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Title page

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

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Abstract

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 the dropping of the sea level to ~-120 m amsl. The combination of these two events triggered the aggradation of the Great Po Plain (GPP), a vast flat area between the Alpine chain, the Italian 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 the Alpine foothills supported more extensive forest stands, due to increased orographic rainfall. These were open boreal forests which persisted throughout the LGM, while open woodlands, steppes, semideserts and wetlands occupied the lowlands. A complex ecogradient, including both an Alpine and a continental timberline, is documented by the fossil records at the NE Alpine border, with a larch-pine forest-steppe belt, in contact with steppes and loess areas extending in the plain, on the dry extreme of the gradient. Still, edaphic wetlands occupied the waterlogged silty soils in the lowlands. Other areas, marked by active geodynamic processes, supported semideserts, i.e. grooves of xerophytic herbs and shrubs. Enhanced aridity and the development of deflation areas, prompted the accretion of loess cover at the northern and southern margins of the GPP. Fauna recorded the gradual disappearance of mammoth, woolly rhino and giant deer, together with cave bear. Gravettian and Epigravettian hunter-gatherer groups inhabited the GPP, although their presence and settlement dynamics at the margins and across this region has long been questioned. As a matter of fact, a handful of archaeological sites composes a patchy record of the peopling of the plain itself. At the northern rim of the GAPR, characterized by a well-developed karst region, several caves and rock shelters record the presence of hunters of bisons and horses at the margins of the GPP and ibexes and cave bears in some hilly landscapes. Nonetheless, evidence of contacts across this area is provided by the exploitation of chert sources and by stylistic and technical similarities in the lithic industries. The work resumes the currently available multidisciplinary data 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 Prealpine and the Apennine foothills, along with the Dinarids, were persistently settled.

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

1. Introduction

Since the time of the Middle Pleistocene Revolution, the increased magnitude of glacial cycles and unstable climatic conditions deeply influenced the human settlement dynamics. It is possible to 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 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 Palaeolithic *Homo sapiens* hunter-gatherers experienced dramatic biological turnovers during the Late Pleistocene as attested by discontinuous archaeological record (Djindjian et al., 1999, Bocquet-Appel et al., 2005). The timing and pattern of multiscalar shifts that occurred from the Last Glacial Maximum (hereafter LGM; 30-16.5 ka *sensu* Lambeck et al., 2014) to the onset of the Late Glacial (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 that led to the build-up of boreal ice sheets (terminology of millennial climatic phases in the following work is in accordance with Rasmussen et al., 2014). Their waxing drove sea level drop 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 major continental shelves (Fig. 1). In the Alps, glaciers were already growing before 30 ka BP (Martinez-Lamas et al., 2020) and reached their maximum extent around 25.0±1.7 ka cal BP (Monegato et al., 2017). It is also known that forested area was very reduced in central Europe and northern Europe was mostly treeless during the late MIS 3 (including GS-5) and MIS 2 (Willis et 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 ecosystems has been thoughtfully investigated in Northern and Eastern Europe (Maier et al., 2016; Tallavaara et al., 2015; Burke et al., 2017; Sinitsyn, 2015). Despite the ecological implications of huge geographic and climate changes (Antonioli and Vai, 2004), in Southern Europe several regions experienced more favourable conditions supporting the development of open boreal forests and highly productive wetlands (Willis, 2000; Monegato et al., 2015; Badino et al., submitted). This offered favorable environmental conditions for several mammal species (Svenning et al., 2008), which could here thrive, while large part of their former distribution areal, in Central and Northern 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 capability to maintain large-scale networks (Soffer and Gamble, 1990; Straus, 1991; Djindjian et al., 1999; Roebroeks et al., 2000; Moreau, 2009). South of the Alps, these more favourable conditions allowed the survival and delayed extinction of important consumers like cave bears (Terlato et al., 2019a).

FIGURE 1 ABOUT HERE

Human groups reacted to the ecological turnovers by increasing their resilience, as shown by a large array of evidence revealed by sites persisting at the middle latitudes. But also large migrations took place through the corridors connecting the European regions, and pronounced changes in 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 poorly understood: Djindjian et al., 1999). Lastly, this deeply contributed to the shaping of our present genetic ancestry (Fu et al., 2016; Posth et al., 2016). However, a full understanding of how Upper Palaeolithic groups modulated their biological, cultural and social adaptation to the Late Pleistocene climate change is still far from being achieved, especially in regions of strategic importance for their geographic position, geomorphological setting and biodiversity. One of these corridors was the vast continental shelf that emerged as consequence of the LGM sea level low stand, extending from the Western Balkan Peninsula to peninsular Italy (Maselli et al., 2014).

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 (hereafter GPP), a vast alluvial landscape composed by the Po Plain (the plain of the Po River and its tributaries, hereafter PP), the Venetian-Friulian Plain (the plain where present-day Venetian and Friulian rivers flow not joining the Po River, hereafter VFP) and the Adriatic Plain (the plain emerged during the LGM lowstand, hereafter AP) (Fig. 2). The GPP was at the centre of the Great Adriatic-Po Region (hereafter GAPR), circumscribed by the northern and central Apennines, the southern side of the Alps, and the Dinarides. The term Alpine (upper case) is used geographically to ecompass the Alps, whereas the term alpine (lower case) indicates the ecological zone above the 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 external sector of the Alps facing the GPP plains is a full mountain range but reaching lower elevations compared to the internal core sector of the Alps, not exeeding the 2,200-2,300 m amsl. We named such an external sector Prealpi (Prealps). It does not correspond to a foothills belt. Additional terms relate the Prealps indicating specific regions (Fig. 2). In this study we focus on the 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.

Aims of the work

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 witnessed vast movements of populations. The human adaptive flexibility expressed by the Gravettian-Epigravettian material culture, human mobility, subsistence and symbolic thinking from 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 circumscribing the GAPR, including the Italian Prealps. The present work aims to resume the current state of the art regarding the paleo-geographic, ecological and anthropogenetic circumstances and the evidence of the Late Pleistocene southern European population. We also present additional original data issued from a new petroarchaeological investigation aimed to reconstruct large-scale circulation patterns in the GAPR. These data consolidate the view that this region was settled and crossed by Gravettian-Epigravettian hunter-gatherers.

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 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 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 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).

2.1. Physical setting

For almost the whole Alps, wide portions of the Apennines and large sectors of the GPP, the LGM represented a morphogenetic phase of paramount importance because of the erosion produced by glacial and periglacial processes in the mountain catchments, and of the depositional phase, sustained by the glaciofluvial and fluvial systems, in the plains. Thus, before the LGM the 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 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 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).

New available data for the Dalmatian coast (Brunović et al., 2020) confirm that, since the end of MIS 5, the relative sea level of the Adriatic basin lowered below -50 m amsl (c.f. Antonioli et al., 2009), leading to a significant increase of the alluvial plain areas in MIS 4. During MIS 3, the marine level was probably between -60 and -90 m amsl (Benjamin et al., 2017), in agreement with the available reconstruction for the Red Sea (Siddall et al., 2003, 2010). At that time, a complex system of isolated lakes occupied part of the valleys exposed in the Kvarner Gulf and along the Dalmatian coast because of the sea-level fall (Miko et al., 2016; Brunović et al., 2020). This area was characterized by a karst landscape and by development of lacustrine environments, during the marine lowstand (Fig. 2). Some valleys in the Prealpine hills were also occupied by lakes, as the area of Fimon, in the Berici Hills (Monegato et al., 2011), and Palù di Livenza, in the Carnic 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 of human groups unlikely. During this cold phase, the GPP lowlands were characterized by highly dynamic environments with semideserts and rocky deserts; open boreal forest occupied the moister areas (see section 2.2). Such climate and environmental conditions are expected to have enhanced 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 moraines (Cremaschi, 1987, 1990; Wacha et al., 2011a, 2011b; Cremaschi et al., 2015; Peresani and Nicosia, 2015; Zerboni et al., 2015, 2018; Frigerio et al., 2017; Fontana and Ferrari, 2020; Badino 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 major Alpine glaciers reached their first maximum advance at the outlet of the valleys only around 26-25 ka cal BP. This is evidenced by the up-building of terminal moraines in the southalpine morainic amphitheatres (Monegato et al., 2007; 2017; Ivy-Ochs et al., 2018; Braakhekke et al., 2020) and the beginning of a consistent aggradation phase of the fluvial systems fed by the southern Alps (Fontana et al., 2014a; Rossato and Mozzi, 2016). The glaciers produced a strong dismantling action in the mountain catchments and supported the efficient transport of the eroded sediment to their fronts in the piedmont belt. Most of the major Alpine rivers acted as glacial outwashes, with a significant water and solid discharge that allowed the progradation and aggradation of alluvial megafans over the plain (Fontana et al., 2008). Those Alpine rivers that were not directly supplied by piedmont glaciers, together with the main Apennine fluvial systems, experienced a significant activity and formed large alluvial fans from their valley outlet (Castiglioni et al., 1997; Fontana et al., 2014a and reference therein). In the western PP, the general tectonic framework provided high accommodation space in the Savigliano basin, leading to the trapping of most of the fluvial sediment yield from the south-western Alps upstream of Torino (Piana et al., 2017). Just downstream of Torino, fluvial sedimentation was confined between terraces of older fluvioglacial 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 compared with the megafans of the central PP and VFP (Fontana et al., 2014a).

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

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

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 in the portion submerged by the Holocene transgression, where extensive and detailed geophysical surveys have been carried out (Trincardi et al., 2011). The recognized paleochannels have a rather small dimension, generally not comparable even to the Holocene ones, suggesting that significant part of water and sedimentary discharge was probably dispersed on the surface of the megafans. Moreover, in the northern sector of the AP, the LGM fluvial network was not incised but aggrading over the plain (Fontana et al., 2014a). North of the present Po River delta only a single small incised fluvial valley has been documented for the LGM, 30 km offshore of Chioggia, but this belonged to 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 NE Italy 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, where most of the rivers had a limited water and sedimentary discharge because of their karst catchments (Pikelj and Juračić, 2013; Felja et al., 2015; Furlani et al., 2016, Novak et al., 2020). Small ice-caps developed in the highest mountains but outwash fans were confined to polje areas (Žebre and Stepišnik, 2015; Žebre et al., 2016; Sarıkaya et al., 2020). It is likely that the related fluvial network was incised in the AP but, for a complete reconstruction of the LGM palaeogeography, a major obstacle is represented by the lack of information from the offshore sector of Croatia.

The idea of an AP with a well-formed and interconnected hydrographic network, as proposed in the first reconstruction by De Marchi (1922) and also described in recent papers (e.g. Amorosi et al., 2016), is hardly applicable to the unstable fluvial systems characterizing the LGM. 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 Adriatic Depression. Between 31.8 and 14.4 ka cal BP the delta aggraded for about 350 m of thickness over the scarp of the continental shelf but, because of the steep slope of the scarp, the coastline shifting was rather limited, in the range of about 30 km during the LGM (cf. Pellegrini et al., 2017, 2018).

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 hunters-gatherers 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 withdrew towards the upland catchments, leading to dramatic changes both in the Alpine valleys and in the alluvial plains. Between 22 and 17.5 ka cal BP part of the fans and megafans did already experience an erosive phase, which led the active channel to entrench in their apical portion. The northern sector of PP experienced the entrenchment of the Alpine rivers up to their junction with the Po River (Marchetti, 2001). The VFP major incised valleys formed in the alluvial megafans of the Tagliamento and Piave Rivers (Carton et al., 2009; Fontana et al., 2014a) between 19 and 15 ka cal BP, while in the Brenta megafan they started after 17.5 ka cal BP (Mozzi et al., 2013). Thus, between 19 and 16 ka cal BP, the GAPR experienced a dramatic change in the geomorphic 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 about 16.5 ka cal BP also the rapid sea-level rise begun (Lambeck et al., 2014), but the position of the Adriatic coastline started to change considerably only after 15 ka cal BP, when the sea stepped over the edge of the continental scarp and could transgress over the AP.

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).

2.2. Ecozones of the Great Adriatic-Po Region in the Last Glacial Maximum, their vegetation 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).

The vegetation of the plain ecozones. Active megafans were pioneered by edaphic semideserts, 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 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 mm; see Badino et al., submitted) that developed in the depressed Adriatic plain. Here we also envisage riverside vegetation relevant both for the mammal fauna and the humans, but the palaeoecological documentation is scarce (Tab. 1). Extensive wetlands developed in the lower 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 Adda megafan (Ravazzi et al., 2018, 2020).

