappable

982 materials used at Gravettian - Epigravettian sites located at far distance from the primary

983 workshops. We selected 27 sites: 16 were previously petroarchaeologically investigated in the last

two decades; six are the subject of this study, and five are left outside from this study for reasonsdue to unaccessible or not yet analysed material (Tab. 4).

986 Geological surveys conducted previously the present work have produced qualitative data on the 987 distribution and properties of the knappable rocks from primary outcrops and secondary deposits in representative type areas. Cherts have been studied with a geological approach, considered as part 988 of the outcropping formations, the latter ratified by the International Commission of Stratigraphy 989 and, for the Italian territory, mapped by the ISPRA. The systematic prospecting and sampling, 990 carried on since the 90's of the 20th century by one of the authors (SB) and other researchers of the 991 Ferrara University, on the Southern Alps and Northern Apennines, allowed to build a large and 992 993 diversified siliceous raw materials collection (lithotheque) stored in the Dipartimento di Studi Umanistici of the University of Ferrara. The lithotheque is widely representative both of the lateral 994 995 (areal) and vertical (stratigraphic) variations of the cherts in the different outcropping formations; it represents a powerful database for analysis and comparisons with the archaeological collections. 996

In addition to this lithoteque, this work has also considered two other raw materials collections. The 997 998 first from the Marche Apennines, in the Gola della Rossa e Frasassi Natural Park, where chert 999 sources were surveyed, mapped and characterized. Moreover, availability and suitability of cherts 1000 were tested through the sampling of selected areas and their classification in accordance with the flaking attitude (Cancellieri, 2015). This collection is stored in the Dipartimento di Studi Umanistici 1001 of the University of Ferrara as well. The second raw materials collection covers Istria and Dalmatia, 1002 where systematic researches on lithic collections and outcropping knappable rocks have been 1003 carried on in the last two decades (Perhoč, 2009; 2020). This lithoteque is stored at Zlatko Perhoč's 1004 1005 home, Mannheim, Germany.

1006 We attributed the archaeological cherts (lithic artefacts) to their respective geological formations through the analysis of diagnostic features such as: color, cortex features, petrographic textures and 1007 1008 structures, micropaleontology, mineralogy and rheology (i.e. Tab. 3, Fig. 8). Chert colors were compared with the Munsell Soil Color Charts® (Munsell Color, 2001) and the Rock-Color Chart® 1009 1010 (Geological Society of America, 1964). In a second step, the geographic provenance of the cherts 1011 was tentatively circumscribed on the basis of laterally variable features within the same formation. 1012 Important additional information was inferred by the presence, on the artefacts, of natural surface features (alterations on cherts and cortexes, patinas, rounding) referable to the collecting contexts of 1013 1014 the cherts like soils or paleosoils, slope, present stream channels and coarse alluvial deposits.

1015 We finally scrutinized under multivariable optical stereomicroscope (Optika SZ series, 45X with

- 1017 microfossils) of the geological and archaeological cherts. Additionally, we analysed with a
- 1018 mineralogy microscope (Olympus BX40) under polarized light the thin sections of some geological1019 cherts of the area.
- 1020 We determined microfossils using comparison atlas (Robaszynski and Caron, 1995; Bolli et al,
- 1021 1985; Premoli Silva and Sliter, 1995, 2002) and other references (among them Cita, 1964; Erba and
- 1022 Quadrio, 1987; Luciani, 1989; Sliter, 1989).
- 1023 FIGURE 8 ABOUT HERE
- 1024
- 1025 **4.3. Results** (Tab. 4 and Fig. 9)
- 1026

1027 Northern Apennine

Piovesello, Gravettian. In this site, the local red and brown radiolarites (Monte Alpe Cherts
formation, Ligurids, Jurassic) were maily exploited but it is also attested the introduction of few
finished hunting implements, domestic tools and one bladelet core made of chert from the AptFoucalquier basin (Vaucluse-Haute Provence, 300 km far), plus the in-site production of bladelet
blanks, retouching and re-tooling (Peresani et al., 2018) (Tab. 4 and Fig. 9a).

1033

1034 Venetian and Friulian Prealps

1035 *Grotta Fumane, Unit D, Gravettian.* Finished hunting tools, blades and bladelets record sporadic
1036 occupations of the cave and attest the exclusive use of the local resources from Lessini mountains
1037 (Bertola et al., 2018) (Tab. 4).

Grotta Rio Secco, layer 6, Gravettian. Chert has been provisioned in a radius of 50 km from this 1038 site in the Carnian Prealps where different Triassic to Cretaceous formations oucrop, uplifted and 1039 deformed from intense and still active tectonic activity: Buchenstein, Soverzene, Igne, Verzegnis, 1040 1041 Fonzaso, Maiolica, Scaglia Variegata Alpina, Scaglia Rossa. Well rounded cobbles are among the finest knappable material, collectable in the Tertiary Flysch and Molasse in the Carnian foothills 1042 1043 and redeposited after erosion on the Tagliamento end-moraine system and the Tagliamento, Isonzo and Cormor alluvial beds, originally included in the Tertiary deposits (Tab. 4 and Fig. 9a). Among 1044 1045 these cobbles, the most appreciable cherts belong to Maiolica and Fonzaso. Cobbles up to 6-8cm were exploited to produce bladelets or short blades. Longer blades were produced from cherts 1046

- gathered on the poorly tectonized outcrops of the Maiolica and Scaglia Variegata Alpina. Common
 tools such as scrapers are frequently made out of flakes or on by-products (Peresani et al., 2011).
- 1049 *Grotta Broion (layers C-E), Gravettian.* There are a few artifacts made with different chert types
 1050 from the Berici Hills and Euganei Hills (5-15 km) and the Lessini Mountains (25-50 km), the latter
 1051 chosen expecially for blade production (Bertola et al., 2018) (Tab. 4 and Fig. 9a).
- 1052 *Riparo Broion, US 1a-d. Gravettian.* Similarly to the Grotta Broion, the exploited raw materials
- 1053 comprehend regional chert types from the Berici, Euganei and the Lessini. There are many affinities
- both in raw material and typology (De Stefani et al., 2005; Bertola et al., 2018) (Tab. 4 and Fig. 9a).
- Grotta Paina, Sala Azzurra, layers 7 and 6, Gravettian and early Epigravettian. Both assemblages 1055 (Bartolomei et al., 1985) contain a few lithic tools (23 and 47 respectively) almost entirely made of 1056 allochtonous chert (78% and 89%; Broglio et al., 2009). Varieties belong to the Maiolica, Marne a 1057 Fucoidi, Scaglia Rossa, Scaglia Variegata (Tab. 3, Figs. 10.7 and 10.8) formations outcropping in 1058 the Umbria-Marche region (Tab. 4, Figs. 9b and 9c). There is no evidence of intra-site flaking or 1059 retouching of these allochtonous raw materials. The scarce Berici-Euganei chert artefacts are all 1060 unretouched and consist of blade and bladelet fragments but also cortical flakes and small flakes 1061 (debris), attesting sporadic flaking activities at the site. Four backed bladelet fragments are made of 1062 1063 excellent Lessini cherts of the Scaglia Variegata Alpina; these pieces were introduced finished onto the site (Broglio et al., 2009; Bertola et al., 2018). 1064
- Grotta Paina, Sala Terminale, layers B-C, 21-29 and 125, Gravettian and early Epigravettian?
 Similar to above considerations could be advanced for the excavations carried out in the Sala
 Terminale (Leonardi and Broglio, 1962). Upper layers are in great part reworked and contain *gravettes* and shouldered points comparable to the Grottina Azzurra series, layer 6. Lower layers
 contain fragmentary armatures without shouldered points, and are comparable to the Grottina
 Azzurra series, layer 7. The raw materials entirely come from the Umbria-Marche region (Broglio
 et al. 2009; Bertola et al., 2018) (Tabs. 3 and 4, Figs. 9c and 10.11).
- 1072 Buso Doppio Broion, layers 1 and RIM, early Epigravettian. Among the 46 studied artifacts
- 1073 (Bertola et al. 2018), 17 are made with allochtonous Umbria-Marche basin cherts, most of them
- shaped like backed and shouldered points together with a few unretouched blades and bladelets.
- 1075 Cherts show greater variability with respect to the previous described assemblages, possibly
- 1076 suggesting different or wider exploitation areas (Tab. 4, Fig. 9c). They belong to the following
- 1077 formations: Bisciaro, Scaglia Cinerea, Scaglia Rossa, Scaglia Bianca, Marne a Fucoidi and Maiolica
- 1078 (Tab. 3, Fig. 10.10). Lessini cherts are represented by seven artefacts, six of them retouched

1079 (backed tools) and one crested bladelet. The Berici-Euganei cherts artefacts (26) were also flaked
1080 on site to produce blade, bladelets and backed tools, but not the shouldered points. (Romandini et al.
1081 2015; Bertola et al., 2018).

Grotta Trene, layer B, early Epigravettian. Of the total assemblage (33 lithics), ten are retouched
tools: nine are made of allochtonous Umbria-Marche cherts (Scaglia Rossa, Maiolica and Marne a
Fucoidi) and one, a leaf point, of Scaglia Variegata Alpina from the Lessini. All the remaining
artefacts are unretouched and made of local cherts from the Berici Hills and Euganei Hills (19) or of
the Lessini (4) (Broglio et al., 2009; Bertola et al. 2018) (Tabs. 3 and 4, Figs. 9c and 10.9).