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., submitted) document the continental boundary of the forested region at the NE Alpine border (Fig. 3). The modern pollen analogues lie in the forest-steppe ecogradient in the Altaj mountains at the Russian-Mongolian border (Chytrý et al., 2008; Magyari et al., 2014; Badino et al., submitted), with a larch-pine forest-steppe belt at the continental timberline limit (300 mm annual rainfall and boreal continental climate; Zhambazhamts and Bat, 1985; Makunina, 2016), in contact with steppes and loess areas on the dry extreme of the gradient. The structure and position of the elevational timberline in the LGM is hardly documented by fossil elevational sites, so far available for the early Late Glacial only (Vescovi et al., 2007; Ravazzi et al., 2012). Based on modern Asian pollen analogues, an ecoclimatic elevational model based on temperature lapse rate (Gorbunov, 1978; Matthews, 1992) allowed estimating the elevation of the Alpine timberline at around 700 m in the NE Prealps (Ravazzi et al., 2004). It is envisaged that *Pinus mugo* dwarf forests played an important role at timberline elevations on areas characterized by carbonate bedrock in the Eastern Prealps (Ravazzi and Vescovi, 2009), especially on south-facing slopes with periglacial activity. According 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 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 MIS 3 stadials (Berici Hills = 10 cm winter snow height) to an advanced phase of the LGM, 21 ka cal BP (Berici Hills = 138 cm winter snow height) (see Barron and Pollard, 2002; Pini et al. 2010, their tab. 4).

The alpine vegetation ecozones. A wide ecotone of alpine grasslands, steppe-grasslands and petrophytic semideserts is predicted to have withstood the LGM on stable unglaciated areas beyond the elevational timberline (Tab. 1). Unfortunately, this figure is still poorly documented by fossil sites and only at low elevation (Fig. 3; Ravazzi et al., 2012). This ecozone supported rich populations of ungulates and preserves hotspots of endemic herbs and invertebrate herbivore communities. The biodiversity in this ecozone experienced great success downhill of its interglacial range, following late MIS 3 forest withdrawal (e.g. Pini et al., 2010). The alpine ecozone is predicted to have expanded downhill over the sunny slopes. Still, these communities were able to settle areas over the valley glaciers (Antonioli and Vai, 2004). The range of many species shifted 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, and back at the Late Glacial climate reversal. Consequently, the LGM refugial areas of mobile 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), 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.

2.3. Zoogeographic setting

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

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 Tyrrhenian side of Italy (Breda, 2002) and which retired in north-eastern Europe as well. This distribution of some elements of the fauna, supports the idea of the existence of two distinct bioprovinces (Sala and Marchetti, 2006). On the contrary, animals such as mammoth, wholly rhino, giant deer and bison dispersed through the entire peninsula, reaching the Tyrrhenian side but also as far south as the Salento (Puglia region, Petronio et al., 1996). However, during the LGM, further immigration from the nearby Pannonian basin did not take place probably because the north-east passage through Slovenia was inaccessible due to the high snow cover (Sala, 2004). So, when 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 pardus*), the cave bear (*Ursus spelaeus*), and the hyena (*Crocuta crocuta*), toward the end of the LGM, they left a much-impoverished fauna (Sala 2007). Particularly, the radiocarbon dating of cave bear remains from the Berici Hills in the subalpine area (n°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 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 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 along the meltwater rivers and wetlands at the edge of the VFP and favourable winter temperatures on low elevation karstic hills allowed their survival here for few additional thousand years. Isotopic 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 settled the same district, were (probably) the forcing factors leading to their final extinction. A similar trend could be envisaged also for *Ursus ingressus*, an intrusive species in this region and representative of the genetically impoverished relict of a larger East European population, as revealed from the sequencing of mitochondrial DNA (Gretzinger et al., 2019).

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°26 in Fig. 3), associated with horse (Riedel, 1980), at Manerba in the glacial amphitheatre surrounding the Garda lake (n°12 in Fig. 3 - Ravazzi et al., 2014), at Settepolesini quarry at the centre of the Po Plain (n°25 in Fig. 3 - Sala, 2001), at Cava a Filo quarry at 225 m of elevation in the nothern slope of the Apennine (n°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 differentiated fauna. Three chronological intervals have been recognised through radiocarbon dating, representing two cold intervals of the LGM and the beginning of the LG (Paronuzzi et al., 2018a). *Megaloceros giganteus* appears in the Cava a Filo 1 association with *Meles meles*, *Lepus timidus* and *Marmota marmota*, which in Cava a Filo 2 association, are joined by *Vulpes vulpes*. Cava a Filo 3 dates to 18.6-17.4 ka cal BP and records an increased diversity with *Sus scrofa* and *Mustela erminea*, in addition to the large mammals already present in the older levels, consistent with a more forested environment and with the climatic amelioration of the beginning of the LG (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* persists beyond 16.4 ka cal BP in virtue of its reduced nutritional requirements that allowed it to thrive also in arid steppes where more demanding herbivores could not survive (Sala and Gallini, 2002).

In the foothills and subalpine area of southeastern Alps, the ibex is the most common species during the LGM. The deer and the roe deer are very rare like the Equidae (Bartolomei et al., 1977). As noted by Sala (2007), in the sites dated to the earliest LG period on the Berici hills and at the foot of the Venetian Prealps, the ibex is still very abundant, together with the chamois where steep slopes are present (e.g. lower levels of Riparo Tagliente; n°30 in Fig. 3 - Fontana et al., 2009). Archaeofaunas from cave deposits also record the presence of carnivores like *Vulpes vulpes*, *Felis silvestris* and *Canis lupus* in addition to the cave bear (Romandini and Nannini, 2012). The moose is recorded and relatively abundant both in the plains along with the bison (e.g. Settepolesini). 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 habitats, it can span a wide variety of environments and climates (Breda, 2001; 2002). Conifer or mixed open forests with grasslands, slow-flowing water bodies and mountain meadows with rocky outcrops are are the habitat predicted by bird assemblages from sites in the Carnic Prealps (Grotta Rio Secco: n°31 in Fig. 3 - Carrera et al., 2018a) and the Berici Hills (Buso Doppio Broion: n°6 in Fig. 3 - Carrera et al., 2018b) alongside with sparse cyprinid and salmonid remains (Romandini et al., 2015). Furthermore, the presence at the onset of LGM of *Bubo scandiacus* and *Surnia ulula*, two cold-adapted species currently distributed at high latitude in the Boreal hemisphere, is a clear 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, along with the horse, and frequently *Equus hydruntinus* as well. In the southern sector of the GAPR (not included in this work), the bison is replaced by the aurochs, which are numerous there, while 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.

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).

3.1. Cultural background

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 the Danube basin to the Mediterranean regions (Montet-White, 1996). Evidence of this is the spread of the Gravettian and Epigravettian cultures, which are recorded with detail up to the southern Adriatic coast (Palma di Cesnola, 2004). Gravettian-Epigravettian societies adapted in response to environment, resources and exploitation strategies; technical hunting behaviour turns out to be a key element in the identification of these phenomena (Wierer, 2013). Backed tools are the most diagnostic trait of the Gravettian and their typological features were used for its tripartite subdivision into early, middle (evolved) and late (final), being the first phase characterized both by invasive backed points and the occurrence of marginally backed points. Among these latter, the specific type *fléchette*, a leaf-shaped point characterized by marginal semi-abrupt retouch sometimes inverse at one or both ends of the blade blank, is rather typical for the early Gravettian as confirmed at Grotta Paglicci, layer 22 (Palma di Cesnola, 2004). This technocultural facies (also 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 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 addition to scrapers made on flake and to splintered pieces. The Gravettian is also known for the vast array of burin types, considered as diagnostic elements of specific cultural facies diffused in a short time-span at the regional or supraregional scale after the early Gravettian. This is the case of the *Noailles* type, a burin spread from Western Europe to the Tyrrhenian coast of Italy (Palma di Cesnola, 2001) and inland until the western slope of the Central Apennine at 28.6-28.0 ka cal BP (Aranguren and Revedin, 2008), but which is completely absent in Adriatic Italy (Gambassini, 2007), the Balkan region (Mihailović and Mihailović, 2007) and Greece (Adam, 2007). Partition of the middle phase of the Gravettian along the Italian Peninsula in two facies based on the presence or absence of burins correlates to the biogeographic zonation described above.

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 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 assimilation of innovations in the technical behaviours of neighbouring regions (Moreau, 2009). This could also have been the main factor leading to the first appearance of the techno-complex with shouldered points (Fig. 5), the iconic tool of the third phase of the early Epigravettian, in western Balkans and the GAPR refugia, settled by late Gravettians coming from the middle Danube region. Kozłowski (1999; 2008) suggested to trace the occupation of this region by the early Epigravettians on a morpho-stylistic comparative analysis with similar eastern types, like the Kostienky and Willendorf ones. To this lane, Broglio (1997) revealed a delayed trend in the appearance of shouldered points according to the latitude position of the sites towards the south of 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 Jama and Šandalja II cave (although challenged from the date of layer 17E – 23.9-23 ka cal BP - at Grotta Paglicci; Palma di Cesnola, 1993). More recently, alternative points of view have been offered. After Borić and Cristiani (2016), it is possible that the design, manufacture and use of shouldered points were transferred as a cultural package along networks developed between populations, rather than these tools were directly spread in consequence of the movement of human groups. Further on, the shouldered point as cultural marker has been challenged by the extension of its chronological range. New dates from Kastritsa cave in Greece and Vrbička cave in Montenegro 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 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 identification of a specific cultural facies (Vukosavljević and Karavanić, 2017), and claims for renewed analyses.

FIGURE 5 ABOUT HERE

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

Correspondingly, the chronological position of the lower boundary of the late Epigravettian is still 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 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 Baracche (Marche area) and Campo delle Piane (central Apennines) at 18.4-17.9 ka cal BP. Both these open-air sites were extensively excavated (Olive, 2017; Peresani et al., 2005), thus yielding a large amount of lithic artifacts with common tools and hunting implements. A later chronology is provided by Tagliente rock-shelter in the Venetian Prealps, where the lowermost layers of the Epigravettian series dating back between 17 and 16 ka cal BP, attest the presence of sporadic items of this typology (Bartolomei et al., 1982; Fontana et al., 2012, 2015, 2018).

Trends driving responsive technology in tool making might have been encouraged by the possibility 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-how 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 available evidence remains too sparse yet.

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

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

TABLE 2 ABOUT HERE

3.2.1. Factors of bias

Speculating about the organization of a settlement system extended in a now submerged geographic zone like the Adriatic Plain could be meaningless due to weakened reliability of any proposed scenario. The loss of a large continental land extent due to the rise of the sea-level during Termination I was the most relevant change in the geographic setting of the GPP, leading to the submersion of the Adriatic Plain. The incision of the Alpine alluvial megafans led to the downstream formation of LG fans (Fontana et al., 2014a) alongside with the Apennine alluvial fans, which also grew over the LGM plain (Amorosi et al., 2016). Wetlands and lowlands patterns on marine coasts or around lakes and marshes, riverside forests, desert landscape were all potentially settled environments, the exploration of which is prevented to us. Furthermore, also the paucity of 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 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 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 local settlement systems.

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

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

3.2.2. Distribution of the radiocarbon dates

Except for some sparse surface findings and very few open-air sites, most Gravettian – Epigravettian sites in the GAPR were radiocarbon dated to the LGM chronological range (Tab. 2 and Fig. 6). Aside Piovesello, Riparo Broion, Stria, Rio Secco, Ponte di Pietra, Paina, Trene, Riparo Tagliente, Romualdova Pećina and Campo delle Piane, only one date is available for each site or layer from multilayered archaeological sites. Charred wood is the most dated material, followed by animal bone, human bone (Tagliente), and organic silt associated with charcoal (Fonte delle 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 information neither about the xilotomic determination for charred wood samples (with the exception of Büs dei Lader: *Larix*), nor about the taphonomy of animal bones (natural or anthropogenic origin?). For most contexts, dispersed charcoal fragments were collected from archaeological layers, with only few cases documenting sampling from fire-places (Riparo Broion, Campo delle 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.