1087 Riparo Tagliente, layers (SU) 15, 15a, 13a, 13a alfa, 13a beta, 250, 300, 360, 307. Early Late *Epigravettian.* In these layers, among a dominant exploitation of the excellent local Lessini cherts, 1088 1089 recent studies have isolated a group of implements made on extra-regional cherts, quite all 1090 belonging to the Umbria-Marche basin Scaglia Rossa lithotypes absent from the same areas 1091 exploited by the late Gravettian and the early Epigravettian hunter-gatherers who settled the area of the Berici Hills. A total of 48 artefacts on Scaglia Rossa (mostly Eocene) and three on Calcari 1092 Diasprigni (upper Jurassic) Umbria-Marche cherts were identified (Tabs. 3 and 4, Figs. 9d and 1093 10.12). The assemblage includes 13 retouched tools (among which nine backed fragments, one 1094 burin, one endscraper, one truncated blade and one pointed piece), 35 unmodified blanks (including 1095 bladelets, flakes, semi-cortical blanks and maintenance elements) and three bladelet cores (Bertola 1096 et al., 2018). Allochthonous Apennine cherts reduce in number in the later times during the LG 1097 interstadial. 1098

1099 FIGURES 9 AND 10 ABOUT HERE

1100

1101 Karst, Istria and Dalmatia

Šandalja II cave, layer C/d, early Epigravettian. In our preliminary study, petrographic 1102 1103 determinations were not completed with computation of the overall assemblage of layer C. Raw materials from different paleogeographic areas have been identified, comprehending local (Istria) 1104 1105 but also more distant sources like the eastern Southern Alps (Friuli/Veneto) and very distant allochtonous ones (Umbria-Marche) (Tabs. 3 and 4, Fig. 11). Prealpine chert was possibly collected 1106 1107 as cobbles in the vast gravelly alluvial plains of the Isonzo and Tagliamento. Among these materials, Triassic (Ladinian) Buchenstein cherts, Jurassic Soverzene/Igne and Fonzaso cherts (Tab. 1108 3, Figs. 11.17 and 11.18) and probably also a kind of Maiolica (with bioturbations, typical of the 1109 Southern Alps) were identified as well. Among the local cherts, there are easily recognizable types, 1110

- 1111 deposited in shallow waters, with evident stripes (stromatolitic laminae, algae) often with a
- 1112 brecciated appearance. Regarding the lithic industry made on raw materials from Umbria-Marche,
- artefacts made on Scaglia Rossa (Eocene layers; Fig. 11.13) and Maiolica (Tab. 3, Fig. 11.15) have
- been also identified, including some shouldered points. Attributing additional lithotypes featured
- 1115 from fine crystalline gray to yellow color, and radiolarians and *Rotalipora* (Albian/Cenomanian)
- 1116 has been more problematic due to the existence of petrographic similitudes in cherts shared between
- 1117 the Umbria-Marche Apennine and the Southern Alps. For these types more detailed analyses will be
- 1118 required. Artefacts made of yellow fine crystalline chert with radiolarians and Rotalipora
- 1119 (Albian/Cenomanian) likely attributable to the Scaglia Variegata Alpina (Southern Alps,
- 1120 Friuli/Veneto regions) or to the Scaglia Bianca (Umbria-Marche) are also present in layer B/C.

1121 Romualdova pećina, no context, early Epigravettian. We identified chert of Umbria-Marche Scaglia

1122 Rossa on one shouldered point (Tabs. 3 and 4, Figs. 9d and 11.14).

- 1123 Vlakno cave, layer 32, early Epigravettian. Blade artifacts document exploitation mainly of eastern
- 1124 Adriatic chert, but also use of chert originating from Umbria-Marche Apennine and Venetian
- 1125 Prealps (Perhoč, 2020) (Tab. 4, Fig. 9d).
- *Zala cave, layers 97, 98, 100, 101 and 102, late Epigravettian.* All the artifacts were made using
 exogenous materials, given the nearest source positioned 30 km from the site along the gravelly bed
- of the Kupa River south of the town of Ozalj. Provisioning area extends south-east in the Likaregion and northern Dalmatia, and west of Istria and more far to the Veneto Prealps. The latter
- 1130 source supplied half of the artifacts (Perhoč, 2020; Vukosavljević et al., 2015) (Tab. 4, Fig. 9d).
- 1131 FIGURE 11 ABOUT HERE
- 1132

1133 Marche-Abruzzi Apennine

Fonte delle Mattinate, layer SU B27, early Gravettian. The exploited cherts are from the UmbriaMarche Scaglia Rossa and Scaglia Variegata, outcropping near the site, but also a coarse-textured
gray chert (Oligocene-Miocene flysch improperly called ftanite) not cropping locally, possibly
collected in the Tiber basin or in a northern area along the Apennine range where the CervarolaFalterona Unit outcrops (Silvestrini et al., 2005a) (Tab. 4, Fig. 9a). This exogenous arenitic chert
was used to produce a point.

1140 *Ponte di Pietra, layer SU 53-64, late Gravettian.* The exploited cherts totally consist of the Umbria-

1141 Marche Scaglia Rossa and Scaglia Variegata, outcropping near the site, but also different types of
Maiolica not cropping locally, possibly collected along the Misa stream gravel bed (De Stefani etal., 2005) (Tab. 4, Fig. 9b and 9c).

Fosso Mergaoni, late Gravettian. Cherts were collected few kilometers away from stream beds and
slope waste deposits in proximity of primary outcrops of Tertiary and Jurassic formations. The best
represented are Tertiary cherts of Maiolica, Scaglia Rossa and Scaglia Variegata provisioned as
large nodules and slabs (Cancellieri, 2015) (Tab. 4, Fig. 9c).

Madonna dell'Ospedale, early Epigravettian. No detailed data on the attribution of the raw material
units are available for the predominant blade and bladelet industry of this site. Its position on an
alluvial terrace along the left slope of a stream valley which dissects Cretaceous marly limestones
(Maiolica and Scaglia) points in favour of local collecting of chert nodules and slabs (Silvestrini et
al., 2008) (Tab. 4).

1153 *Baracche, late Epigravettian.* Similarly to the previous, the blade and bladelet industry of this site

has been macroscopically subdivided in raw material units, but no detailed studies have been done.

1155 Anyway, the exploitation of the local Maiolica and Scaglia cherts is very likely (Peresani et al.,

1156 2005) (Tab. 4, Fig. 9d).

Campo delle Piane CDP 7, Late Epigravettian. The lithic assemblage found in layer 24 is made of
Scaglia Rossa and Maiolica cherts provisioned in local gravel deposits and also in primary outcrops
in the surroundings at least 5 km to the west, in the Gran Sasso Massif (Olive, 2017) (Tab. 4, Fig.
9d).

1161

5. Collected on the sea shore: an overview on the circulation of marine shells beads

Perforated marine shells were found at Ponte di Pietra and Riparo Tagliente, the only sites on the 1163 western Adriatic that yielded gastropods and bivalves. The commonest species used during the 1164 Gravettian is Homalopoma sanguineum, an herbivorous gastropod associated with sea grassland 1165 (es: Posidonia) and rocky seabeds and distributed in the Mediterranean Sea from the intertidal belt 1166 1167 to 50 m of depth. Currently, it lives in a variety of pericoastal environments in the lower Adriatic, Ionian and Tyrrhenian Sea. It is the only species found at Ponte di Pietra, with nine specimens, all 1168 1169 perforated (Gurioli, 2005). Since the Uluzzian, but mostly in the Protoaurignacian, H. sanguineum 1170 is a shared cultural-symbolic element in Southern Europe and also in the GAPR as observed at 1171 Grotta Fumane (Peresani et al., 2019). This bright red colored appealing shell was selected for ornamental purpose also thanks to its morphology and size, as observed throughout most of the 1172 1173 Upper Palaeolithic in a vast area extending from the south-west of Europe to the Eastern

Mediterranean, up to the middle course of the Rhine River (Bosinski, 1999), and to the east of the 1174 Carpatians (Alvarez-Fernández, 2006; Vanhaeren and D'Errico, 2006; Morales et al., 2019; Perlès, 1175 2018; Nitu et al., 2019). Its use has been recorded on the Tyrrhenian side at Riparo Mochi (Stiner 1176 1999), Grotta di Castelcivita (Tassoni, 2019), Grotta La Cala (Tassoni, 2019) and Grotta Serratura 1177 (Martini et al., 2003) and along the eastern side of the Italian Peninsula at Grotta Cavallo (Arrighi et 1178 al., 2020). The Homalopoma specimens found at Ponte di Pietra testify the use of this gastropod at 1179 the end of the Gravettian. The thickness of the shell wall may have also been an important feature, 1180 as personal ornaments made of thicker shells might require greater manufacturing skills and time. 1181 The use of this species' shell decreases considerably during the Late Epigravettian, being replaced 1182 by Tritia sp. and Columbella rustica as the main ornamental components (Cristiani et al., 2014; 1183 Martini et al., 2003; Perlès, 2018). The oldest settlement phase of the Late Epigravettian 1184 1185 stratigraphic series of Riparo Tagliente (SUs 13a alpha, 13a beta and 300) shows a complex composition of the ornamental shell assemblage. The dominating shell is *Tritia* (more than 90%) 1186 with prevailing *T. neritea* followed by *T. pellucida*. All other species are either represented by few 1187 specimens each (Dentalium cf. inaequicostatum, H. sanguineum, Nassarius cf. pygmeus) or by just 1188 1189 by one item (Aporrhais pespelecani, cf. Neverita josephinia, Gastropoda indet., Glycymeris sp., Nassarius costulatus cuvierii). 1190 A shell beads assemblage was also discovered in the late Upper Palaeolithic layers of Zala, dated to 1191 the end of LGM. The assemblage consists of 15 marine Cyclope neritea perforated shells. A 1192 fragment of Pecten jacobaeus shell provides additional evidence for contacts between LGM coast 1193 and the inland where Zala is located (Vukosavljević and Karavanić, 2015). 1194 A variety of hard animal materials has been deliberately modified to shape beads. However, 1195 1196 investigations on these findings are still at an embrionic state, even long after their discovery. This

is especially the case of the seven atrophic red deer canines associated to Gravettian lithics at Grotta
Broion (Leonardi and Broglio, 1960). Aside deliberate polishing and perforations, at present there is
no further information on these teeth, as regarding the manufacture techniques or the possible use of
additional substances such as ochre and other residues. Two modified teeth of *Cervus elaphus* were
found in Šandalja layer C/d (Cvitkušić, 2017).

1202

1203 6. Discussion

1204 6.1. Human groups across the Great Adriatic–Po Plain: a questioned scenario

The ensemble of evidence illustrated in the previous chapters points to the GAPR as a suitable land 1205 for Gravettian and Epigravettian hunter-gatherers. The view that the mountain ranges and their 1206 forelands around the GPP could have provided profitable habitats for the subsistence of human 1207 populations was questioned several times since the end of the 80's of the 20th century. A major 1208 point of discussion regards the role played by the plain in facilitating the seasonal aggregation of 1209 bands from both sides of the sea. According to Mussi (1990), the gap in the early Gravettian 1210 archaeological record of Italy and the gradual disappearance of items like funerary goods or mobile 1211 art bringing complex symbolic significance observed up to the end of the Gravettian should be 1212 related to slackening in the social relations established among human groups, presumably correlated 1213 to the general decrease in population density. Southern Europe did not escape the consequent 1214 disruption of networks and disappearance of long-range social relationships. Isolated by the 1215 glaciated Alps, the GAPR was connected to the sparsely inhabited western Balkans, sporadically 1216 exploited by small groups. Mussi (1990) suggests, in disagreement to a more consistent evidence of 1217 repeated human frequentations at the multilayered sites distributed along the Tyrrhenian belt and in 1218 1219 the southernmost area of the peninsula, that the GAPR flatland was an arid and steppe-like environment delimited by instable shorelines and denudated landscapes at the foot of the mountain 1220 1221 ranges. According to this Author, the GAPR was not settled permanently because of hostile climatic and environmental conditions and too sparse resources to sustain movements of people (Mussi, 1222 2001). The Karst, at the north-eastern edge of the VFP and AP was also considered to be an 1223 inhospitable land during the LG, unforested and generally poor in vegetation, because of its 1224 1225 dryeness (Boschian and Fusco, 2007).

1226 Contrasting positions supported at times the view that the plain was rich in game, water and a variety of resources, especially along the water courses, across ecotones, around the lakes and on 1227 the coastal and estuarine environments, and thus attractive for human populations (Van Andel, 1228 1989; Shackleton et al., 1984; Bailey and Gamble, 1990). Based on archaeofaunal data from Istria 1229 and the Kvarner region (Miracle, 1994-1995, 2007), conceives this vast land as seasonally crossed 1230 by large migratory game. He arguments that all this game is representative of a rich and diverse 1231 mammal biome exploited by humans at the margins of the eastern AP and that the karstic inland 1232 was sporadically settled on a strictly seasonal basis and careful planning (Miracle, 1994-95). 1233

1234

6.2. Great Po Plain and Great Adriatic-Po Region ecological conditions and sustainability during the LGM

As highlighted above, previous ideas about the sustainability of the GAPR for hunter-gatherers are
somewhat conflicting. Hereafter, we examine the GAPR ecological pattern in view of the spatial
diversity of environmental resources in the LGM. Besides, we discuss the effects of the
environmental changes intervening in the LG.

In spite of the semiarid land expansion in the GARP lowlands during the late MIS 3 and MIS 2 cold 1241 1242 phases (Badino et al., 2020), meltwater discharge provided an extra-contribution to water resource available to the lowland ecosystems. Here, edaphic moisture stored by fine-grained sediments and 1243 reduced evapotraspiration triggered the development of wetlands (see Tab. 1, Fig. 2). A striking 1244 mosaic with contrasting treeless shrubby semidesert and short-grass steppes with highly productive 1245 1246 mires is envisaged for the lower megafan belt (around -20 to +100 m amsl). Water resources were enhanced by summer snow and ice melting implying increased biomass production and hunting 1247 1248 potential during summertime. However, in the lowstand AP, the availability of surface water and soil water regimes are debatable, due to uncertainties in reconstructing the hydrographic network 1249

1250 (Fig. 2, see section 2.1) and, most important, the watertable levels.

1251 The ecogradient linking the higher, coarse-grained megafans belt with the Alpine piedmont and the mountains can be traced thanks to the palaeoecological record (sections 2.1 and 2.2.) and, 1252 1253 remarkably, by consistent indications for modern ecological analogues in the mountain-piedmont systems of Central Asia (see Tab. 1, Fig. 4, and references herein). Several biomes existed along 1254 this ecoclimate elevational gradient, compressed in a space of a few tens of kilometers - from short 1255 grass steppes supporting a rich megafauna, to boreal forests with its resources; to alpine grasslands 1256 supporting ungulates; to cold rocky semideserts. Additionally, eco- and biodiversity were increased 1257 by bedrock variability, especially the extensive denudated limestone lands widespread in the GAPR. 1258 All these phenomena during the LGM triggered habitat diversification, along with karstic 1259 conservative habitats and stable climatic microrefugia (Dobrowsky, 2011). These contexts in the 1260 GPP sustained herbivores population, largely composed by the steppe bison (*Bison priscus*), 1261 alongside with moose (Alces alces) and, possibly auroch (Bos primigenius). The ecology of the 1262 1263 steppe bison, as inferred from fossil evidence and through comparison with living relatives, the 1264 American bison (Bison bison) and the European bison or wisent (Bison bonasus) points to a grazer of wooded steppe mosaics (for the American bison), while wisents were present in a more diverse 1265 1266 environment and adopted a more variable diet (Brugal et al., 1999; Kerley et al., 2012; Bocherens et 1267 al., 2015; Soubrier et al., 2016). B. priscus diet included grass from typical steppe and grassland 1268 (C3) including lichens in eastern Ukraine 18.5 ka cal BP (Julien et al., 2012), partly complemented by woody plant as also inferred from frozen remains dated 36 ka cal BP in Alaska (Guthrie, 1990). 1269

1270 Comparably to *B. bison* and *B. bonasus*, Late Pleistocene bisons were gregarious, the size and
1271 structure of the herds varing in function of the seasonally available resources (Plumb et al., 2009;
1272 Krasinska and Krasinski, 2013). Although sparse, zooarchaeological data point to consider these
1273 large herbivores as a targeted game for Gravettian and Epigravettian hunters.

The limestone Berici Hills (Fig. 2 for location) may serve as an example. Here, fossil pollen records 1274 1275 from caves and shelters document rocky steppe and semideserts already in Late MIS 3, but expanding during the latest MIS 3 and LGM (Cattani and Renault-Miskovsky, 1983; Bartolomei et 1276 1277 al., 1985; Pini, unpublished pollen spectra). Downhills, the Berici were fringed by boreal forests and wetlands throughout the LGM, although their extension was subject to submillennial climate 1278 1279 variability (Pini et al., 2010; Badino et al., 2020; submitted). The Berici hills could be envisaged as a condensed segment of the Alpine-piedmont ecogradient (see above) including a dry extreme of 1280 1281 karstic rocky steppe with ibex, a foothills forest belt (with giant deer and deer) and a wetland mosaic in the plains. This latter ecozone represented an auroch and moose hunting for Late 1282 Mousterian up to Gravettian groups (Terlato et al., 2019b; Romandini and Nannini, 2012) and a 1283 foraging area for the cave bear (Terlato et al., 2019a). This ecogradient was condensed in a linear 1284 space from 1 to 5 km. Paleolithic hunther-gatherers dwelled this area throughout the LGM, also in 1285 reason of caves availability (see sect. 3.3). 1286

1287 It would be misleading to claim the Karst itself as a desolated land. Its proximity to high mountains 1288 promoted ecodiversity and enhanced resources. Water resources were provided by hypogean 1289 watercourses and springs fed by the melting of glaciers in the Julian Alps and Dinarides. An 1290 additional input of orographic climate moisture is testified by the persistence of boreal forest at the 1291 foothills of Alps-Dinarides junction during all the LGM (Monegato et al., 2015). Indeed, as testified 1292 at Abri Kontija 002, Istria was repeteadly settled during the Gravettian (Janković et al., 2015).

1293

1294 **6.3. Impact of vegetation changes intervening at the Late Glacial onset**

1295 An important challenge for the history of human-environment interaction in GAPR are the rapidly changing conditions developed since the LGM / LG transition which is chronologically constrained 1296 at 18/17.5 ka cal BP south of the Alps (Ravazzi et al., 2007; Vescovi et al., 2007; Finsinger et al., 1297 2008; Wirsig et al., 2016), slightly anticipating the collapse of the ice-sheets (the end of the LGM 1298 according to Lambeck et al., 2014). At the Alpine foothills, a forest progression started immediately 1299 with increasing insolation, so that trees witnessed the glacier collapse just after 17.5 ka cal BP 1300 1301 (Kromer et al., 1998; Ravazzi et al., 2014; Monegato and Ravazzi, 2018). In about a thousand years, formerly glaciated forelands experienced a rapid vegetation chronosequence from glacial desert to 1302

pine-larch woodlands. However, forest progression in elevation was initially limited and only 1303 reached over 1500 m amsl after the onset of the LG interstadial (Gehrig, 1997; Heiss et al., 2005). 1304 Furthermore, summer drought limited forest progression over steppic hills and sunny slopes, and, in 1305 connection with increased fuel availability, enhanced fire propagation and frequency. During the 1306 early LG, even in the distal sector of the megafans, fluvial activity of the main Alpine rivers was 1307 limited to the incised valleys, thus maintaining open dynamic vegetations such as shrubby 1308 1309 semideserts. Being these landscapes inhabited by bisons and other large herbivores hunters, we cannot exclude that Gravettian and early Epigravettian human groups might have targeted bison 1310 herds on a seasonal base, similarly to Neanderthals (Terlato et al., 2019b). Unfortunately, there are 1311 no migratory-related ethological data about bisons in the GAPR. Taking as a reference the 1312 European bison leaving in the forest-field landscape in Poland, no historical data are known on its 1313 seasonal movements, despite altitudinal shifts in mountain areas are not excluded (Krasinska and 1314 Krasinski, 2013). Taking as a close reference the American plains, bisons forage on open 1315 bottomlands and lower adjacent slopes and may seasonally move until as much as 250 km, also in 1316 1317 crossing forest areas and steep slopes (Meagher, 1989). By reference to historical ethnographic and ecological data from Northamerican natives (Roos et al., 2018), it cannot be excluded that 1318 Gravettian and early Epigravettian hunting strategies had an impact on fire regimes. 1319

1320

1321 6.4. Hunter-gatherers in the Great Adriatic-Po Region: rhytms and circulation

1322 During the the LGM and early LG, European hunter-gatherers inhabited with variable continuity cold, cold-temperate and often moister biomes. The western regions of the continent are estimated 1323 to have represented the most settled area (Tallavaara et al., 2015; Burke et al., 2017), traditionally 1324 1325 considered a cradle of remarkable cultural changes following the Gravettian in comparison to the patchy settlement scenario currently known from central-eastern Europe. However, of the huge 1326 1327 amount of archaeological evidence recorded between the Rhine and the Volga, the most striking points to long distances covered by the circulation of chert and other stones used to manufacture 1328 domestic tools, hunting implements and mobile art artifacts. Petroarchaeological cases examined by 1329 1330 Féblot-Augustins (1997) in her seminal study, record distances up to 160 km of provenance for 1331 lithic artifacts recovered at Dolní Vestonice and Pavlov in Moravia and in the Váh river valley and even up to 300 km in eastern Slovakia, the Svabian Jura and Rhenania (Scheer, 2000). Raw blocks, 1332 1333 prepared cores and other artifacts were interpreted as an expression of embedded provisionings of 1334 cherts made by groups or individuals during their seasonal yearly circulation, as supposed for certain items in Pavlov and in other sites in Moravia positioned along the main river courses (Oliva, 1335

2000). Longer-distance social networks encompass the 450 km recorded in lower Austria, with
obsidian provisioned in the Carpathian mountain range (Féblot-Augustins, 1997; Dobosi, 2000) or
the perforated *Homalopoma sanguineum* ornamental shells brought at Poiana Cireşului (northern
Carpatians), over 900 km of distance from the sea (Nitu et al., 2019).