The dates cover with discontinuity the LGM range, being the Pećina kod Rovinjskog Sela 1 (Pećina Cave near Rovinjskog Selo 1), Piovesello, Grotta Broion and Riparo Broion, Rio Secco and Fonte delle Mattinate positioned in the 33-29 ka cal BP interval. Radiocarbon chronology at Grotta

Fumane in the Lessini Mountains marks one of the oldest range ever recorded in Europe for an early Gravettian industry and it is currently under discussion. Sporadic lithic artefacts, backed bladelets and one Vachons point were discovered in association with an extended accumulation of charcoal in layer D1d, embedded in the detrital macro unit D, whose deposition filled-up the main entrance of the cave (Falcucci and Peresani, in press). Following this first group of sites after a gap of few thousands years, human presence is testified on the Berici Hills, the foot of the Marche Apennine and in the Karst, starting from 25 ka cal BP in the late/final Gravettian and all along the early Epigravettian until 21 ka cal BP. Dated sites are very sparse in the three following millennia, provided by only one site in the Berici Hills (Stria) and in Northern Dalmatia (Vlakno) and by the exception of Büs dei Lader, a small cavity in the Prealpine foothills west of the Garda glacier front. Although the charcoal fragment from Büs dei Lader was determined as *Larix*, its association with the only artifact found in 1956 during a survey remains uncertain (Biagi, 2000). Starting from 18 ka cal BP, late Epigravettian groups settled at the foot of the Marche Apennine and then in Istria and inland. Interestingly, after the collapse of the Garda glacier, human groups frequented persistently the foothills of the Veneto Prealps (Tagliente) and inland in Western Mountain Croatia (Zala). Given this distribution of the archaeological dated evidence across the LGM, the peopling of the 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-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 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 support a complete scenario of settlement dynamics during the Gravettian.

FIGURE 6 ABOUT HERE

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 layers C, D and E in the main cavern (Sala Grande) and in a small lateral cavity (Grottina delle Marmotte) (Leonardi and Broglio, 1951, 1954). Riparo Broion was settled before and in the same chronological range as Grotta Broion. Typological features of the backed points and backed 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* and *microgravettes* and backed bladelets and, in addition to the presence of impact fractures on these artifacts, points to interpreting this settlement as strictly related to hunting parties (De Stefani et al., 2005). The previous attribution (De Stefani et al., 2005) of these layers to the early Epigravettian was based on the presence of fragmented shouldered points, unifacial leaf pieces and 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 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 shouldered points at Riparo 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 end-scraper, burin-cores), backed points and bladelets recovered sparse in layers 4 and 6 where remnants of fire-places were also brought to light (Peresani et al., 2014).

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 by lithics, faunal bones and marine shells was produced from a survey in 2007.

A context partly comparable to Piovesello has been reconstructed from geoarchaeological 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 - 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 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 constraining human mobility in the innermost zone of the central Apennine (Giaccio et al., 2004; Silvestrini et al., 2005a).

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

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

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 points to an exclusive presence of open-air sites, close to streams and major rivers, at the lower end of gorges. Such sites were devoted to extractive and productive activities undertaken during short-term visits. The set of available radiocarbon dates, for instance, constrains the occupation of Ponte di Pietra and Fosso Mergaoni sites between 25.2 and 20.9 ka cal BP and between 22.5 and 21.4 ka cal BP. Ponte di Pietra is situated along the river Misa, in a district plenty of excellent lithic resources (Lollini et al., 2005). Fosso Mergaoni is mainly featured by two groups of lithic workshops scattered on the alluvial ground. The spatial pattern with intra and inter-workshop refittings, the paucity in retouched implements, the technological composition of the lithic artifacts concentrations, the low incidence of use-wear related to the acquisition of alimentary resources and to the processing of animal resources observed on a sample of artifacts, prove that the site was 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).

3.2.5. Early Epigravettian

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 bladelets, shouldered points and *microgravettes* backed points. Minimal archaeological remains 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 weapons for huntings (backed points and backed bladelets) together with unretouched blade and bladelet blanks. Shouldered projectile points found at Paina and Trene bear impact scars, which consistently provide hints for interpreting these contexts like short-lived campsites and hunting stands (Broglio et al., 1993; 2009). At Buso Doppio Broion, recent excavations brought to light a sequence where the uppermost layer 1tt.1I and reworked sediments yielded backed and shouldered points (Romandini et al., 2015). According to the radiocarbon date, the presence of fragmented shouldered points and of unifacial leaf pieces mentioned above, Riparo Broion was settled during the early Epigravettian (De Stefani et al., 2005). A marginally retouched point is the only archaeological find recovered at Büs dei Lader (Biagi, 1976). No data on the early Epigravettian settlement at Stria Cave have been produced yet.

The site Madonna dell'Ospedale lies on a fluvial terrace along the Rudielle stream valley, one of the incisions which dissects the Cingoli Mountain ridge (Marche Apennines). Chert in this zone, especially from Maiolica and Scaglia, is of the most excellent in the Marche Apennines. The site has been culturally attributed on a tecnological and typological basis (shouldered points) and interpreted as specialized for the production of blanks and the manufacture of hunting weapons (Silvestrini et al., 2008; Cancellieri, 2015). In the north-western Balkans, the earliest spread of the early Epigravettian comes from Šandalja II. In the Slovenian karst, reference sites for the early Epigravettian are Zakajeni Spodmol, Ovčja Jama, Županov Spodmol and Jama V Lozi (with one shouldered point) (Montet-White, 1996). A shouldered point was found at Romualdova pećina, another site on the Lim channel in Istria also known for cave paintings likely attributed to the Aurignacian (Ruiz-Redondo et al., 2019). Similarly to the Berici area, cave and sheltered sites are generally interpreted as temporary encampments located along mobility routes used by small groups of hunters, which is suggested by the limited amount of tools and the ephemeral indications of knapping activity. In some cases, like at Županov Spodmol, Epigravettian groups reached the cave equipped with finished tool kits as well as some cores that were further exploited on site. In the case of Ovčja Jama, a more intensive use of the site is documented, along with a possible longer-term occupation (Montet-White, 1996).

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).

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

The evidence from Riparo Tagliente is more consistent than the sites described above. This site attests the first re-occupation of the south-eastern Alps at the end of the LGM, starting from 17 ka 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 location along the corridor of Valpantena giving access to the Lessini plateau and the inner Alps have enhanced its intense occupation along time (Fontana et al., 2009). All late Epigravettian layers document an intense activity of exploitation of the Lessini abundant chert outcrops and ochre deposits (Fontana et al., 2015; Cavallo et al., 2017), while in the area protected by the over-hang of the shelter several dwelling structures were uncovered (Fontana et al., 2018). Tagliente has also yielded one of the most important Epigravettian collections of tools made of animal hard materials and ornamental objects, as well as a series of mobile art objects and a burial dated to 16.6-15.5 ka cal BP (Guerreschi and Veronese, 2002; Gazzoni et al., 2013).

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 lithic artefacts. Blades are produced off site, backed bladelets are the most frequent tool type, 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).

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

3.3. Exploitation of faunal resources

Only a handful of sites has produced zooarchaeological data testifying for game hunting. This is the 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 observed on cervids (*Cervus elaphus* and *Alces alces*), caprids and wild boar as well as on cave bears (*Ursus spelaeus*, sensu lato) at Paina, Trene and Buso doppio Broion (Romandini and Nannini, 2012; Romandini et al., 2015). Cut-marks on several bear remains enable a reconstruction 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 zooarchaeological evidence. At Zala, hunters targeted red deer and moose more than auroch (*Bos primigenius*). Similarly to the Berici Hills caves, carnivores like brown bear (*Ursus arctos*) and wolf (*Canis lupus*) were processed, as attested from butchery marks (Radović, 2015).

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

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 their high mobility across the GAPR is given by petrographic data on the provenance of lithic raw materials, complemented by similarities in lithic industries from sites in north-eastern Italy, Slovenia and Istria (Broglio, 1994). However, our knowledge on the use and circulation of cherts from the GAPR is sparse and biased by differences in the development of investigations. Some information is available in the literature for most of the sites taken into account in this work and additional data are provided from new studies presented here. For the purpose of this investigation aimed to achieve indicators of chert provenance, petroarchaeological data are presented only at qualitative level. For access to computations of each lithic assemblage see references in tables 2 and 4.

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

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 distribution according to the regional palaeogeographic domains. Southern Alps, Dinarides and Eastern Alps share a common paleogeographic and tectonic evolution since late Triassic and each domain was composed of different sub-domains such as shallow-water platforms, submarine 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 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

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 (Calcari Grigi, Rosso Ammonitico, Maiolica, Scaglia Variegata Alpina, Scaglia Rossa, Scaglia Cinerea) with abundant chert nodules and beds, some of them with exceptional rheological properties due to their fine texture and homogeneity. Over the submarine plateaus, the series are much more condensed and with different features both in sedimentary sequences and chert properties. In adjacent areas such as the Karst or Dalmatia, where sea depths were shallower during 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 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 and Tab. 3); this basin was delimited to the south by the Ancona-Anzio line, separating from the Lazio-Abruzzi shallow shelves.

FIGURE 7 AND TABLE 3 ABOUT HERE

Since the Oligo-Miocene, at the foot of the Alps, the Venetian-Friulian foreland basin developed (Massari et al., 1986; Stefani et al., 2007) and the cherts, eroded from the Southern Alps, were redistributed in the clastic wedge; the coarser are preserved in the Montello, and other conglomerates (Massari et al., 1974). At the same time, at the front of the Apennine chain, very deep foreland basins formed, and the distribution of the Oligo-Miocene cherts in the northern Apennines is mainly linked to the evolution of these basins NW-SE or even N-S oriented. In this 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 developed at different times, thus giving distinct features to each group of cherts.

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

In the Karst and Dalmatia, cherts are scarce and confined to few epicontinental basins. Allochthonous siliceous clastic deposits of the Triassic, devitrified tuff and siliceous claystone (green stone), and only a minor degree radiolarite and chert, occur on the northern side of the Velebit Mountain (Sokač, 2009) and in primary exposures in the hinterland of Dalmatia in the vicinity of Muć (Šćavničar et al.,1984), as well as on the Island of Palagruža (Korbar et al., 2009). Upper Jurassic chert of poor quality to knapping are documented on islands in Dalmatia (Velić and Vlahović, 2009). Conversely, upper Cretaceous (Cenomanian – Maastrichtian) chert of markedly different quality is provisionable on limited outcrops scattered throughout Dalmatia and on the Dalmatian islands of Korčula, Brač, Dugi Otok and in the subregion Zagora (Fuček, 2009; Perhoč, 2009, 2020). Chert is largely more frequent in the Lower to Middle Eocene Foraminifera limestones and in the Middle to Upper Eocene Flysch exposures than in the upper Cretaceous one (Sikošek, 1971; Perhoč 2020). Also, in Istria chert is embedded in Cretaceous limestone (Šikić and Pleničar, 1975; Polšak, 1970; Šikić and Polšak, 1973), exceptionally in Jurassic deposits of plate limestone (Polšak and Šikić, 1973). Small outcrops are scattered through the region, with highest 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 northern Istria.

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

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

Investigating human mobility across the GAPR requires detailed determinations on the knappable materials used at Gravettian - Epigravettian sites located at far distance from the primary 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 reasons due to unaccessible or not yet analysed material (Tab. 4).

Geological surveys conducted previously the present work have produced qualitative data on the 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 of the outcropping formations, the latter ratified by the International Commission of Stratigraphy and, for the Italian territory, mapped by the ISPRA. The systematic prospecting and sampling, carried on since the 90's of the 20th century by one of the authors (SB) and other researchers of the Ferrara University, on the Southern Alps and Northern Apennines, allowed to build a large and 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 (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.

In addition to this lithoteque, this work has also considered two other raw materials collections. The first from the Marche Apennines, in the Gola della Rossa e Frasassi Natural Park, where chert sources were surveyed, mapped and characterized. Moreover, availability and suitability of cherts 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 of the University of Ferrara as well. The second raw materials collection covers Istria and Dalmatia, where systematic researches on lithic collections and outcropping knappable rocks have been carried on in the last two decades (Perhoč, 2009; 2020). This lithoteque is stored at Zlatko Perhoč's home, Mannheim, Germany.

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 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® (Geological Society of America, 1964). In a second step, the geographic provenance of the cherts was tentatively circumscribed on the basis of laterally variable features within the same formation. 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 the cherts like soils or paleosoils, slope, present stream channels and coarse alluvial deposits.

We finally scrutinized under multivariable optical stereomicroscope (Optika SZ series, 45X with camera Moticam 3+ USB 3) the microfacies (petrography, mineralogy, microstructures, inclusions, microfossils) of the geological and archaeological cherts. Additionally, we analysed with a mineralogy microscope (Olympus BX40) under polarized light the thin sections of some geological cherts of the area.

We determined microfossils using comparison atlas (Robaszynski and Caron, 1995; Bolli et al, 1985; Premoli Silva and Sliter, 1995, 2002) and other references (among them Cita, 1964; Erba and Quadrio, 1987; Luciani, 1989; Sliter, 1989).

FIGURE 8 ABOUT HERE

4.3. Results (Tab. 4 and Fig. 9)

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 Apt-Foucalquier 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).