Regarding the GAPR, connections between sites located over 250 km apart from another do not 1340 1341 contradict the scenario drawn in the innermost continental Europe. Our petroarchaeological evidence confirms that the GPP was systematically crossed by the Gravettians and the early 1342 Epigravettians. Stable terraces along the Apennine belt were potential areas to settle on a seasonal 1343 base or maintain a network of exchanges between different groups. The same holds for the wide 1344 1345 alluvial plain with its main river courses, alluvial terraces and sand dunes. Despite the absence of direct evidence, we cannot deny that the suitability of these riverine environments could have 1346 1347 favoured the installation of residential camps. Another land suitable for settling was the northern Adriatic Sea shore and the Po River delta, thanks to its environmental variability and the direct 1348 connection to Dalmatia. 1349

Although data about human mobility during the Middle (Evolved) Gravettian are too sparse in the 1350 GAPR to reconstruct the settlement dynamics in this landscape, a marked trend can be highlighted 1351 starting with the Late (Final) Gravettian early Epigravettian and up to the early Late Epigravettian. 1352 This event coincides with a renewal in hunting weaponry around 24 ka cal BP, mainly consisting in 1353 the introduction of shouldered points rather than other backed implements. The long-range 1354 circulation of these points encompasses several macro-regions of Europe and could be related to 1355 new mobility strategies or changes in human groups and their way of exploiting resources in this 1356 territory. Furthermore, too poor or biased archaeological contexts do not support enough 1357 assessments on the possibility that the Gravettian to early Epigravettian techno and socio-economic 1358 changes were accompanied by profound renewals in ornamental sets. Not enough evidence is in fact 1359 currently available in the sites of the GAPR, for examining the relations between the Gravettian and 1360 its shared use of beads made of perforated H. sanguineum shells all over southern Europe and the 1361 1362 following culture. The early Epigravettian replaced the former around 24 ka cal BP, broadly in 1363 coincidence of the GI-2, a climatic threshold marking major cultural changes in western Eurasia. Extensive renewals in the variety of marine species used as ornaments are recorded only during the 1364 1365 Late Epigravettian, hence leaving incertitude on a wide chronological range.

1366 Therefore, further chronological assessments are required to refine the timing of the Gravettian -

1367 early Gravettian replacement and correlate it to the major ecological turnovers in the GAPR.

1368 Traditionally, the large-scale circulation of different categories of items is likely to be considered

one of the most reliable indicators to explain the emplacement of the post-Gravettian cultural 1369 mosaic in Europe, a vast ethno-geographic phenomena leading to the rapid spread of the Solutrean, 1370 Badegoulian, Magdalenian and other complexes in the western Atlantic regions and the 1371 Epigravettian in Mediterranean France, the Italian penisula, the Balkan area and towards the East. 1372 Long-range mobility in the GAPR is clearly attested by the tracing of fine-quality cherts used to 1373 manufacture should red points or to maintain the provisioning of individuals through the circulation 1374 of cores or semi-finished products from the Apennines to hunting camps and short-term settlements 1375 on the opposite side of the GPP, but also reversely from the Eastern Prealpine belt to caves in 1376 northern Dalmatia. Caves and rockshelters positioned in proximity of the ecotones or in other 1377 contexts characterized by environmental variability supported the peopling of the GAPR on a 1378 seasonal base. Currently, evidence is not available to ascertain whether the alluvial megafans of the 1379 northern PP and of the VFP were settled. Although the continuous sedimentary aggradation made 1380 these large elements of the GPP landscape unsuitable to settle on unstable surfaces, we cannot deny 1381 that particular environments, such as the spring belts could have been considered worthy of placing 1382 the camps on the base of their ecological actractiveness. 1383

1384 A second major turnover in settlement dynamics in the GAPR relates to the end of the LGM and the corresponding collapse after 18 ka cal BP of the Alpine glaciers, starting their final withdrawal and 1385 triggering the fluvial incision of the fans and megafans of PP and VFP. The largest portion of these 1386 landforms became free of floods and stable, while the development of active riverine environments 1387 and new wetlands was limited along the incised valleys cutting the plain and the groundwater-fed 1388 rivers. Such quick geomorphological changes are expected to have produced effects on human 1389 occupation, however not yet detected, along the river terraces in the plain. In the Prealpine foothills, 1390 Riparo Tagliente is a location persistently settled by human groups for the exploitation of the local 1391 biotic and abiotic resources which marks one of the first steps of the pioneering exploitation of the 1392 inner Prealpine belt on relatively stable areas. However, evidence of this phase is still very limited 1393 and such scarcity of data hampers the reconstruction of the peopling of the Italian Eastern Alps and 1394 the Dinarides triggered by the climatic amelioration of the LG interstadial starting at 14.7/14.5 ka 1395 1396 cal BP. In the LG interstadial, the progressive rise of the Adriatic coastline combined to the expansion of the treeline up to 1700-1800 m amsl in the SE-Alps (Ravazzi et al., 2007) are among 1397 the key factors leading human groups to intensely occupy the interior mountain ranges along new 1398 1399 routes and to expand their settlements (Bertola et al., 2007; Naudinot et al., 2014).

1400

6.5. Human groups across continental shelves and bridges: comparing the Great Adriatic-Po Region

1403 The emergence of the continental shelves around the European continent as a consequence of the LGM lowering of the sea level, profoundly changed its geography, especially off the present-day 1404 low coastal belts (Fig. 1). This process exerted the highest magnitude both in the southern and 1405 1406 northern latitudes, as along the Channel, the North Sea, the Atlantic western and northern coast of France, the North Black Sea and other smaller traits along the Mediterranean and Atlantic littorals. 1407 Climate-ecological modelling predicts that some of these extreme landscapes, close to the ice 1408 sheets, were left uninhabited (Tallavaara et al., 2015; Burke et al., 2017). This was the case of the 1409 338.000 km² vast land of western and northern Europe that emerged as a consequence of the retreat 1410 of the Channel and the North Sea. This flat region connecting the British Islands with the continent 1411 1412 was wind-lashed and unsuitable for human settlements roughly since the onset of the LGM (Roebroeks, 2000, but see Jacobi and Higham, 2008), until the gradual warming phase at 19-17.5 ka 1413 1414 cal BP, when population started to expand northward from the core areas in southwest and central France. The two ephemeral exceptions being the late Gravettian frequentation at Renancourt 1 (60 1415 1416 km south-east of the present-day Channel coast - Paris et al., 2017) and the Solutrean frequentation in the southern part of the Paris Basin (Bodu et al., 2019). Oisy and Grotte du Renne, France, testify 1417 to more reliable frequentations at 47.5° N than sites in Normandy, Pas-de-Calais, and during H1 in 1418 England, Germany and Belgium (Miller, 2012). Magdalenian northern expansion towards the north 1419 1420 European plain began during the fairly rapid increase in temperature started 16.5 ka cal BP. The 1421 first hunter-gatheres occupations occurred in the Paris Basin and in Belgium; then England was settled 14.7-14.1 ka cal BP during GI-1e, to be extensively occupied during the Bølling (Otte, 1990; 1422 Gamble et al., 2006; Miller, 2012). Fluvial systems with river channels, plains, wetlands and 1423 estuaries would have exerted an attractive force on prehistoric hunter-gatherers (Gupta et al., 2008; 1424 Momber et al., 2016). 1425

The shelf emerged off the Atlantic coast of France was another vast land inhabitable during the 1426 LGM and connected to the north with the Channel shelf (Farr et al., 2017). No evidence suggests 1427 the frequentation of this 55,000 km² large land from the coast of Aquitaine up to the Molène 1428 archipelago. Aside the biases due to surveying constraints in the submarine landscape, this gap 1429 1430 could be partly related to the environmental conditions in the Landes region. Here, the sand cover extended so much into the hinterland to make conditions inhospitable for human settlement and 1431 1432 favouring the persistence of a cultural barrier between Pyrenees - Cantabria and Charente - Périgord (Bertran et al., 2013) through all the Gravettian, Solutrean and part of the Magdalenian. Given the 1433

peopling of both these regions south and north of this deserted area, it has been suggested thathunter-gatherers circulated along the coastline of the submerged shelf (Billard et al., 2020).

Large regions remained uninhabited also at more southern latitudes, as in the case of the Great 1436 North Black Sea region. This 122,000 km² large flat landscape included the coastal lowland, the 1437 lower Dniester, Dnieper and Don alluvial plains expanded over 200 km to the south during the 1438 1439 LGM lowering, when the Black Sea turned its water composition to brackish and saline lake as a consequence of being isolated from the Sea of Marmara and the Mediterranean by the Bosphorus 1440 1441 sill (Kaplin and Selivanov, 2004). The Crimea, the rim of the Azov Sea and the north-western Russian Caucasus belonged to this region. The dominant biomes, the periglacial steppe and the 1442 1443 grass-herb steppe in the southernmost belt (Velichko and Zelikson, 2005) were not attractive for the Gravettian hunter-gatherers, adapted to the northern periglacial steppe zone with permafrost and 1444 1445 mammoths. The general decline in population of Central Europe during H2 (Maier and Zimmermann, 2017) also explains human absence in the Great North Black Sea region until 25 ka 1446 cal BP, when Epi-Aurignacians settled the western part of Ukraine and the plains east of the Azov 1447 Sea for few thousands years until 23 ka cal BP, hunting bisons, but still leaving uninhabited the 1448 1449 southernmost areas of the region. Predictive models have been proposed for testing the expectation of finding submerged Late Palaeolithic settlements in the watershed plateau, river terraces and 1450 slopes, river valleys and hills around the Dniester-Kuyalnik interfluve (Kadurin et al., 2020), far 1451 from the marshy lowmarine coast. Starting from 23 ka cal BP, the early Epigravettians populated 1452 1453 the steppic region basing their subsistence on the hunting of bisons (Demidenko, 2008) and extended their presence in south-eastern Europe. 1454

1455 In the western Mediterranean, the southern shifting of the coast in the Gulf of Lyon originated a 12.000 km² land mass used as a transition corridor by bearers of the Solutrean, Salpetrian and 1456 Middle Madgalenian cultural complexes. Evidence ascribed to the human presence in proximity of 1457 this corridor is represented by the extraordinary paintings dated to the Gravettian and Epigravettian 1458 in the partly submerged Cosquer cave on the Marseilles Calanques, at the eastern edge of this 1459 1460 continental shelf (Valladas et al., 2017). Decorations include seals, auks, fishes and jellyfish. 1461 Further indirect evidence of the exploitation of the marine shore resources is recorded through shells used as beads at inland Middle Madgalenian sites (Bazile, 1997). 1462

1463 Due to the dominant extension of its steep coasts, the Iberian Peninsula increased its extension

1464 limitedly to the middle Mediterranean zone in the Valencia gulf up to the Ebro Delta. Data on

1465 human subsistence remain however too scanty to infer models on mobility and subsistence of the

1466 Solutrean groups who settled this margin extended over 17,500 km² and are limited to record no

evidence of marine resources in inland sites, compared to the increasing number of evidence ofmarine fishery in the LG (Aura Tortosa et al., 2019).

1469 Also, the western border of southern Iberia extended far into the ocean. The region concerned was 1470 the Estremadura, bordered by the Tagus and Mondego rivers and by mountain ranges peacking at 2000 m, to the east. The total land extended over $12,000 \text{ km}^2$ where the 60% was the littoral shelf 1471 (Zilhão, 1997). This land mass sustained Solutrean groups who established their territories along the 1472 main river courses and hunted red-deer, horse and wild boar. Human groups settled in caves and 1473 open-air sites, with caves used as temporary and specialized shelters for small groups of hunters. On 1474 the contrary, several open-air locations provide so high amount of evidence to infer continuous 1475 1476 residential settling also supported by the proximity to sources of provisionable chert. Although biased by unextensive surveying, the absence of base-camps from the present-day coastal area 1477 1478 suggests that the submerged littorals with their estuarine and coastal aquatic resources as much as the inland garrigues, were at the edges of the settled landscape (Zilhão, 1997). Considered all 1479 together, these lands supported a productive Soultrean unit of estimated 500 individuals with a 1480 relatively stable ethnic entity but open to social and cultural relations with the rest of Iberia. 1481 Given the multidisciplinary and petroarchaeological data illustrated in this chapter and in the 1482 chapters above, the GAPR supports comparison with the largest LGM continental shelves of Europe 1483 but differentiates from these due to the presence of palaeontological and archaeological sites 1484

scattered on its sides. This particular morphological structure makes possible to track movements
from on side to another across lowlands or along the coastal belt, an opportunity, which is precluded
in others geographic areas.

1488

1489 6.6. Demography and turnovers inferred from ancient human DNA

1490 Palaeogenetic studies focusing on hunter-gatherer individuals revealed that several population transformations took place across Palaeolithic and Mesolithic Europe (Fu et al., 2016; Posth et al., 1491 2016). Previous analyses of mitochondrial DNA (mtDNA) genomes have shown that, while some 1492 of the pre-existing mtDNA diversity was lost during the LGM, most of the European maternal gene 1493 1494 pool survived this severe population bottleneck. However, a population turnover was observed through a sharp shift in mtDNA haplogroup frequencies around 14.5 ka cal BP, coinciding in time 1495 1496 with the Bølling/Allerød (Posth et al., 2016). Nuclear DNA analyses later demonstrated that this genetic discontinuity was due to the spread of individuals sharing distinctive affinity to present-day 1497 populations from the Near East. This incoming genetic component largely replaced the ancestry 1498 1499 identified in older Magdalenian-related individuals from central Europe (Fu et al., 2016). The oldest

genome harbouring the Near Eastern link is Villabruna, an Epigravettian individual retrieved in Riparo Villabruna, Veneto Prealps and dated to 14.2-13.8 ka cal BP (Aimar et al., 1992; Vercellotti et al., 2008). Two demographic scenarios were proposed to explain the expansion of the Villabrunarelated genetic cluster, and involved either (1) a long-range migration from the Near East to Europe, which took place at least 6 ka years before the Neolithic farming expansion, or (2) a double genetic dispersal of a southern European population, both towards the east and the west, which was responsible for drawing these distinct ancestries together.

Mesolithic individuals from the Iron Gates region in Serbia and Romania showed evidence of interaction with Near Eastern populations, as some of them carried mtDNA haplogroups that are most prevalent in ancient and contemporary individuals from the Near East (Mathieson et al., 2018). However, recent genomic analyses of a 15ky old individual from central Anatolia suggested that the Iron Gates group did not simply derived from a unidirectional gene flow from Near Eastern to European hunter-gatherers. On the contrary, an additional genetic influx from populations

ancestral to southern Europeans into the Near East has been proposed (Feldman et al., 2019).

Ancient human DNA data of individuals older that 14 ka cal BP is still missing from the Balkansand the GAPR impeding a genetic characterization of the groups living in this area during the

1516 Gravettian and early Epigravettian. Nevertheless, described genetic contacts with groups from

1517 southwestern European fringes might provide an indirect evidence for the presence of the

1518 Villabruna-related component in southern Europe well before the Bølling/Allerød. In fact, it has

been recently shown that the genetic make-up of hunter-gatherers from Iberia dated after ~19 ka cal

1520 BP was formed through the admixture of two divergent ancestries. One ancestry was associated

1521 with Magdalenian individuals older than 15 ka cal BP and the other with members of the

1522 Villabruna-related cluster, so far only younger than 14 ka cal BP. Interestingly, the oldest

representative of the Magdalenian-related cluster, dated to around 18.6 ka cal BP from El Miron

1524 cave in Spain, was found to be substantially admixed with a group related to the Villabruna

1525 individual (Villalba-Mouco et al., 2019). This suggests the arrival of the Villabruna-related genetic

1526 component in Iberia before 14 ka cal BP, implying that this cluster was widespread in southern1527 Europe several thousands of years before the age of its oldest genome described until now.

1528 Taken together, these palaeogenetic results support the idea that, from at least 19 ka cal BP,

southern European populations were broadly interconnected across the GAPR and beyond.

1530 Additional genome-wide data of individuals older than 14 ka cal BP from this region is essential to

understand the distribution of such ancestry through time in southern European climatic refugia.

1532 This will allow a better comprehension of the population dynamics that accompanied modern 1533 human re-expansion into Europe towards the end of the coldest period of the LGM.

1534

1535 **7. Conclusions**

The Great Po Plain is the largest alluvial plain ever existed in the Mediterranean basin since the 1536 onset of the Middle Pleistocene, and expanded to reach its maximum size in the LGM. Meanwhile it 1537 1538 greatly pulsated with glacial cycles, pacing the high magnitude sea-level changes related to land ice mass size. This land hosted human groups, surviving during the LGM and settling their camps in 1539 different ecological contexts, ranging from the Alpine vegetation to the Alpine timberline, down to 1540 low-elevational open boreal forest and finally to semiarid ecotones below the continental 1541 timberline. Semiarid ecozones developed especially in the Alpine foreland and in the Adriatic plain. 1542 Fauna impoverished in consequence of gradual disappearance of mammoth, woolly rhino and giant 1543 1544 deer, together with cave bear, a spieces targeted by the Epigravettian hunters. The steppe bison was the most iconic herbivorous species in the plain and together with ibexin the lower hilly landscapes 1545 of the GAPR. 1546

Unexpected archaeological evidence dated to GS-5 on the watershed of the northern Apennine 1547 range also indicates that open, extreme landscapes were the edge of elevational logistical 1548 movements of human groups along mountain ecozones. Despite the sparseness of the 1549 archaeological record with its uneven distribution of sites and the relatively limited evidence of 1550 human presence, the GPP seems to have been crossed and inhabited all along the LGM from the 1551 early Gravettian to the first part of the late Epigravettian. This has been clearly established through 1552 the circulation of finished or semifinished early Epigravettian artefacts made of chert coming from 1553 1554 the formations of the Umbria-Marche Apennines in the subalpine zone, Istria and Dalmatia. Given the functional nature of the most extensively investigated sites, it can be inferred that provisioning 1555 1556 of chert was not embedded in a broad strategy of resource acquisition but, rather, was the outcome of specialized planned activities. These activities were likely within the framework of seasonal 1557 displacement and aggregation of groups in settlements, the existence of which can only be supposed 1558 given the inaccessibility of the submerged plain. It is reasonable to think that the wide open spaces 1559 1560 of the GAPR favoured a great mobility of human groups in the framework of a cultural identity extending into southern Europe. 1561

The Alpine Late Glacial onset was a turning point for bio-geographic evolution also in this area marked by the loss of large continental plains, thus implying an overall rearrangement of all ecozones of human populations, and airmass circulation patterns, triggering phylogeographic

bottlenecks. As a consequence of the Late Glacial interstadial warming, a large-scale Epigravettiancolonization of the Alps, the Apennine, the Dinarides and other mountain ranges started.

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1579 original petroarchaeological data, A.F., G.M., P.M., L.R., S.R. and A.Z. geomorphological

1580 framework, C.R., R.P. and G.F. plant ecological framework, M.B. vertebrate palaeontology

1581 framework, M.P., F.F., I.J., I.K. and N.V. cultural framework, S.B., M.P. and Z.P. chert

1582 petroarchaeological framework; C.P. curated chapter 6.6; D.M. drawn the maps of figures 1, 2, 3, 9

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2670 Tables captions

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2672 **Table 1.** A frame of predicted ecological zones and summary of potential vegetation formations in the Great Adriatic - Padanian Region (GAPR) during the LGM and early LG (30 - 16 ka cal BP). 2673 2674 The ecosystem classification here adopted relies on the recognition that ecosystem properties are 2675 closely tied to both physical and biotic site factors (see e.g. McLaughlan et al., 2010). The 2676 application of this approach to past environments embraces both the identification of predicting abiotic factors, provided by Quaternary geology (see sections xxx in this paper) and the biodiversity 2677 provided by a number of fossil palaeoecological sites. * - taxa documented by the pollen record; § -2678 taxa documented by the macrofossil record. 2679

2680 Sites references: 1. Cerete (Ravazzi et al., 2012); 2. Piovesello (Peresani et al., 2018); 3. Lake

2681 Alserio (Wick, 2000); 4. Lake Annone (Wick, 1996); 5. Azzano Decimo (Pini et al., 2009); 6.

Broion Cave (Cattani and Renault-Miskovsky, 1983); 7. Lago della Costa (Gubler et al., 2018); 8.

Lake Fimon (Pini et al., 2010); 9. Lake Ganna (Schneider and Tobolski, 1985); 10. Lake Origlio

2684 (Tinner et al., 1999); 11. Paina Cave (Bartolomei et al., 1985); 12. Paul di Manerba (Ravazzi et al.,

2685 2014); 13. Lago Piccolo di Avigliana (Finsinger et al., 2008); 14. Renče (Monegato et al., 2015);

2686 15. Revine (Casadoro et al., 1976; Wick, 2000); 16. Trana (Schneider, 1975); 17. Cà Fornera (Miola

et al., 2003); 18. Casaletto Ceredano (Ravazzi et al., 2020); 19. Galzignano (Miola and Gallio,

26881998); 20. Ghedi (Pini, unpublished data); 21. San Donà di Piave (Miola et al., 2003); 22. Venice

Lagoon (Serandrei-Barbero et al., 2005); 23. Lake Vrana (Schmidt et al., 2000); 24. Valun Bay

2690 (Schmidt et al., 2001).

Table 2. List of the Gravettian-Epigravettian sites and radiocarbon dates in the GAPR mentioned in

this work. Notes: Elev, elevation above modern sea level; Ty, type of site (OA - Open air, C - Cave,

2693 RS - Rockshelter); CC, cultural complex (G – Gravettian, EE - early Epigravettian, LE - Late

2694 Epigravettian, ND - not determinable); Mat, material (C - charcoal, B – bone, HB – human bone,

2695 S+C sediment and charcoal particles); ETH-79368 date is from a cut-marked cave bear bone;

samples from Baracche were collected on the surface of the quarried deposits in association with

the lithic arifacts. Conventional ages are expressed in 14C years BP and are calibrated in IntCal 13(Reimer et al., 2013.)