Venetian and Friulian Prealps

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

Grotta Rio Secco, layer 6, Gravettian. Chert has been provisioned in a radius of 50 km from this site in the Carnian Prealps where different Triassic to Cretaceous formations oucrop, uplifted and deformed from intense and still active tectonic activity: Buchenstein, Soverzene, Igne, Verzegnis, 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 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 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 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).

Grotta Broion (layers C-E), Gravettian. There are a few artifacts made with different chert types from the Berici Hills and Euganei Hills (5-15 km) and the Lessini Mountains (25-50 km), the latter chosen expecially for blade production (Bertola et al., 2018) (Tab. 4 and Fig. 9a).

Riparo Broion, US 1a-d. Gravettian. Similarly to the Grotta Broion, the exploited raw materials 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 (Bartolomei et al., 1985) contain a few lithic tools (23 and 47 respectively) almost entirely made of allochtonous chert (78% and 89%; Broglio et al., 2009). Varieties belong to the Maiolica, Marne a Fucoidi, Scaglia Rossa, Scaglia Variegata (Tab. 3, Figs. 10.7 and 10.8) formations outcropping in the Umbria-Marche region (Tab. 4, Figs. 9b and 9c). There is no evidence of intra-site flaking or retouching of these allochtonous raw materials. The scarce Berici-Euganei chert artefacts are all unretouched and consist of blade and bladelet fragments but also cortical flakes and small flakes (*debris*), attesting sporadic flaking activities at the site. Four backed bladelet fragments are made of excellent Lessini cherts of the Scaglia Variegata Alpina; these pieces were introduced finished onto the site (Broglio et al., 2009; Bertola et al., 2018).

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).

Buso Doppio Broion, layers 1 and RIM, early Epigravettian. Among the 46 studied artifacts (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. Cherts show greater variability with respect to the previous described assemblages, possibly suggesting different or wider exploitation areas (Tab. 4, Fig. 9c). They belong to the following formations: Bisciaro, Scaglia Cinerea, Scaglia Rossa, Scaglia Bianca, Marne a Fucoidi and Maiolica (Tab. 3, Fig. 10.10). Lessini cherts are represented by seven artefacts, six of them retouched (backed tools) and one crested bladelet. The Berici-Euganei cherts artefacts (26) were also flaked on site to produce blade, bladelets and backed tools, but not the shouldered points. (Romandini et al. 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).

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, recent studies have isolated a group of implements made on extra-regional cherts, quite all belonging to the Umbria-Marche basin Scaglia Rossa lithotypes absent from the same areas 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 Diasprigni (upper Jurassic) Umbria-Marche cherts were identified (Tabs. 3 and 4, Figs. 9d and 10.12). The assemblage includes 13 retouched tools (among which nine backed fragments, one burin, one endscraper, one truncated blade and one pointed piece), 35 unmodified blanks (including bladelets, flakes, semi-cortical blanks and maintenance elements) and three bladelet cores (Bertola et al., 2018). Allochthonous Apennine cherts reduce in number in the later times during the LG interstadial.

FIGURES 9 AND 10 ABOUT HERE

Karst, Istria and Dalmatia

Šandalja II cave, layer C/d, early Epigravettian. In our preliminary study, petrographic 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) 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 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. 3, Figs. 11.17 and 11.18) and probably also a kind of Maiolica (with bioturbations, typical of the Southern Alps) were identified as well. Among the local cherts, there are easily recognizable types, deposited in shallow waters, with evident stripes (stromatolitic laminae, algae) often with a 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 from fine crystalline gray to yellow color, and radiolarians and *Rotalipora* (Albian/Cenomanian) has been more problematic due to the existence of petrographic similitudes in cherts shared between the Umbria-Marche Apennine and the Southern Alps. For these types more detailed analyses will be required. Artefacts made of yellow fine crystalline chert with radiolarians and Rotalipora (Albian/Cenomanian) likely attributable to the Scaglia Variegata Alpina (Southern Alps, Friuli/Veneto regions) or to the Scaglia Bianca (Umbria-Marche) are also present in layer B/C.

Romualdova pećina, no context, early Epigravettian. We identified chert of Umbria-Marche Scaglia Rossa on one shouldered point (Tabs. 3 and 4, Figs. 9d and 11.14).

Vlakno cave, layer 32, early Epigravettian. Blade artifacts document exploitation mainly of eastern Adriatic chert, but also use of chert originating from Umbria-Marche Apennine and Venetian 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 Lika region and northern Dalmatia, and west of Istria and more far to the Veneto Prealps. The latter source supplied half of the artifacts (Perhoč, 2020; Vukosavljević et al., 2015) (Tab. 4, Fig. 9d).

FIGURE 11 ABOUT HERE

Marche-Abruzzi Apennine

Fonte delle Mattinate, layer SU B27, early Gravettian. The exploited cherts are from the Umbria-Marche 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 Cervarola-Falterona Unit outcrops (Silvestrini et al., 2005a) (Tab. 4, Fig. 9a). This exogenous arenitic chert was used to produce a point.

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

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

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 western Adriatic that yielded gastropods and bivalves. The commonest species used during the Gravettian is *Homalopoma sanguineum*, an herbivorous gastropod associated with sea grassland (es: *Posidonia*) and rocky seabeds and distributed in the Mediterranean Sea from the intertidal belt 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 perforated (Gurioli, 2005). Since the Uluzzian, but mostly in the Protoaurignacian, *H. sanguineum* is a shared cultural-symbolic element in Southern Europe and also in the GAPR as observed at 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 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 Carpatians (Alvarez-Fernández, 2006; Vanhaeren and D'Errico, 2006; Morales et al., 2019; Perlès, 2018; Niţu et al., 2019). Its use has been recorded on the Tyrrhenian side at Riparo Mochi (Stiner 1999), Grotta di Castelcivita (Tassoni, 2019), Grotta La Cala (Tassoni, 2019) and Grotta Serratura (Martini et al., 2003) and along the eastern side of the Italian Peninsula at Grotta Cavallo (Arrighi et al., 2020). The *Homalopoma* specimens found at Ponte di Pietra testify the use of this gastropod at the end of the Gravettian. The thickness of the shell wall may have also been an important feature, as personal ornaments made of thicker shells might require greater manufacturing skills and time.

The use of this species' shell decreases considerably during the Late Epigravettian, being replaced by *Tritia* sp. and *Columbella rustica* as the main ornamental components (Cristiani et al., 2014; Martini et al., 2003; Perlès, 2018). The oldest settlement phase of the Late Epigravettian 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%) with prevailing *T. neritea* followed by *T. pellucida*. All other species are either represented by few specimens each (*Dentalium cf. inaequicostatum*, *H. sanguineum*, *Nassarius cf. pygmeus*) or by just by one item (*Aporrhais pespelecani*, *cf. Neverita josephinia*, *Gastropoda* indet., *Glycymeris* sp., *Nassarius costulatus cuvierii*).

A shell beads assemblage was also discovered in the late Upper Palaeolithic layers of Zala, dated to the end of LGM. The assemblage consists of 15 marine *Cyclope neritea* perforated shells. A fragment of *Pecten jacobaeus* shell provides additional evidence for contacts between LGM coast and the inland where Zala is located (Vukosavljević and Karavanić, 2015).

A variety of hard animal materials has been deliberately modified to shape beads. However, 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).

6. Discussion

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 for Gravettian and Epigravettian hunter-gatherers. The view that the mountain ranges and their forelands around the GPP could have provided profitable habitats for the subsistence of human populations was questioned several times since the end of the 80's of the 20th century. A major point of discussion regards the role played by the plain in facilitating the seasonal aggregation of bands from both sides of the sea. According to Mussi (1990), the gap in the early Gravettian archaeological record of Italy and the gradual disappearance of items like funerary goods or mobile art bringing complex symbolic significance observed up to the end of the Gravettian should be related to slackening in the social relations established among human groups, presumably correlated to the general decrease in population density. Southern Europe did not escape the consequent disruption of networks and disappearance of long-range social relationships. Isolated by the glaciated Alps, the GAPR was connected to the sparsely inhabited western Balkans, sporadically exploited by small groups. Mussi (1990) suggests, in disagreement to a more consistent evidence of repeated human frequentations at the multilayered sites distributed along the Tyrrhenian belt and in 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 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, 2001). The Karst, at the north-eastern edge of the VFP and AP was also considered to be an inhospitable land during the LG, unforested and generally poor in vegetation, because of its dryeness (Boschian and Fusco, 2007).

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 the coastal and estuarine environments, and thus attractive for human populations (Van Andel, 1989; Shackleton et al., 1984; Bailey and Gamble, 1990). Based on archaeofaunal data from Istria and the Kvarner region (Miracle, 1994-1995, 2007), conceives this vast land as seasonally crossed by large migratory game. He arguments that all this game is representative of a rich and diverse mammal biome exploited by humans at the margins of the eastern AP and that the karstic inland was sporadically settled on a strictly seasonal basis and careful planning (Miracle, 1994-95).

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 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 reduced evapotraspiration triggered the development of wetlands (see Tab. 1, Fig. 2). A striking mosaic with contrasting treeless shrubby semidesert and short-grass steppes with highly productive 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 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 (Fig. 2, see section 2.1) and, most important, the watertable levels.

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, 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 this ecoclimate elevational gradient, compressed in a space of a few tens of kilometers - from short grass steppes supporting a rich megafauna, to boreal forests with its resources; to alpine grasslands supporting ungulates; to cold rocky semideserts. Additionally, eco- and biodiversity were increased by bedrock variability, especially the extensive denudated limestone lands widespread in the GAPR. All these phenomena during the LGM triggered habitat diversification, along with karstic conservative habitats and stable climatic microrefugia (Dobrowsky, 2011). These contexts in the GPP sustained herbivores population, largely composed by the steppe bison (*Bison priscus*), alongside with moose (*Alces alces*) and, possibly auroch (*Bos primigenius*). The ecology of the steppe bison, as inferred from fossil evidence and through comparison with living relatives, the 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 environment and adopted a more variable diet (Brugal et al., 1999; Kerley et al., 2012; Bocherens et al., 2015; Soubrier et al., 2016). *B. priscus* diet included grass from typical steppe and grassland (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).

Comparably to *B. bison* and *B. bonasus*, Late Pleistocene bisons were gregarious, the size and structure of the herds varing in function of the seasonally available resources (Plumb et al., 2009; Krasinska and Krasinski, 2013). Although sparse, zooarchaeological data point to consider these 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 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 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 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 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 Mousterian up to Gravettian groups (Terlato et al., 2019b; Romandini and Nannini, 2012) and a foraging area for the cave bear (Terlato et al., 2019a). This ecogradient was condensed in a linear space from 1 to 5 km. Paleolithic hunther-gatherers dwelled this area throughout the LGM, also in reason of caves availability (see sect. 3.3).

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

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

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 at 18/17.5 ka cal BP south of the Alps (Ravazzi et al., 2007; Vescovi et al., 2007; Finsinger et al., 2008; Wirsig et al., 2016), slightly anticipating the collapse of the ice-sheets (the end of the LGM according to Lambeck et al., 2014). At the Alpine foothills, a forest progression started immediately with increasing insolation, so that trees witnessed the glacier collapse just after 17.5 ka cal BP (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 pine-larch woodlands. However, forest progression in elevation was initially limited and only reached over 1500 m amsl after the onset of the LG interstadial (Gehrig, 1997; Heiss et al., 2005). Furthermore, summer drought limited forest progression over steppic hills and sunny slopes, and, in connection with increased fuel availability, enhanced fire propagation and frequency. During the early LG, even in the distal sector of the megafans, fluvial activity of the main Alpine rivers was limited to the incised valleys, thus maintaining open dynamic vegetations such as shrubby 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 herds on a seasonal base, similarly to Neanderthals (Terlato et al., 2019b). Unfortunately, there are no migratory-related ethological data about bisons in the GAPR. Taking as a reference the European bison leaving in the forest-field landscape in Poland, no historical data are known on its seasonal movements, despite altitudinal shifts in mountain areas are not excluded (Krasinska and Krasinski, 2013). Taking as a close reference the American plains, bisons forage on open bottomlands and lower adjacent slopes and may seasonally move until as much as 250 km, also in 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 Gravettian and early Epigravettian hunting strategies had an impact on fire regimes.

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

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 to have represented the most settled area (Tallavaara et al., 2015; Burke et al., 2017), traditionally 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 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 domestic tools, hunting implements and mobile art artifacts. Petroarchaeological cases examined by Féblot-Augustins (1997) in her seminal study, record distances up to 160 km of provenance for 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, prepared cores and other artifacts were interpreted as an expression of embedded provisionings of 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, 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 Cireșului (northern Carpatians), over 900 km of distance from the sea (Niţu et al., 2019).

Regarding the GAPR, connections between sites located over 250 km apart from another do not 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 Epigravettians. Stable terraces along the Apennine belt were potential areas to settle on a seasonal base or maintain a network of exchanges between different groups. The same holds for the wide 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 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 connection to Dalmatia.

Although data about human mobility during the Middle (Evolved) Gravettian are too sparse in the GAPR to reconstruct the settlement dynamics in this landscape, a marked trend can be highlighted starting with the Late (Final) Gravettian early Epigravettian and up to the early Late Epigravettian. This event coincides with a renewal in hunting weaponry around 24 ka cal BP, mainly consisting in the introduction of shouldered points rather than other backed implements. The long-range circulation of these points encompasses several macro-regions of Europe and could be related to new mobility strategies or changes in human groups and their way of exploiting resources in this territory. Furthermore, too poor or biased archaeological contexts do not support enough assessments on the possibility that the Gravettian to early Epigravettian techno and socio-economic changes were accompanied by profound renewals in ornamental sets. Not enough evidence is in fact currently available in the sites of the GAPR, for examining the relations between the Gravettian and its shared use of beads made of perforated *H. sanguineum* shells all over southern Europe and the following culture. The early Epigravettian replaced the former around 24 ka cal BP, broadly in 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 Late Epigravettian, hence leaving incertitude on a wide chronological range.

Therefore, further chronological assessments are required to refine the timing of the Gravettian - early Gravettian replacement and correlate it to the major ecological turnovers in the GAPR. 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 mosaic in Europe, a vast ethno-geographic phenomena leading to the rapid spread of the Solutrean, Badegoulian, Magdalenian and other complexes in the western Atlantic regions and the Epigravettian in Mediterranean France, the Italian penisula, the Balkan area and towards the East. Long-range mobility in the GAPR is clearly attested by the tracing of fine-quality cherts used to manufacture shouldered points or to maintain the provisioning of individuals through the circulation of cores or semi-finished products from the Apennines to hunting camps and short-term settlements on the opposite side of the GPP, but also reversely from the Eastern Prealpine belt to caves in northern Dalmatia. Caves and rockshelters positioned in proximity of the ecotones or in other contexts characterized by environmental variability supported the peopling of the GAPR on a seasonal base. Currently, evidence is not available to ascertain whether the alluvial megafans of the northern PP and of the VFP were settled. Although the continuous sedimentary aggradation made these large elements of the GPP landscape unsuitable to settle on unstable surfaces, we cannot deny that particular environments, such as the spring belts could have been considered worthy of placing the camps on the base of their ecological actractiveness.

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 triggering the fluvial incision of the fans and megafans of PP and VFP. The largest portion of these landforms became free of floods and stable, while the develpoment of active riverine environments and new wetlands was limited along the incised valleys cutting the plain and the groundwater-fed rivers. Such quick geomorphological changes are expected to have produced effects on human occupation, however not yet detected, along the river terraces in the plain. In the Prealpine foothills, Riparo Tagliente is a location persistently settled by human groups for the exploitation of the local biotic and abiotic resources which marks one of the first steps of the pioneering exploitation of the inner Prealpine belt on relatively stable areas. However, evidence of this phase is still very limited and such scarcity of data hampers the reconstruction of the peopling of the Italian Eastern Alps and the Dinarides triggered by the climatic amelioration of the LG interstadial starting at 14.7/14.5 ka 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 the key factors leading human groups to intensely occupy the interior mountain ranges along new routes and to expand their settlements (Bertola et al., 2007; Naudinot et al., 2014).

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

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 low coastal belts (Fig. 1). This process exerted the highest magnitude both in the southern and 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. Climate-ecological modelling predicts that some of these extreme landscapes, close to the ice sheets, were left uninhabited (Tallavaara et al., 2015; Burke et al., 2017). This was the case of the 338,000 km^2 vast land of western and northern Europe that emerged as a consequence of the retreat of the Channel and the North Sea. This flat region connecting the British Islands with the continent 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 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 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 to more reliable frequentations at 47.5° N than sites in Normandy, Pas-de-Calais, and during H1 in England, Germany and Belgium (Miller, 2012). Magdalenian northern expansion towards the north European plain began during the fairly rapid increase in temperature started 16.5 ka cal BP. The 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; Gamble et al., 2006; Miller, 2012). Fluvial systems with river channels, plains, wetlands and estuaries would have exerted an attractive force on prehistoric hunter-gatherers (Gupta et al., 2008; Momber et al., 2016).

The shelf emerged off the Atlantic coast of France was another vast land inhabitable during the LGM and connected to the north with the Channel shelf (Farr et al., 2017). No evidence suggests the frequentation of this 55,000 km^2 large land from the coast of Aquitaine up to the Molène archipelago. Aside the biases due to surveying constraints in the submarine landscape, this gap 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 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 peopling of both these regions south and north of this deserted area, it has been suggested that hunter-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 North Black Sea region. This 122,000 km^2 large flat landscape included the coastal lowland, the lower Dniester, Dnieper and Don alluvial plains expanded over 200 km to the south during the 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 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 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 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 cal BP, when Epi-Aurignacians settled the western part of Ukraine and the plains east of the Azov Sea for few thousands years until 23 ka cal BP, hunting bisons, but still leaving uninhabited the 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 slopes, river valleys and hills around the Dniester-Kuyalnik interfluve (Kadurin et al., 2020), far from the marshy lowmarine coast. Starting from 23 ka cal BP, the early Epigravettians populated the steppic region basing their subsistence on the hunting of bisons (Demidenko, 2008) and extended their presence in south-eastern Europe.

In the western Mediterranean, the southern shifting of the coast in the Gulf of Lyon originated a 12,000 km^2 land mass used as a transition corridor by bearers of the Solutrean, Salpetrian and Middle Madgalenian cultural complexes. Evidence ascribed to the human presence in proximity of this corridor is represented by the extraordinary paintings dated to the Gravettian and Epigravettian in the partly submerged Cosquer cave on the Marseilles Calanques, at the eastern edge of this continental shelf (Valladas et al., 2017). Decorations include seals, auks, fishes and jellyfish. 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).

Due to the dominant extension of its steep coasts, the Iberian Peninsula increased its extension limitedly to the middle Mediterranean zone in the Valencia gulf up to the Ebro Delta. Data on human subsistence remain however too scanty to infer models on mobility and subsistence of the Solutrean groups who settled this margin extended over 17,500 km^2 and are limited to record no evidence of marine resources in inland sites, compared to the increasing number of evidence of marine fishery in the LG (Aura Tortosa et al., 2019).

Also, the western border of southern Iberia extended far into the ocean. The region concerned was 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 km^2 where the 60% was the littoral shelf (Zilhão, 1997). This land mass sustained Solutrean groups who established their territories along the main river courses and hunted red-deer, horse and wild boar. Human groups settled in caves and open-air sites, with caves used as temporary and specialized shelters for small groups of hunters. On the contrary, several open-air locations provide so high amount of evidence to infer continuous 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 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 together, these lands supported a productive Soultrean unit of estimated 500 individuals with a relatively stable ethnic entity but open to social and cultural relations with the rest of Iberia.

Given the multidisciplinary and petroarchaeological data illustrated in this chapter and in the chapters above, the GAPR supports comparison with the largest LGM continental shelves of Europe but differentiates from these due to the presence of palaeontological and archaeological sites 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.

6.6. Demography and turnovers inferred from ancient human DNA

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., 2016). Previous analyses of mitochondrial DNA (mtDNA) genomes have shown that, while some of the pre-existing mtDNA diversity was lost during the LGM, most of the European maternal gene 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 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 populations from the Near East. This incoming genetic component largely replaced the ancestry 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 Villabruna-related 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 Balkans and the GAPR impeding a genetic characterization of the groups living in this area during the Gravettian and early Epigravettian. Nevertheless, described genetic contacts with groups from southwestern European fringes might provide an indirect evidence for the presence of the 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 BP was formed through the admixture of two divergent ancestries. One ancestry was associated with Magdalenian individuals older than 15 ka cal BP and the other with members of the 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 cave in Spain, was found to be substantially admixed with a group related to the Villabruna individual (Villalba-Mouco et al., 2019). This suggests the arrival of the Villabruna-related genetic component in Iberia before 14 ka cal BP, implying that this cluster was widespread in southern Europe several thousands of years before the age of its oldest genome described until now.

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. 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.

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

7. Conclusions

The Great Po Plain is the largest alluvial plain ever existed in the Mediterranean basin since the onset of the Middle Pleistocene, and expanded to reach its maximum size in the LGM. Meanwhile it 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 different ecological contexts, ranging from the Alpine vegetation to the Alpine timberline, down to low-elevational open boreal forest and finally to semiarid ecotones below the continental timberline. Semiarid ecozones developed especially in the Alpine foreland and in the Adriatic plain. Fauna impoverished in consequence of gradual disappearance of mammoth, woolly rhino and giant 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 of the GAPR.

Unexpected archaeological evidence dated to GS-5 on the watershed of the northern Apennine range also indicates that open, extreme landscapes were the edge of elevational logistical movements of human groups along mountain ecozones. Despite the sparseness of the archaeological record with its uneven distribution of sites and the relatively limited evidence of human presence, the GPP seems to have been crossed and inhabited all along the LGM from the early Gravettian to the first part of the late Epigravettian. This has been clearly established through the circulation of finished or semifinished early Epigravettian artefacts made of chert coming from 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 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 displacement and aggregation of groups in settlements, the existence of which can only be supposed given the inaccessibility of the submerged plain. It is reasonable to think that the wide open spaces of the GAPR favoured a great mobility of human groups in the framework of a cultural identity extending into southern Europe.

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 Epigravettian colonization of the Alps, the Apennine, the Dinarides and other mountain ranges started.

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Tables captions

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). 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. McLaughlan et al., 2010). 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., 2020); 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).

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, RS - Rockshelter); CC, cultural complex (G – Gravettian, EE - early Epigravettian, LE - Late Epigravettian, ND - not determinable); Mat, material (C - charcoal, B – bone, HB – human bone, 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, 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 - Open air, C - Cave, RS - Rockshelter); CC, Cultural Complex (G – Gravettian, EE - early Epigravettian, LE - Late Epigravettian, ND - not determinable);

Figures captions

Figure 1. Map of Europe with the largest continental shelves emerged during the Last Glacial Maximum. 1. Doggerland/North Sea, English Channel and Bristol Channel; 2. Bay of Biscay and France Atlantic Coast; 3. North-central Portugal Atlantic Coast; 4. Catalunya and Valencia Coasts; 5. Gulf of Lion; 6. Great Po Plain; 7. Northern Black Sea Coast (Sea of Azov and Chorne Sea); 8. Other LGM emerged areas; 9. Scandinavian and British Islands ice sheets; 10. Mountain Glaciers; 11. Major rivers and lakes. Technical notes: Coordinate system ETRS89 / UTM zone 32N (EPSG 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 (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 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., 2015). Alpine glaciers downloaded from https://booksite.elsevier.com/9780444534477/and modified in the Italian side using updated reconstructions (Ravazzi et al., 2012; Monegato et al., 2017; Gianotti et al., 2015; Ivy-Ochs et al., 2018; Rossato et al., 2013, 2018). Major European and 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 references to colour in this figure legend, the reader is referred to the Web version of this article).

Figure 2. Palaeogeographic map of the Great Adriatic-Po Region (GAPR) with the Great Po Plain (GPP) composed by the Po Plain (PP), the Adriatic Plain (AP) and the Venetian - Friulian Plain (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 (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

the sectors between the Dora Riparia and the Brenta valley outlets; Garda glacier, GG; Tagliamento glacier, TG); 2. Lakes (based on Miko et al., 2017); 3. megafan bodies above the current sea level (B Mgf, Brenta megafan; P Mgf, Piave megafan; T Mgf, Tagliamento megafan; Fontana et al., 2008, 2014a); 4. megafan bodies sunken under the current sea level; 5. Upper proximal megafan belt; 6. Po River floodplain (Amorosi et al. 2017, http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/complessi-idrogeologici); 7, Po River delta (Pellegrini et al., 2018); 8, stable surfaces supporting deeply weathered soils and loess. These surfaces belong to the following main physiographic units: ancient, terraced alluvial units; hills emerging from the plain (BH, Berici Hills); karstic plateaux at low elevatio□; 9, DEM □olor s□ale -130 – 4.808.