Table 3. Main features (natural shape, color, microfacies and micropalaeontology) of the cherts

shown in the Figs. 7, 9 and 10; numbers in the first column are corresponding. See also Fig. 6 for

the stratigraphic position of the samples. Notes: U-M basin, Umbria-Marche basin; C-B basin,

2702 Carnia-Belluno basin.

- **Table 4**. Summary of the evidence produced from this study and from previous petroarchaeological
- analyses of Gravettian and Epigravettian assemblages in the GAPR. Notes: Ty, Type of site (OA -
- 2705 Open air, C Cave, RS Rockshelter); CC, Cultural Complex (G Gravettian, EE early
- 2706 Epigravettian, LE Late Epigravettian, ND not determinable);
- 2707
- 2708

2709 Figures captions

2710

Figure 1. Map of Europe with the largest continental shelves emerged during the Last Glacial 2711 Maximum. 1. Doggerland/North Sea, English Channel and Bristol Channel; 2. Bay of Biscay and 2712 France Atlantic Coast; 3. North-central Portugal Atlantic Coast; 4. Catalunya and Valencia Coasts; 2713 5. Gulf of Lion; 6. Great Po Plain; 7. Northern Black Sea Coast (Sea of Azov and Chorne Sea); 8. 2714 Other LGM emerged areas; 9. Scandinavian and British Islands ice sheets; 10. Mountain Glaciers; 2715 11. Major rivers and lakes. Technical notes: Coordinate system ETRS89 / UTM zone 32N (EPSG 2716 2717 25832); Digital Elevation Model (base topography – Copernicus Land Monitoring Service (CLMS), 2019 and General Bathymetric Chart of the Oceans (GEBCO), 2019). Sea level drop at - 130 m 2718 2719 (Pellegrini et al., 2017; 2018). Scandinavian and British Islands ice sheets after Hughes et al. (2016) at 22 ka. The mountain glaciers from Ehlers et al. (2011) with updated reconstructions in the Tatra 2720 2721 Mountains (Zasadni and Klapyta, 2014), Dinarides (Kuhlemann et al., 2009; Žebre and Stepišnik, 2014, 2015; Temovski et al., 2018), Pyrenees (Delmas, 2015), Cantabrian range (Serrano et al., 2722 2723 2015). Alpine glaciers downloaded from https://booksite.elsevier.com/9780444534477/and 2724 modified in the Italian side using updated reconstructions (Ravazzi et al., 2012; Monegato et al., 2725 2017; Gianotti et al., 2015; Ivy-Ochs et al., 2018; Rossato et al., 2013, 2018). Major European and 2726 eastern European lakes and rivers after Toucanne et al. (2015) and Verheul et al. (2015), Adriatic lakes (Miko et al., 2017) and rivers simplified from Maselli et al. (2014) (For interpretation of the 2727 references to colour in this figure legend, the reader is referred to the Web version of this article). 2728 Figure 2. Palaeogeographic map of the Great Adriatic-Po Region (GAPR) with the Great Po Plain 2729 (GPP) composed by the Po Plain (PP), the Adriatic Plain (AP) and the Venetian - Friulian Plain 2730 2731 (VFP) in the Last Glacial Maximum. Main physiographic units at the last glacier culmination in the piedmont at the southern side of the Alps, 26 to 22 ka cal BP (LGM p.p.). Key: 1. Glaciers 2732 2733 (according to Ehlers et al. 2011 with updatings by Ravazzi et al., 2012; Monegato et al., 2017; Gianotti et al., 2015; Ivy-Ochs et al., 2018; Rossato et al., 2013, 2018; Braakhekke et al., 2020 in 2734

- the sectors between the Dora Riparia and the Brenta valley outlets; Garda glacier, GG; Tagliamento 2735 glacier, TG); 2. Lakes (based on Miko et al., 2017); 3. megafan bodies above the current sea level 2736 (B Mgf, Brenta megafan; P Mgf, Piave megafan; T Mgf, Tagliamento megafan; Fontana et al., 2737 2008, 2014a); 4. megafan bodies sunken under the current sea level; 5. Upper proximal megafan 2738 belt; 6. Po River floodplain (Amorosi et al. 2017, http://www.sinanet.isprambiente.it/it/sia-2739 ispra/download-mais/complessi-idrogeologici); 7, Po River delta (Pellegrini et al., 2018); 8, stable 2740 surfaces supporting deeply weathered soils and loess. These surfaces belong to the following main 2741 physiographic units: ancient, terraced alluvial units; hills emerging from the plain (BH, Berici 2742 Hills); karstic plateaux at low elevatio \Box 9, DEM \Box olor s \Box ale -130 – 4.808. 2743 2744 Technical note. Coordinate system ETRS89 / UTM zone 32N (EPSG 25832); Digital Elevation Model (base topography – Copernicus Land Monitoring Service (CLMS), 2019 and General 2745 2746 Bathymetric Chart of the Oceans (GEBCO), 2019). Sea level drop at – 130 m (Pellegrini et al., 2015; 2017; 2018). The mountain glaciers (pale blue) from Ehlers et al. (2011). Dinarides from 2747 Žebre and Stepišnik (2015). Alpine glaciers downloaded from 2748 https://booksite.elsevier.com/9780444534477/ and modified in the Italian side using updated 2749 2750 reconstructions (Ravazzi et al., 2012; Monegato et al., 2017; Gianotti et al., 2015; Ivy-Ochs et al., 2018; Rossato et al., 2018; Braakhekke et al., 2020). Adriatic lakes (Miko et al., 2017). Stable areas 2751 (middle and lower Pleistocene alluvial deposits, aeolian sediments, Loess) (Zerboni et al., 2018; 2752 Geological Map 1:50.000 Iseo, Bergamo, Vimercate sheets; Geomorphological Map of the Po Plain 2753 2754 (Giuliano et al., 1998), selected area with slope range 0-10% of Geological Map of Slovenia 1:1.000.000). Alluvial fans and megafans along the southern side of the Alps (Fontana et al., 2755 2756 2014a). Alluvial fans along the northeastern side of the Apennine (Amorosi et al., 2017; Bruno et al., 2018). Po river delta area (Pellegrini et al., 2018) and Po channel belt (Amorosi et al., 2017; 2757 Bruno et al., 2018; Carta Complessi idrogeologici http://www.sinanet.isprambiente.it/it/sia-2758 ispra/download-mais/complessi-idrogeologici). Gravelly sector of the plain (Castiglioni et al., 2759 1997). Distal plain. (For interpretation of the references to colour in this figure legend, the reader is 2760 referred to the Web version of this article). 2761 2762 2763 Figure 3. Map of the Great Adriatic-Po Region showing the location of Palaeobotanical, Palaeontological and Palaeolithic sites mentioned in the text. Palaeobotanical sites: 1. Cerete; 2. 2764 2765 Piovesello (including the Piovesello Paleolithic site); 3. Lake Alserio; 4. Lake Annone; 5. Azzano 2766 Decimo; 6. Grotta Broion (including the Riparo Broion and Grotta Buso Doppio Broion Paleolithic
- sites); 7. Lago della Costa; 8. Lake Fimon; 9. Lake Ganna; 10. Lake Origlio; 11. Grotta Paina

- 2768 (including the Grotta Stria and Grotta Trene Paleolithic sites); 12. Paul di Manerba; 13. Lago
- Piccolo di Avigliana; 14. Renče; 15. Revine; 16. Trana; 17. Cà Fornera; 18. Casaletto Ceredano; 19.
- 2770 Galzignano; 20. Ghedi; 21. San Donà di Piave; 22. Venice Lagoon; 23. Lake Vrana; 24. Valun Bay;
- 2771 <u>Palaeontological sites</u>: 25. Settepolesini; 26. Grotta Tilde; 27. Cava a Filo;
- 2772 <u>Palaeontological and Palaeolithic sites</u>: 28. Büs dei Lader; 29. Grotta Fumane; 30. Riparo Tagliente;
- 2773 31. Grotta Rio Secco; 32. Ovčja Jama and Županov Spodmol; 33. Zala cave; 34. Abri Kontija 002,
- 2774 Romualdova pećina and Pećina kod Rovinjskog Selo 1; 35. Šandalja II cave and Ljubićeva pećina;
- 2775 36. Vlakno cave; 37. Fornace San Damiano; 38. Fonte delle Mattinate; 39. Fosso Mergaoni; 40.
- 2776 Ponte di Pietra; 41. Madonna dell'Ospedale and Baracche; 42. Campo delle Piane. (For
- interpretation of the references to colour in this figure legend, the reader is referred to the Webversion of this article).
- **Figure 4.** 3D ecographic sketch of the ecoclimatic gradient spanning the Kurai steppe and the
- 2780 northern slope of the Chuya mountains, SW Altai, Russia, 50°12'48'' N, 87°56'27'' E. It provides a
- 2781 modern analogue, predicted by palaeoecological data, for the elevational structure of the ecozones
- at the southern fringe of the Alps during the LGM. (drawn on the Google Earth Satellite image,
- June 2017; interpreted on the base of Blyakharchuk et al., 2008; Kuneš et al., 2008; Makunina,
- 2784 2016; Badino et al., submitted; elaboration by the Lab. Palynology, CNR Milano).
- **Figure 5.** Selection of Epigravettian shouldered backed points (nn. 1 to 5) and *microgravettes* (nn.
- 6-7) from: 1, 2 and 7. Paina Grottina Azzurra; 3. Buso Doppio Broion; 4 and 6. Trene; 5. Šandalja
- 2787 II (from Broglio et al., 2009; Vukosavljević and Karavanić, 2017).
- **Figure 6.** Distribution of calibrated dates in the 35 15 ka interval reported in Table 2.
- 2789 Figure 7. Comparative stratigraphic sketches of the Apennines Umbria-Marche Basin and Southern
- 2790 Alps Trento Plateau series with highlighted the distribution of the cherts. The numbers on the right
- of the Umbria-Marche column resume the stratigraphic position of the archaeological and
- 2792 geological samples shown in the Figs. 8, 10 and 11.
- 2793 Figure 8. Micrographs of Umbria-Marche Basin cherts from primary exposures. 1. Oligocene
- 2794 Scaglia Cinerea; 2. Eocene Scaglia Rossa; 3. Middle Cretaceous Scaglia Bianca; 4. Middle
- 2795 Cretaceous Marne a Fucoidi; 5-6. Lower Cretaceous Maiolica (scale bar = 1 mm; for interpretation
- of the references to colour in this figure legend, the reader is referred to the Web version of thisarticle).
- Figure 9. Maps of the GAPR at different time intervals (32-29, 26-23, 23-19, 18-16 ka cal BP)
 showing the simplified palaeogeographic units, the Gravettian Epigravettian radiocarbon dated