Technical note. Coordinate system ETRS89 / UTM zone 32N (EPSG 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 (Pellegrini et al., 2015; 2017; 2018). The mountain glaciers (pale blue) from Ehlers et al. (2011). Dinarides from Žebre and Stepišnik (2015). Alpine glaciers downloaded from https://booksite.elsevier.com/9780444534477/ and modified in the Italian side using updated 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 (middle and lower Pleistocene alluvial deposits, aeolian sediments, Loess) (Zerboni et al., 2018; Geological Map 1:50.000 Iseo, Bergamo, Vimercate sheets; Geomorphological Map of the Po Plain (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., 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; Bruno et al., 2018; Carta Complessi idrogeologici http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/complessi-idrogeologici). Gravelly sector of the plain (Castiglioni et al., 1997). Distal plain. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

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. Piovesello (including the Piovesello Paleolithic site); 3. Lake Alserio; 4. Lake Annone; 5. Azzano 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

(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. Galzignano; 20. Ghedi; 21. San Donà di Piave; 22. Venice Lagoon; 23. Lake Vrana; 24. Valun Bay; Palaeontological sites: 25. Settepolesini; 26. Grotta Tilde; 27. Cava a Filo; Palaeontological and Palaeolithic sites: 28. Büs dei Lader; 29. Grotta Fumane; 30. Riparo Tagliente; 31. Grotta Rio Secco; 32. Ovčja Jama and Županov Spodmol; 33. Zala cave; 34. Abri Kontija 002, Romualdova pećina and Pećina kod Rovinjskog Selo 1; 35. Šandalja II cave and Ljubićeva pećina; 36. Vlakno cave; 37. Fornace San Damiano; 38. Fonte delle Mattinate; 39. Fosso Mergaoni; 40. 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 Web version of this article).

Figure 4. 3D ecographic sketch of the ecoclimatic gradient spanning the Kurai steppe and the northern slope of the Chuya mountains, SW Altai, Russia, 50°12‘48‘‘ N, 87°56‘27‘‘ E. It provides a 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, 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 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.

Figure 7. Comparative stratigraphic sketches of the Apennines Umbria-Marche Basin and Southern 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 geological samples shown in the Figs. 8, 10 and 11.

Figure 8. Micrographs of Umbria-Marche Basin cherts from primary exposures. 1. Oligocene Scaglia Cinerea; 2. Eocene Scaglia Rossa; 3. Middle Cretaceous Scaglia Bianca; 4. Middle 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 this article).

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

sites and the sites that produced indication of allochthonous chert provenance (black arrows). Key: 1, DEM color scale -130 – 4,808 m amsl; 2. Glaciers; 3. Lakes; 4. Upper proximal megafan belt; 5. Po River floodplain; 6, Po River delta; 7, stable surfaces supporting deeply weathered soils and loess. For details on references and explanations of the legend see figure 2 and section 2.1. For discussion on the chronological frame and cultural attribution of each site see section 3.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Figure 9a. Simplified map for the interval 32-29 ka cal BP. Sites: 2. Piovesello; 6. Grotta Broion and Riparo Broion; 11. Paina; 31. Rio Secco; 34. Pećina kod Rovinjskog Sela 1; 38. Fonte delle Mattinate.

Figure 9b. Simplified map for the interval 26-23 ka cal BP. Sites: 11. Paina, Trene and Stria; 32. Ovčja Jama (note that layer 4 is culturally attributed to the early Epigravettian); 35. Šandalja II (note that layer C/d is culturally attributed to the early Epigravettian); 40. Ponte di Pietra.

Figure 9c. Simplified map for the interval 23-19 ka cal BP2. Sites: 6. Riparo Broion and Buso Doppio Broion; 11. Stria, Trene and Paina; 28. Büs dei Lader; 34. Romualdova; 35. Šandalja II; 36, Vlakno; 39. Fosso Mergaoni; 40. Ponte di Pietra (note that these last two sites are culturally attributed to the late Gravettian).

Figure 9d. Simplified map of the eastern GAPR for the interval 18-16 ka cal BP. Sites: 30. Tagliente; 33. Zala; 34. Romualdova; 35. Ljubićeva; 41. Baracche; 42. Campo delle Piane.

Figure 10. Berici Hills (7-11) and Lessini Mountains (12). Micrographs of allochtonous cherts from the Umbria-Marche Basin taken on Epigravettian artifacts: 7. Oligocene Scaglia Cinerea (Paina Cave - Grottina Azzurra layer 6); 8. Eocene Scaglia Rossa (Paina - Grottina Azzurra layer 6); 9. Eocene Scaglia Rossa (Trene, complex B); 10. Middle Cretaceous Marne a Fucoidi (Buso Doppio del Broion, layer Rim); 11. Lower Cretaceous Maiolica (Paina - Sala Terminale layer 125); 12. Middle Jurassic Calcari Diasprigni (Tagliente, SU 300) (scale bar = 1 mm; for interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Figure 11. Istria. Micrographs of allochtonous cherts from the Umbria-Marche Basin (13-15) and the Carnia-Belluno Basin (16-18) taken on Epigravettian artifacts: 13. Eocene Scaglia Rossa (Šandalja II, layer C/d); 14. Eocene Scaglia Rossa (Romualdova pećina); 15. Lower Cretaceous Maiolica (Šandalja II, layer C/d); 16. Lower Cretaceous Maiolica (Šandalja II, layer C/d); 17. Middle Jurassic Soverzene (Šandalja II, layer C/d); 18. Triassic Buchenstein (Šandalja II, layer C/d) (scale bar = 1 mm; for interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

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

					6	Poz-41208	C	28300±260	32977 31471	Peresani et al., 2014
					6	MAMS-15906	C	28995±135	33609 32816	Talamo et al., 2014
					6	MAMS-15907	C	29390±135	32839 31735	Talamo et al., 2014
Fonte delle Mattinate	Marche Apennine	760	OA	G	B-27	--	C	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	C	19940±471	25273 22942	Lollini et al., 2005
					II, su 66	CRG-1019	C	18515±618	23934 20926	Lollini et al., 2005
Fosso Mergaoni	Marche Apennine	180	OA	G	4a2	UtC-11551	C	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	C	14920±95	18385 17896	Peresani et al., 2005
					--	LTL172A	C	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	C	14810±120	18332 17713	Olive, 2017
Ovčja Jama	Karst	586	C	G	4	KN-48	C	19540±500	24856 22450	Osole, 1974
Zala	W mount. Croatia	270	C	LE	100	Beta-334806	B	14100±60	17414 16924	Šošić Klindžić et al., 2015
				LE	12	Beta-228734	B	13840±50	16986 16509	Karavanić et al., 2007
				LE	102	Beta-334805	B	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	C	G	B	Poz-80127	B	26730±300	31290 30405	Unpublished (DK)
Ljubićeva pećina	Istria	170	C	LE	D (4)	Beta-249371	C	13230±70	16136 15676	Percan et al., 2009 Simonet, 2013
Romualdova pećina	Istria	110	C	EE	2	Beta-465338	C	13970±50	17174 16692	Ruiz-Redondo et al., 2019
					2	OxA-36127	C	14250±80	17592 17099	Ruiz-Redondo et al., 2019
Šandalja II	Istria	70	C	EE	C/d	Z-193	C	20750±400	25840 24085	Srdoč et al., 1973
Vlakno	Dugi otok Island	38	C	EE	32	Beta-302247	C	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	5-15	5-300	Peresani et al., 2018
			Provence	300		
Fumane	G	Venetian Prealps	Lessini Plateau	5-15	5-15	This study
Grotta Broion Riparo Broion	G	Venetian Prealps	Berici Hills	5-15	5-50	Bertola et al., 2018
			Lessini Plateau	25-50		
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	--	--	--	--
Fonte delle Mattinate	G	Marche Apennine	Umbria-Marche Apennine	0-15	0-50	Silvestrini et al., 2005a; Cancellieri, 2018
			High Tiberine valley	25-50		
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
Paina, layer 7	G	Venetian Prealps	Berici Hills	5-15	5-270	Broglio et al., 2009; Bertola et al., 2018
			Lessini Plateau	25-50		
			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
Paina, layer 6	EE	Venetian Prealps	Berici Hills	5-15	5-270	Broglio et al., 2009; Bertola et al. 2018
			Lessini Plateau	25-50		
			Umbria-Marche Apennine	250-270		
Trene	EE	Venetian Prealps	Berici Hills	5-15	5-270	Broglio et al., 2009; Bertola et al. 2018
			Lessini Plateau	25-50		
			Umbria-Marches Apennines	250-270		
Buso Doppio Broion	EE	Venetian Prealps	Berici Hills	5-15	5-270	Romandini et al. 2015; Bertola et al. 2018
			Lessini Plateau	25-50		
			Umbria-Marche Apennine	250-270		
Col de La Stria	EE	Venetian Prealps	--	--	--	--
Šandalja II, layer C/d	EE	Istria	Istria	5-15	5-200	This study
			Friulan plain	25-50		
			Umbria-Marche Apennine	150-200		
Madonna dell'Ospedale	EE	Marche Apennine	Umbria-Marche Apennine	0-15	0-15	Cancellieri et al., 2015
Vlakno	EE	Dugi otok Island	Northern Dalmatia	20	20-350	Perhoč, 2020
			Umbria-Marche Apennine	180		
			Veneto Prealps	350		
Romualdova pećina	EE	Istria	Umbria-Marche Apennine	200	200	This study

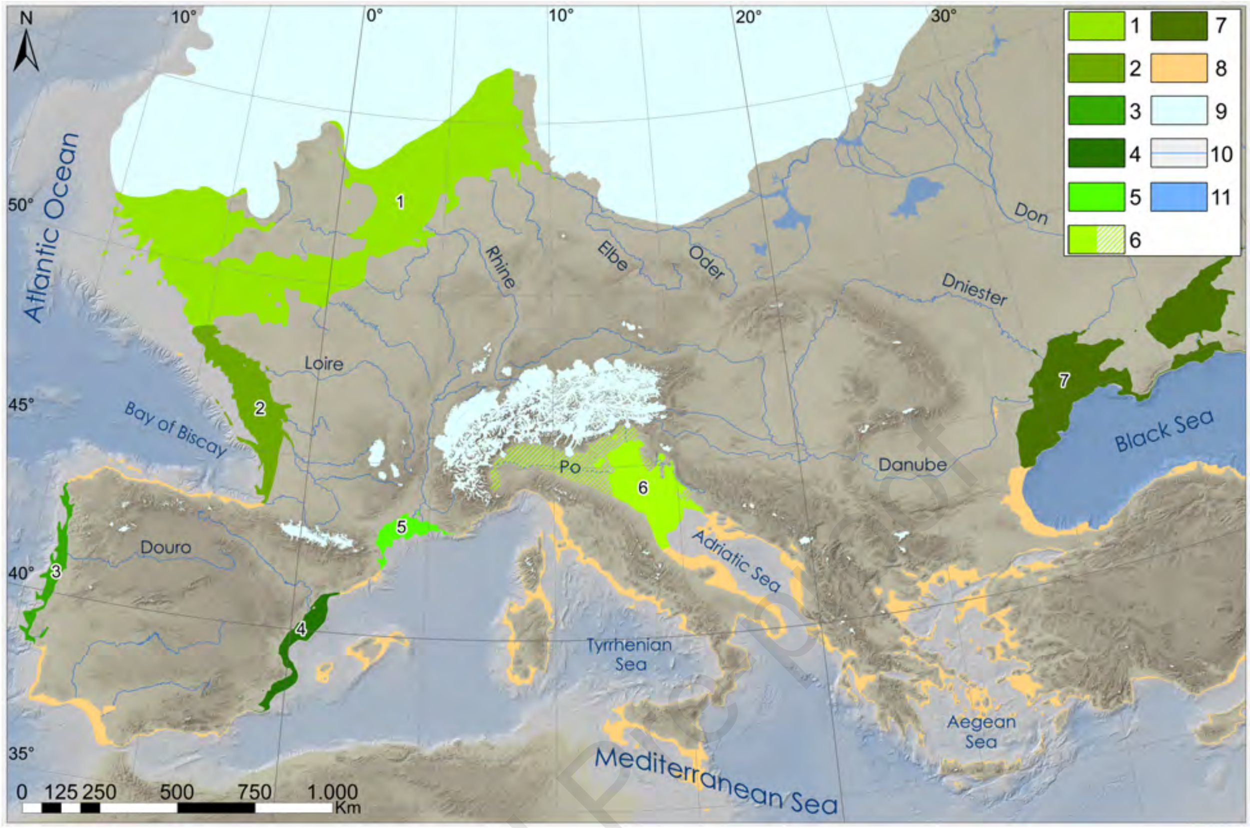
Tagliente	LE	Venetian Prealps	Lessini Plateau	0-15	0-270	Bertola et al. 2018
Ljubićeva pećina	LE	Istria	--	--	--	--
Zala	LE	W. mountain Croatia	Kupa River	30	30-300	Vukosavljević et al., 2015; Perhoč, 2020
			Lika region	75		
			Istria	100		
			Northern Dalmatia	115		
			Lessini Plateau	300		
Baracche	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
Alpine vegetation ecozones **(**unglaciated areas beyond the Alpine timberlines**)**	bare ice and debris covered glaciers	**Cushion vegetation** on fresh moraine ridges Other petrophytic vegetation **Cryonival algal and microbial communities**	No ancient ice preserved
	other areas under active geomorphic processes	**Alpine rockfields and steeplands**	Cerete[1], Piovesello[2]
	nival to sunny slopes (including nunataks)	**Petrophytic deserts** with *Plantago alpina* type*, *Armeria**, Dipsacaceae* **Rocky steppe** **Steppe-grasslands** with *Carex humilis*, *Stipa* sspp. and xerophilous chamaephytes (*Helianthemum**, *Artemisia**, *Juniperus**, etc.) **Alpine grasslands** with *Festuca* sspp. *Carex* sspp, *Sesleria varia*	
	cold waterscapes	**e.g. Cold spring herb communities, cold limnic ecosystems**	
Alpine timberline			
Mountain-piedmont ecozones under a moist climate	stable or stabilized fields, no edaphic drought, especially on gentle slopes	**Forests and woodlands.** *Pinus mugo* dwarf forests at the alpine timberline mainly in the Eastern Calcareous Alps; open boreal forests; larch-scots pine woodlands at the continental timberline.	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], Renče[14], Revine[15], Trana[16]
	edaphic drought, especially on limestone plateau, ridges, and sunny slopes	**Grasslands, steppes, rocky steppes, alpine rockfields and steeplands** (see above)	
	cold waterscapes	***Salix*** **and tall-herbs riverside formations; cold limnic ecosystems**	
	thermal springs (Euganei Hills)	**Patches of thermophilous woody formations** with *Corylus*, deciduous *Quercus*, *Tilia*, *Ulmus*, *Fagus*, etc (cryptorefugium) .	
Continental timberline			