2800	sites and the sites that produced indication of allochthonous chert provenance (black arrows). Key:
2801	1, DEM color scale -130 – 4,808 m amsl; 2. Glaciers; 3. Lakes; 4. Upper proximal megafan belt; 5.
2802	Po River floodplain; 6, Po River delta; 7, stable surfaces supporting deeply weathered soils and
2803	loess. For details on references and explanations of the legend see figure 2 and section 2.1. For
2804	discussion on the chronological frame and cultural attribution of each site see section 3.2. (For
2805	interpretation of the references to colour in this figure legend, the reader is referred to the Web
2806	version of this article).
2807	Figure 9a. Simplified map for the interval 32-29 ka cal BP. Sites: 2. Piovesello; 6. Grotta Broion
2808	and Riparo Broion; 11. Paina; 31. Rio Secco; 34. Pećina kod Rovinjskog Sela 1; 38. Fonte delle
2809	Mattinate.
2810	Figure 9b. Simplified map for the interval 26-23 ka cal BP. Sites: 11. Paina, Trene and Stria; 32.
2811	Ovčja Jama (note that layer 4 is culturally attributed to the early Epigravettian); 35. Šandalja II
2812	(note that layer C/d is culturally attributed to the early Epigravettian); 40. Ponte di Pietra.
2813	Figure 9c. Simplified map for the interval 23-19 ka cal BP2. Sites: 6. Riparo Broion and Buso
2814	Doppio Broion; 11. Stria, Trene and Paina; 28. Büs dei Lader; 34. Romualdova; 35. Šandalja II; 36,
2815	Vlakno; 39. Fosso Mergaoni; 40. Ponte di Pietra (note that these last two sites are culturally
2816	attributed to the late Gravettian).
2817	Figure 9d. Simplified map of the eastern GAPR for the interval 18-16 ka cal BP. Sites: 30.
2818	Tagliente; 33. Zala; 34. Romualdova; 35. Ljubićeva; 41. Baracche; 42. Campo delle Piane.
2819	Figure 10. Berici Hills (7-11) and Lessini Mountains (12). Micrographs of allochtonous cherts from
2820	the Umbria-Marche Basin taken on Epigravettian artifacts: 7. Oligocene Scaglia Cinerea (Paina
2821	Cave - Grottina Azzurra layer 6); 8. Eocene Scaglia Rossa (Paina - Grottina Azzurra layer 6); 9.
2822	Eocene Scaglia Rossa (Trene, complex B); 10. Middle Cretaceous Marne a Fucoidi (Buso Doppio
2823	del Broion, layer Rim); 11. Lower Cretaceous Maiolica (Paina - Sala Terminale layer 125); 12.
2824	Middle Jurassic Calcari Diasprigni (Tagliente, SU 300) (scale bar = 1 mm; for interpretation of the
2825	references to colour in this figure legend, the reader is referred to the Web version of this article).
2826	Figure 11. Istria. Micrographs of allochtonous cherts from the Umbria-Marche Basin (13-15) and
2827	the Carnia-Belluno Basin (16-18) taken on Epigravettian artifacts: 13. Eocene Scaglia Rossa
2828	(Šandalja II, layer C/d); 14. Eocene Scaglia Rossa (Romualdova pećina); 15. Lower Cretaceous
2829	Maiolica (Šandalja II, layer C/d); 16. Lower Cretaceous Maiolica (Šandalja II, layer C/d); 17.
2830	Middle Jurassic Soverzene (Šandalja II, layer C/d); 18. Triassic Buchenstein (Šandalja II, layer C/d)
2831	(scale bar = 1 mm; for interpretation of the references to colour in this figure legend, the reader is
2832	referred to the Web version of this article).

Site	Geography	Elev	Ту	CC	Context	Lab. ID	Mat	¹⁴ C age	Cal. age BP	Reference
Piovesello	Emilian Apennine	870	OA	G	7	LTL13257A	С	26020±80	30681 29899	Peresani et al., 2018
					7	LTL14195A	С	25650±100	30235 29444	Peresani et al., 2018
Büs dei Lader	Lombard Prealps	310	С	ND	infill	GrA-216	С	17040±80	20802 20301	Biagi, 2000
Riparo Tagliente	Lessini Plateau	226	RS	LE	13a alpha	LTL4441A	В	13986±60	17219 16687	Fontana et al., 2012
				LE	300	Lyon-10030	В	13920±80	17160 16555	Fontana et al., 2018
				LE	15-16	R-605a	C	13430±180	16761 15660	old date no ref.
				LE	15-16	R-605	C	13330±160	16537 15548	old date no ref.
					352	OxA-29834	В	13600±60	16638 16179	Soubrier et al., 2016
				LE	13a	Lyon-10031	В	13450±70	16438 15941	Fontana et al., 2018
				LE	10e (OL3)	OxA-3532	С	13270±170	16426 15371	old date no ref.
					10c (OL2)	OxA-3531	C	13070±170	16147 15176	old date no ref.
					13trincea	Lyon-10033	В	13250±80	16186 15684	Fontana et al., 2018
					13burial	OxA-10672	HB	13190±90	16149 15532	Gazzoni et al., 2013
Grotta Broion	Berici Hills	145	С	G	D	UtC-2694	В	24700±400	29656 27890	Broglio and Improta, 1995
				G	Е	UtC-2693	В	25250±280	30150 28705	Broglio and Improta, 1995
Riparo Broion	Berici Hills	135	RS	G	1b	Utc-13320	С	28460±260	33220 31598	De Stefani et al., 2005
					1balfa	UtC-10504	С	27960±300	32702 31216	De Stefani et al., 2005
					1b - S1	UtC-10506	С	17830±100	21890 21282	De Stefani et al., 2005
					1c	UtC-13321	С	25860±200	30657 29532	De Stefani et al., 2005
Buso Doppio Broion	Berici Hills	135	С	EE	1t1I		-			Romandini et al., 2015
				G	2-1tt.II-IV 1base		-			Romandini et al., 2015
Grotta Paina	Berici Hills	335	С	EE	5	ETH-79366	В	19686±54	23948 23489	Terlato et al., 2019a
				EE	6	UtC-2696	В	20120±220	24875 23660	Broglio and Improta, 1995
					6	UtC-2043	В	19430±150	23810 22985	Broglio and Improta, 1995
				G	7A	UtC-2697	В	20200±240	25040 23730	Broglio and Improta, 1995
Grotta Col de La Stria	Berici Hills	370	С	EE	2cl	LTL-2638A	С	16037±100	19609 19050	Romandini and Nannini, 2012
				EE	2cl	LTL-2639A	С	16802±90	20522 20017	Romandini and Nannini, 2012
					2base	LTL-2147A	В	19485±200	23780 23107	Romandini and Nannini, 2012
Grotta Trene	Berici Hills	360	С	EE	BI	UtC-2691	В	17640±140	21761 20930	Broglio and Improta, 1995
					BI	ETH-79368	В	19948±55	25476 22821	Terlato et al., 2019a
					BII	UtC-2692	В	18630±150	22909 22174	Broglio and Improta, 1995
Grotta Rio Secco	Carnic Prealps	580	С	G	6	Poz-41207	С	27080±230	31380 30807	Peresani et al., 2014

					6	Poz-41208	С	28300±260	32977 31471	Peresani et al., 2014
					6	MAMS-15906	С	28995±135	33609 32816	Talamo et al., 2014
					6	MAMS-15907	С	29390±135	32839 31735	Talamo et al., 2014
Fonte delle Mattinate	Marche Apennine	760	OA	G	B-27		С	28300±790	33964 31039	Silvestrini et al., 2005a
				G	C1	GU-9426	S+C	25930±325	30851 29414	Giaccio et al., 2004
Ponte di Pietra	Marche Apennine	225	OA	G	II, su 65	CRG-1018	С	19940±471	25273 22942	Lollini et al., 2005
					II, su 66	CRG-1019	С	18515±618	23934 20926	Lollini et al., 2005
Fosso Mergaoni	Marche Apennine	180	OA	G	4a2	UtC-11551	С	18160 ± 240	22503 21389	Silvestrini et al., 2005b
Madonna dell'Ospedale	Marche Apennine		OA	EE			-			Silvestrini et al., 2008
Baracche	Marche Apennine	350	OA	LE		LTL169A	С	14920±95	18385 17896	Peresani et al., 2005
						LTL172A	С	14929±110	18431 17884	Peresani et al., 2005
Campo delle Piane – CDP 7	Abruzzi Preapennine	350	OA	LE	24	GifA-99158	C	14590±120	18055 17465	Olive, 2017
					24	GifA-100542	С	14810±120	18332 17713	Olive, 2017
Ovčja Jama	Karst	586	С	G	4	KN-48	С	19540±500	24856 22450	Osole, 1974
Zala	W mount. Croatia	270	С	LE	100	Beta-334806	В	14100±60	17414 16924	Šošić Klindžić et al., 2015
				LE	12	Beta-228734	В	13840±50	16986 16509	Karavanić et al., 2007
				LE	102	Beta-334805	В	13340±60	16250 15831	Šošić Klindžić et al., 2015
Abri Kontija 002	Istria	46	RS	G			-			Janković et al., 2015
Pećina kod Rovinjskog Sela 1	Istria	71	С	G	В	Poz-80127	В	26730±300	31290 30405	Unpublished (DK)
Ljubićeva pećina	Istria	170	C	LE	D (4)	Beta-249371	С	13230±70	16136 15676	Percan et al., 2009 Simonet, 2013
Romualdova pećina	Istria	110	С	EE	2	Beta-465338	С	13970±50	17174 16692	Ruiz-Redondo et al., 2019
				\mathbf{O}	2	OxA-36127	С	14250±80	17592 17099	Ruiz-Redondo et al., 2019
Šandalja II	Istria	70	C	EE	C/d	Z-193	С	20750±400	25840 24085	Srdoč et al., 1973
Vlakno	Dugi otok Island	38	С	EE	32	Beta-302247	С	16330±70	19955 19515	Cvitkušić et al., 2018