Mountain-piedmont ecozones under a semiarid climate	stable terraced piedmont areas with loess accumulation and isohumic soils development under grasslands	**Steppes and semideserts** with Gramineae, Compositae, *Hippophäe*, Erica, Berberis?, Rhamnus** **Tree grooves** (*Betula, Pinus*)	
Plain ecozones *(mostly depending on edaphic moisture)*	active megafans - bars, dunes and abandoned riverbeds on coarse-grained sediments	**Edaphic semideserts** with xerophytic herbs and shrubs (*Artemisia**, Chenopodiaceae*, *Hippophae**, *Juniperus**, Ephedraceae*, etc.)	Azzano Decimo[5], Cà Fornera[17], Casaletto Ceredano[18] Galzignano[19], Ghedi[20], San Donà di Piave[21], Venice Lagoon[22], L. Vrana[23], Valun Bay[24]
	stable surfaces - dune and loess fields under semiarid climate	**Climatic semideserts and deserts** with *Artemisia* and Gramineae (poorly documented by fossil sites)	
	active river channels in lower megafan belts	**Riverside vegetations** with tree *Betula** and *Alnus incana* patches, and tall herbs (Umbelliferae). In drier spots, riverbed lithophyte communities with *Juniperus** heaths and *Pinus sylvestris** parkland, with Fabaceae, *Erica, Ephedra*.*	