Figure	Formation	Age	Provenance	Nat. shape	Color	Microfacies and micropalaeontology
8.1, 10.7	Scaglia Cinerea	Oligocene	U-M basin	nodules	grey to black	Pelagic cherty limestone with radiolarians and plancktic foraminifers (Globigerina and Pseudohastigerina)
8.2, 10.8-9, 11.13-14	Scaglia Rossa	Eocene	U-M basin	nodules	reddish brown	Pelagic cherty limestone with radiolarians and plancktic foraminifers (Globigerina, Morozovella and Acarinina)
8.4, 10.10	Marne a Fucoidi	Aptian	U-M basin	layers	green	Pelagic cherty marly limestone with radiolarians and bad preserved pre-globotruncanids and planomalinids
8.5-6, 10.11, 11.15	Maiolica	Valanginian- Barremian	U-M basin	nodules and layers	grey	Very fine texture pelagic cherty limestone with radiolarians and limestone remains
10.12	Calcari Diasprigni	Kimmeridgian -Tithonian	U-M basin	nodules and layers	dark red to violet	Pelagic cherty limestone with radiolarians, Saccocoma and Aptici
11.16	Maiolica	Valanginian- Barremian	C-B basin	nodules and layers	grey	Pelagic cherty limestone with resedimented radiolarians and sponge spicules
11.17	Soverzene	Hettangian- Pliensbachian	C-B basin	layers	dark grey to black	Bituminous cherty dolomitic limestones with sponge spicules and radiolarians
11.18	Buchenstein	Ladinian	C-B basin	layers	grey to green	Pelagic cherty limestone with volcaniclastic detrital inputs and bad preserved radiolarians
8.3	Scaglia Bianca	Cenomanian	U-M basin	nodules and layers	grey to black	Laminated cherty marly limestone rich in organic matter, radiolarians and planktic foraminifers (Rotalipora)
8.4	Marne a Fucoidi	Albian	U-M basin	layers	green	Pelagic marly limestone with radiolarians and well preserved planktic foraminifers (Planomalina)

Table 3

Site	CC	Geographic location	Provisioning Area	PD	Range	Reference
Piovesello	G	Emilian Apennine	Nure valley Provence	5-15 300	5-300	Peresani et al., 2018
Fumane	G	Venetian Prealps	Lessini Plateau	5-15	5-15	This study
Grotta Broion Riparo Broion	G	Venetian Prealps	Berici Hills Lessini Plateau	5-15 25-50	5-50	Bertola et al., 2018
Rio Secco	G	Carnic Prealps	Carnic and Friulan Prealps	5-50	5-50	This study
Abri Kontija 002	G	Istria				
Pećina Kod Rovinjskog Sela 1	G	Istria		Ť,		
Fonte delle Mattinate	G	Marche Apennine	Umbria-Marche Apennine High Tiberine valley	0-15 25-50	0-50	Silvestrini et al., 2005a; Cancellieri, 2018
Ponte di Pietra	G	Marche Apennine	Umbria-Marche Apennine	0-15	0-15	Lollini et al. 2005; this study
Fosso Mergaoni	G	Marche Apennine	Umbria-Marche Apennine	0-15	0-15	Silvestrini et al. 2005b; Cancellieri, 2015
			Berici Hills	5-15		
Paina, layer 7	G	Venetian Prealps	Lessini Plateau	25-50	5-270	Broglio et al., 2009; Bertola et al., 2018
			Umbria-Marches Apennines	250-270		
Ovčja jama	G	Notranjska region				
Büs dei Lader	ND	Lombard Prealps	Baldo/Lessini Plateau	25-50	25-50	This study
			Berici Hills	5-15		
Paina, layer 6	EE	Venetian Prealps	Lessini Plateau	25-50	5-270	Broglio et al., 2009; Bertola et al. 2018
			Umbria-Marche Apennine	250-270		
			Berici Hills	5-15		
Trene	EE	Venetian Prealps	Lessini Plateau	25-50	5-270	Broglio et al., 2009; Bertola et al. 2018
			Umbria-Marches Apennines	250-270		
			Berici Hills	5-15		
Buso Doppio Broion	EE	Venetian Prealps	Lessini Plateau	25-50	5-270	Romandini et al. 2015; Bertola et al. 2018
			Umbria-Marche Apennine	250-270		
Col de La Stria	EE	Venetian Prealps				
			Istria	5-15		
Šandalja II, layer C/d	EE	Istria	Friulan plain	25-50	5-200	This study
			Umbria-Marche Apennine	150-200		
Madonna dell'Ospedale	EE	Marche Apennine	Umbria-Marche Apennine	0-15	0-15	Cancellieri et al., 2015
			Northern Dalmatia	20		
Vlakno	EE	Dugi otok Island	Umbria-Marche Apennine	180	20-350	Perhoč, 2020
			Veneto Prealps	350		
Romualdova pećina	EE	Istria	Umbria-Marche Apennine	200	200	This study

Tagliente	LE	Venetian Prealps	Lessini Plateau	0-15	0-270	Bertola et al. 2018
Ljubićeva pećina	LE	Istria				
			Kupa River	30		
			Lika region	75		
Zala	LE	W. mountain Croatia	Istria	100	30-300	Vukosavljević et al., 2015; Perhoč, 2020
			Northern Dalmatia	115		
			Lessini Plateau	300		
Baracche	LE	Marche Apennine	Umbria-Marche Apennine	0-15	0-15	Peresani et al., 2005
Campo d. Piane CPD7	LE	Abruzzi Apennine	Apennine foot	5-25	5-25	Olive et al., 2017

Vegetation ecozones	Main ecoregions	Potential vegetation formations, characteristic plant taxa, and main predicting pollen and macrofossils types (marked with an * and a $^{\$}$, respectively)	Fossil sites in the ecozones	
	bare ice and debris covered glaciers	Cushion vegetation on fresh moraine ridges Other petrophytic vegetation Cryonival algal and microbial communities	No ancient ice preserved	
Alpine vegetation	other areas under active geomorphic processes	Alpine rockfields and steeplands	Cerete ¹ , Piovesello ²	
ecozones (unglaciated areas beyond the Alpine timberlines)	nival to sunny slopes (including nunataks)	Petrophytic deserts with <i>Plantago alpina</i> type*, <i>Armeria</i> *, Dipsacaceae* Rocky steppe Steppe-grasslands with <i>Carex humilis</i> , <i>Stipa</i> sspp. and xerophilous chamaephytes (<i>Helianthemum</i> *, <i>Artemisia</i> *, <i>Juniperus</i> *, etc.) Alpine grasslands with <i>Festuca</i> sspp. <i>Carex</i> sspp, <i>Sesleria varia</i>		
	cold waterscapes	e.g. Cold spring herb communities, cold limnic ecosystems		
Alpine timberline				
	stable or stabilized fields, no edaphic drought, especially on gentle slopes	Forests and woodlands. <i>Pinus mugo</i> dwarf forests at the alpine timberline mainly in the Eastern Calcareous Alps; open boreal forests; larch-scots pine woodlands at the continental timberline.		
<i>Mountain-piedmont ecozones under a moist climate</i>	edaphic drought, especially on limestone plateau, ridges, and sunny slopes	Grasslands, steppes, rocky steppes, alpine rockfields and steeplands (see above)	L. Alserio ³ , L. Annone ⁴ , Azzano Decimo ⁵ , Broion Cave ⁶ , L. della Costa ⁷ , L. Fimon ⁸ , L. Ganna ⁹ , L. Origlio ¹⁰ , Paina Cave ¹¹ , Paul di Manerba ¹² , L. Piccolo di Avigliana ¹³ , Pončo ¹⁴ , Povino ¹⁵ , Trana ¹⁶	
	cold waterscapes	<i>Salix</i> and tall-herbs riverside formations; cold limnic ecosystems		
	thermal springs (Euganei Hills)	Patches of thermophilous woody formations with <i>Corylus</i> , deciduous <i>Quercus</i> , <i>Tilia</i> , <i>Ulmus</i> , <i>Fagus</i> , etc (cryptorefugium)		

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<i>Mountain-piedmont ecozones under a semiarid climate</i>	stable terraced piedmont areas with loess accumulation and isohumic soils development under grasslands	Steppes and semideserts with Gramineae, Compositae, <i>Hippophäe*, Erica, Berberis?, Rhamnus*</i> Tree grooves (<i>Betula, Pinus</i>)	
	active megafans - bars, dunes and abandoned riverbeds on coarse- grained sediments	Edaphic semideserts with xerophytic herbs and shrubs (<i>Artemisia</i> *, Chenopodiaceae*, <i>Hippophae</i> *, <i>Juniperus</i> *, Ephedraceae*, etc.)	
Plain ecozones	stable surfaces - dune and loess fields under semiarid climate	Climatic semideserts and deserts with <i>Artemisia</i> and Gramineae (poorly documented by fossil sites)	Azzano Decimo ⁵ , Cà Fornera ¹⁷ , Casaletto Ceredano ¹⁸
(mostly depending on edaphic moisture)	active river channels in lower megafan belts	Riverside vegetations with tree <i>Betula</i> * and <i>Alnus incana</i> patches, and tall herbs (Umbelliferae). In drier spots, riverbed lithophyte communities with <i>Juniperus</i> * heaths and <i>Pinus sylvestris</i> * parkland, with Fabaceae, <i>Erica, Ephedra</i> *.	Galzignano ¹⁹ , Ghedi ²⁰ , San Donà di Piave ²¹ , Venice Lagoon ²² , L. Vrana ²³ , Valun Bay ²⁴
	fine-grained sediments under water- saturated conditions	Wetlands (<i>Carex</i> sspp., <i>Eriophorum</i> sspp., mosses, e.g. <i>Scorpidium</i> [§]), birch (<i>B. pubescens</i> [§]), poplar and alder swamps	

Tab. 1 - A frame of predicted ecological zones and summary of potential vegetation formations in the Great Adriatic - Po Region (GAPR) during the LGM and early Lateglacial (30 - 16 ka cal BP). The ecosystem classification here adopted relies on the recognition that ecosystem properties are closely tied to both physical and biotic site factors (see e.g. McLaughan et al., 2010; in mountain areas: xxx). The application of this approach to past environments embraces both the identification of predicting abiotic factors, provided by Quaternary geology (see sections xxx in this paper) and the biodiversity provided by a number of fossil palaeoecological sites. * - taxa documented by the pollen record; § - taxa documented by the macrofossil record.

Sites references: 1. Cerete (Ravazzi et al., 2012); 2. Piovesello (Peresani et al., 2018); 3. Lake Alserio (Wick, 2000); 4. Lake Annone (Wick, 1996); 5. Azzano Decimo (Pini et al., 2009); 6. Broion Cave (Cattani and Renault-Miskovsky, 1983); 7. Lago della Costa (Gubler et al., 2018); 8. Lake Fimon (Pini et al., 2010); 9. Lake Ganna (Schneider and Tobolski, 1985); 10. Lake Origlio (Tinner et al., 1999); 11. Paina Cave (Bartolomei et al., 1985); 12. Paul di Manerba (Ravazzi et al., 2014); 13. Lago Piccolo di Avigliana (Finsinger et al., 2008); 14. Renče (Monegato et al., 2015); 15. Revine (Casadoro et al., 1976; Wick, 2000); 16. Trana (Schneider, 1975); 17. Cà Fornera (Miola et al., 2003); 18. Casaletto Ceredano (Ravazzi et al., in prep.); 19. Galzignano (Miola and Gallio, 1998); 20. Ghedi (Pini, unpublished data); 21. San Donà di Piave (Miola et al., 2003); 22. Venice Lagoon (Serandrei-Barbero et al., 2005); 23. Lake Vrana (Schmidt et al., 2000); 24. Valun Bay (Schmidt et al., 2001)



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