	fine-grained sediments under water-saturated conditions	**Wetlands** (*Carex* sspp., *Eriophorum* sspp., mosses, e.g. *Scorpidium*§), birch (*B. pubescens*§), 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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Mediterranean Sea
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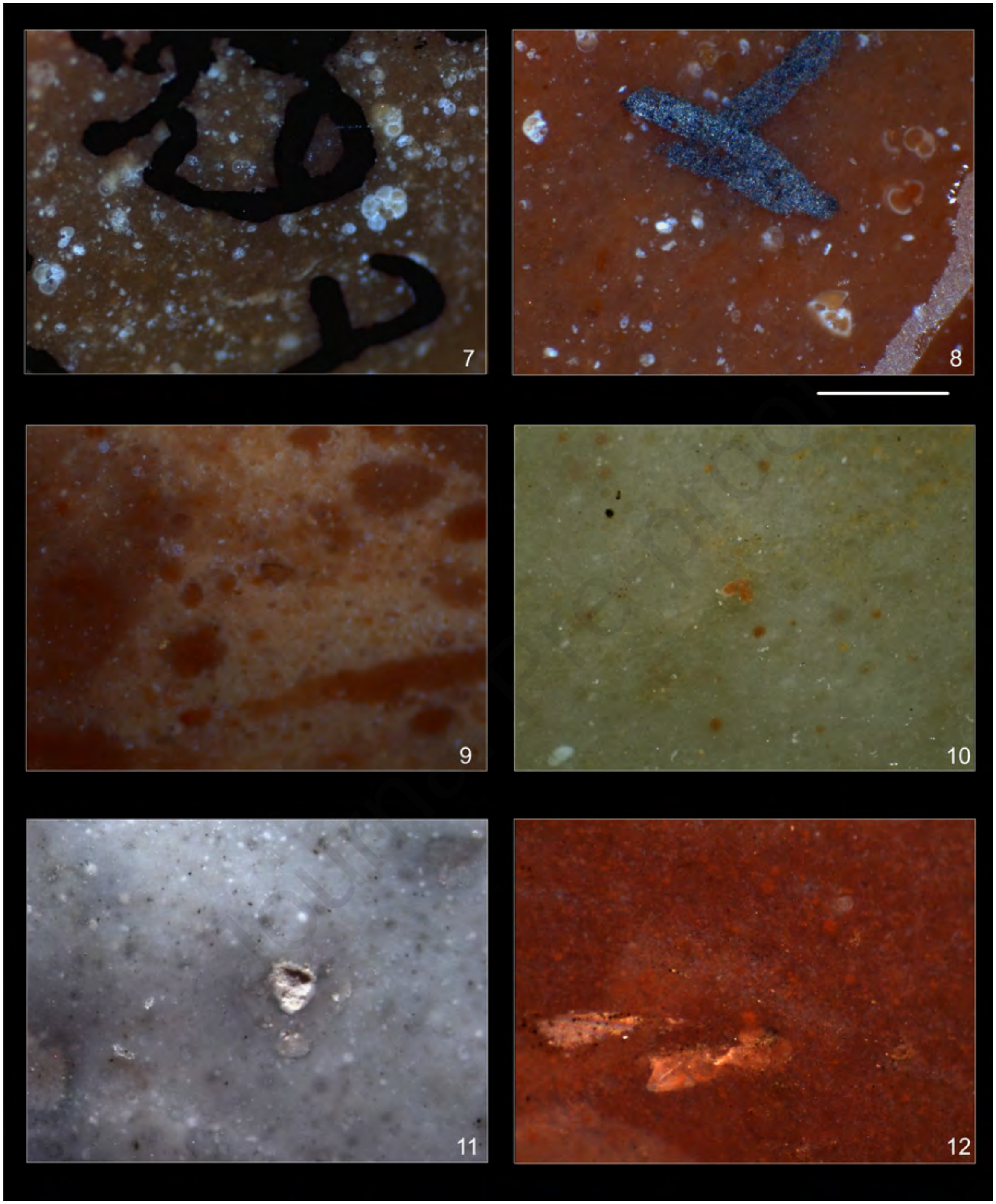
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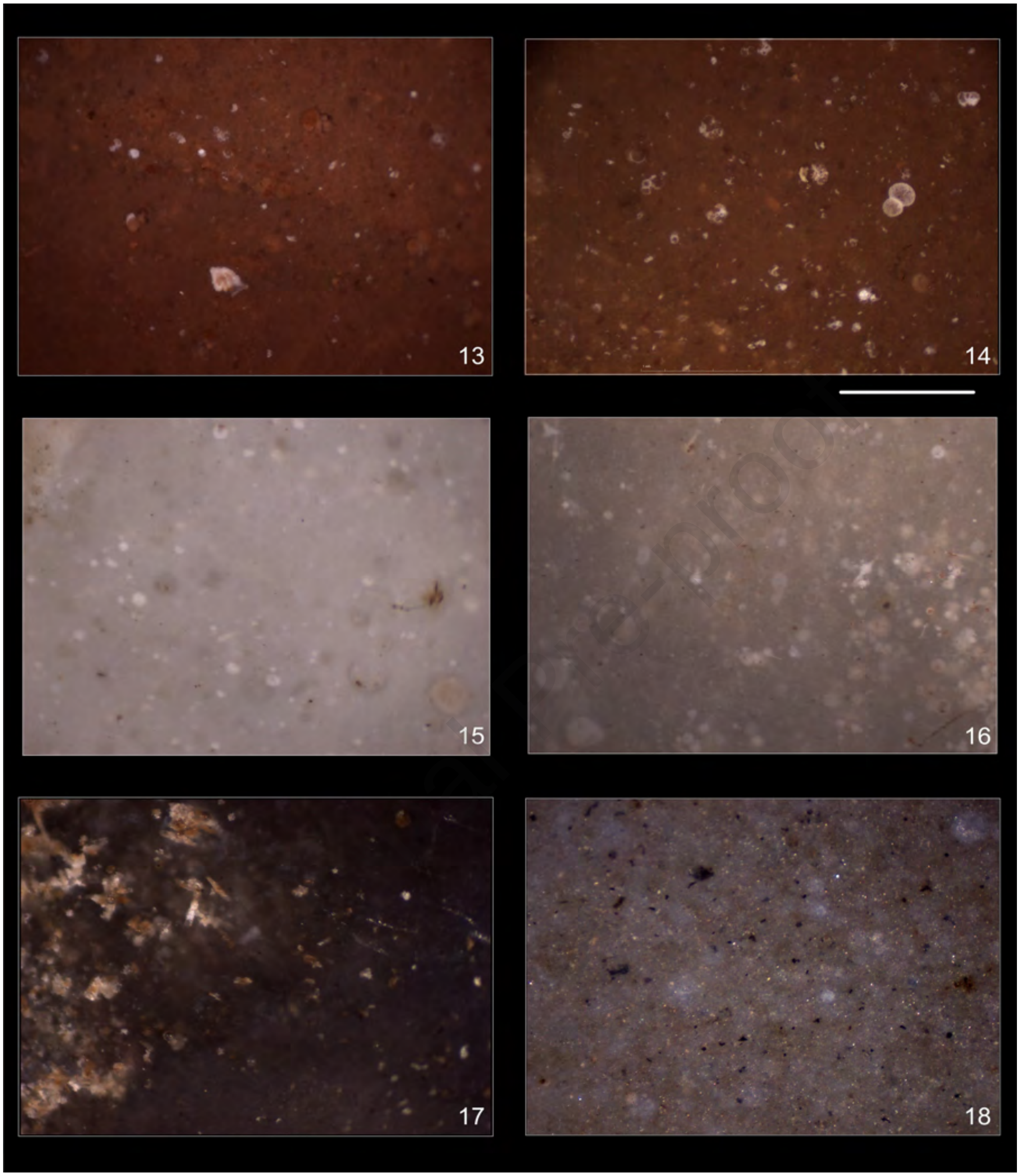
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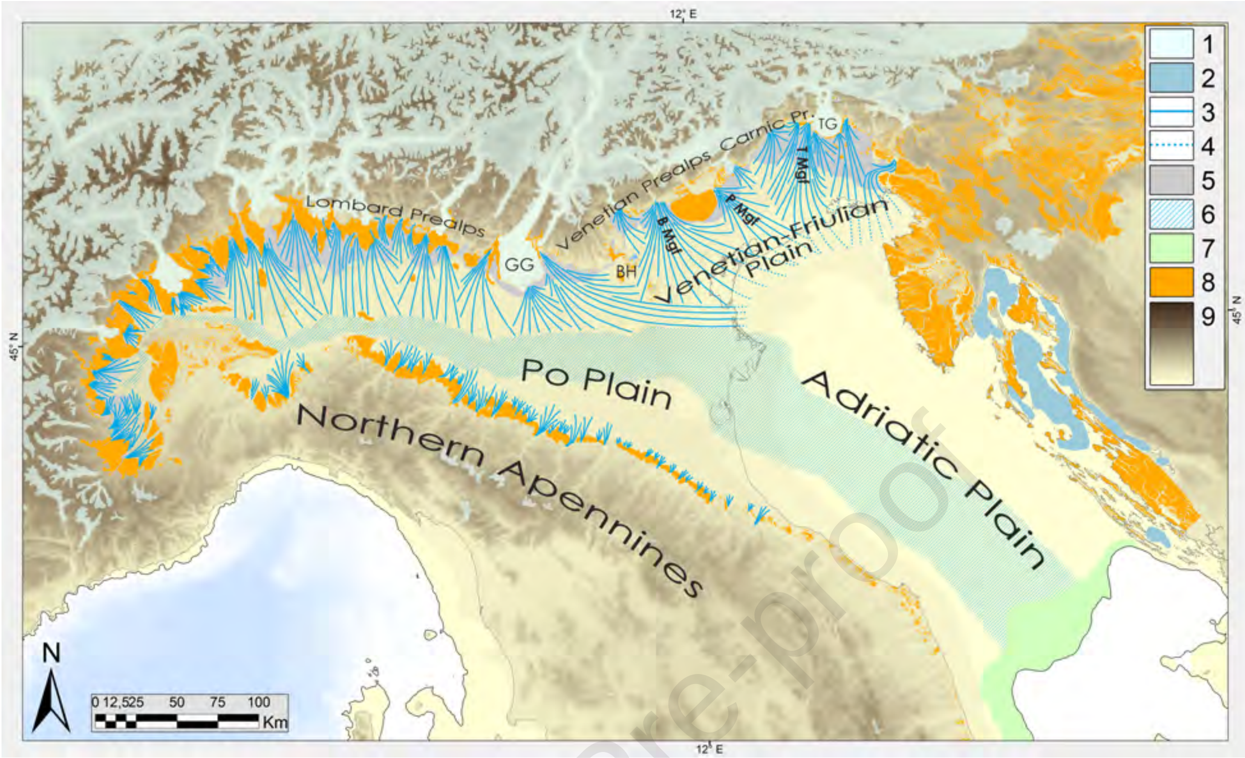
12° E
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45° N
Lombard Prealps
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Carnic Pr.
TG
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BH
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Po Plain
Adriatic Plain
Northern Apennines
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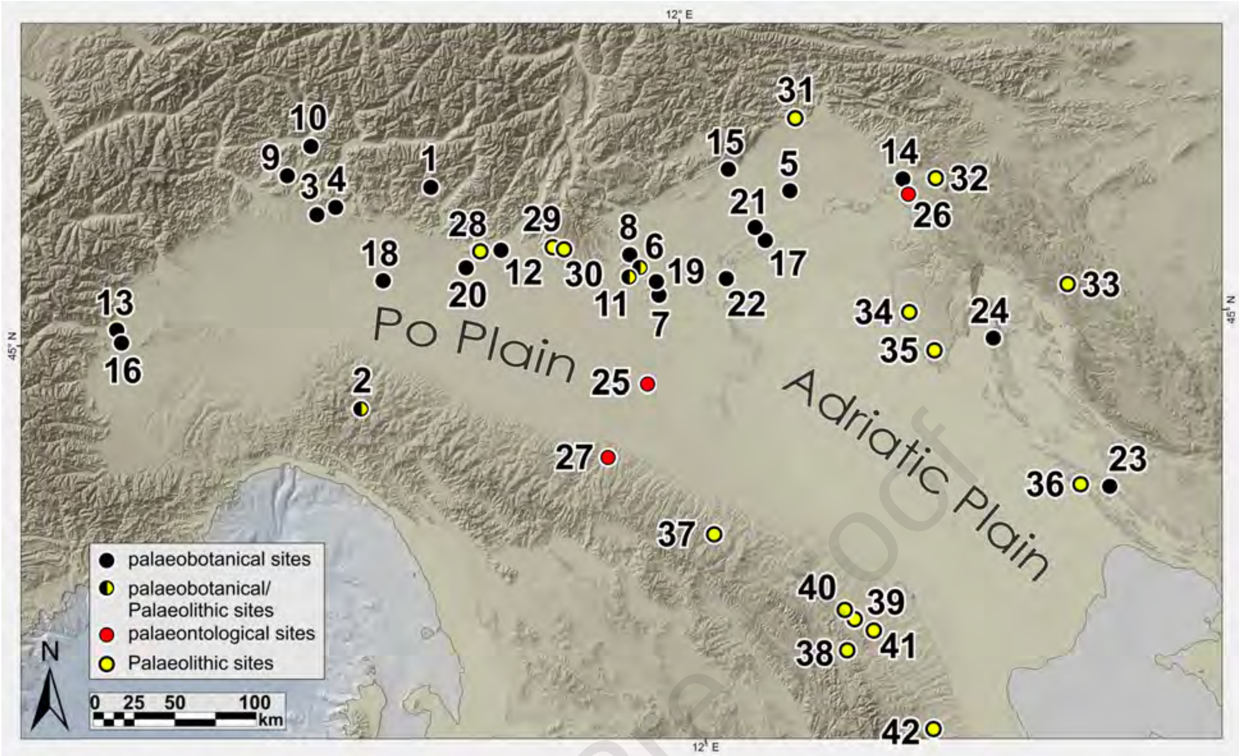
12° E
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Po Plain
Adriatic Plain
palaeobotanical sites
palaeobotanical/ Palaeolithic sites
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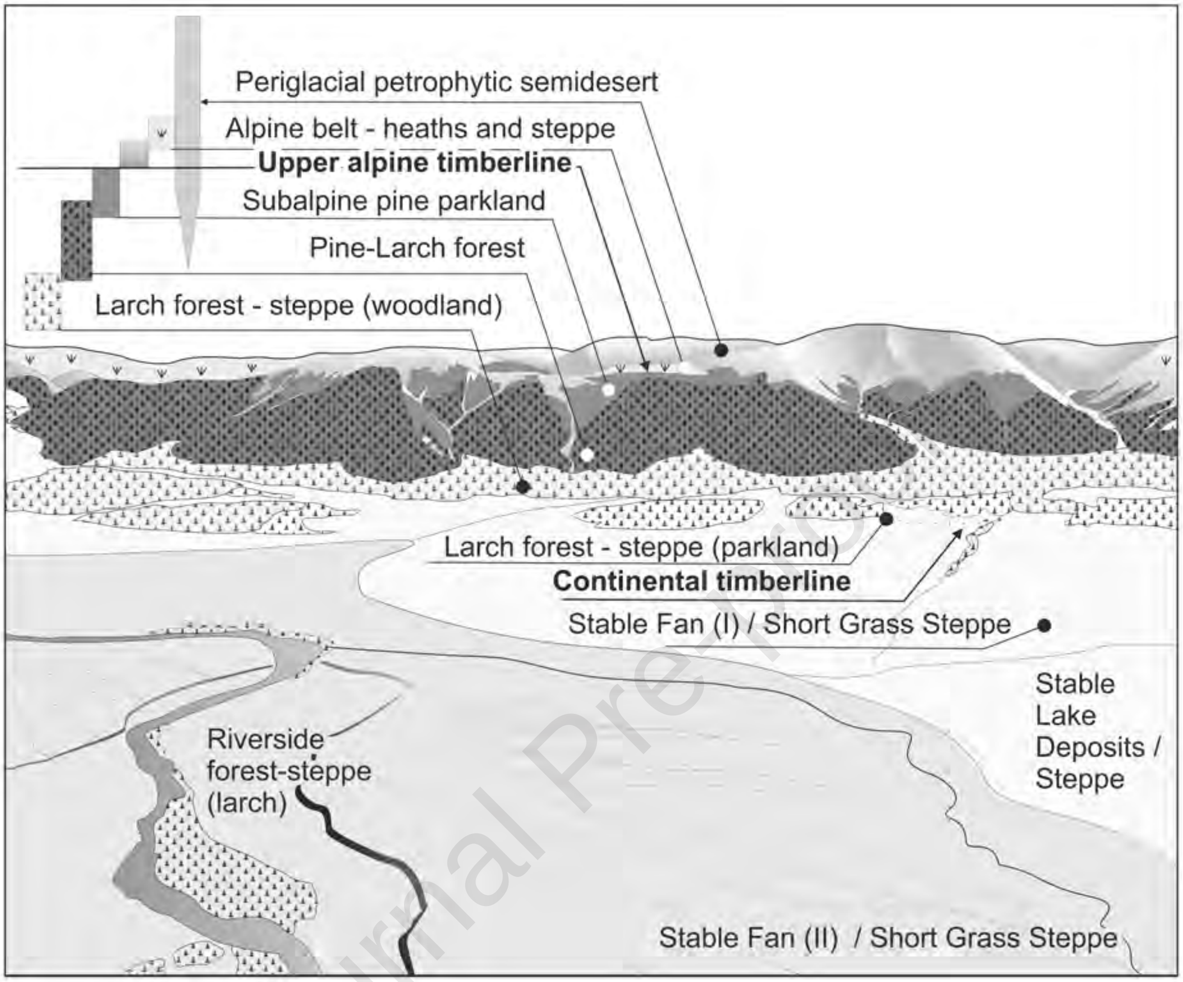
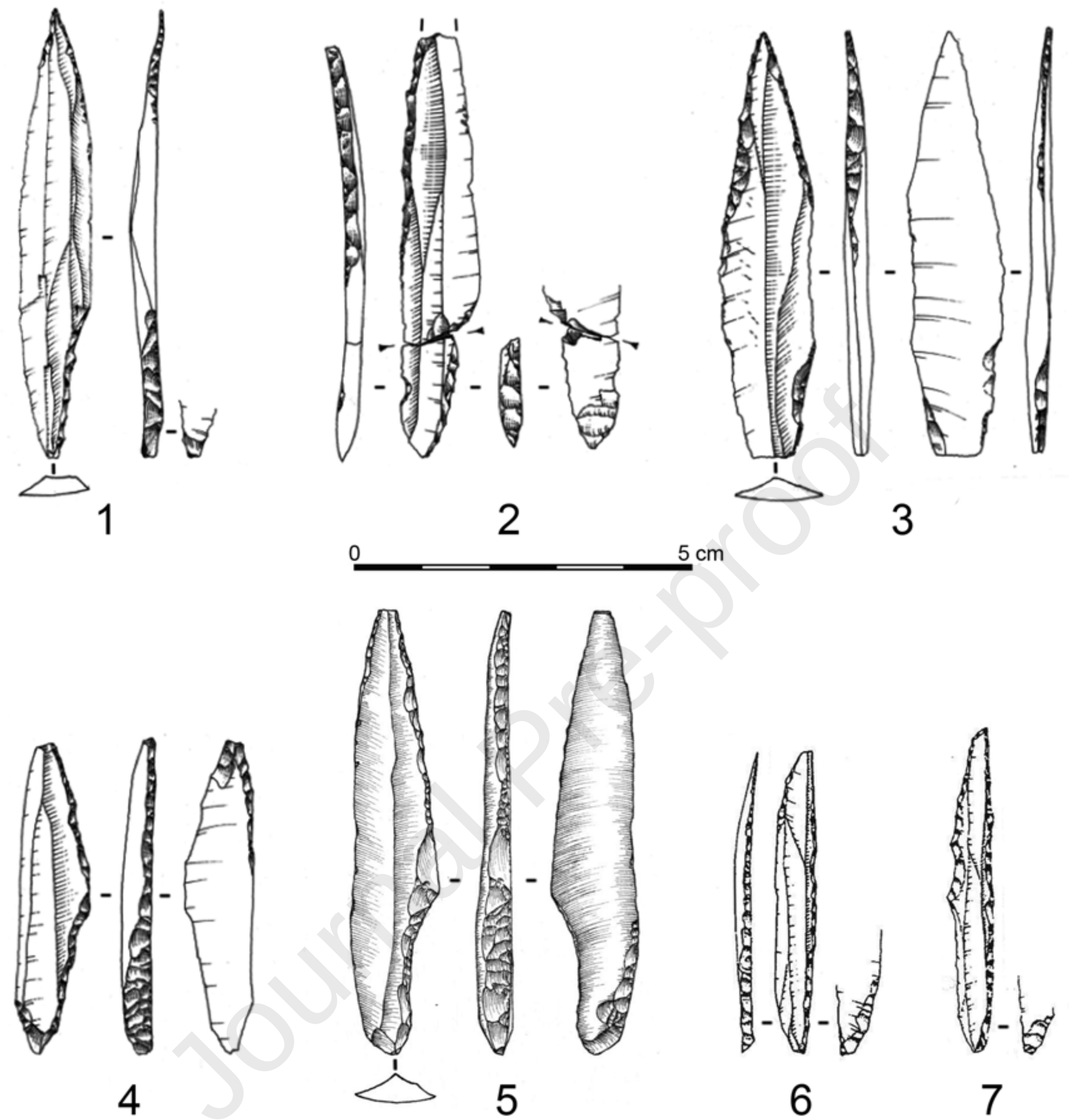


Periglacial petrophytic semidesert
Alpine belt - heaths and steppe
Upper alpine timberline
Subalpine pine parkland
Pine-Larch forest
Larch forest - steppe (woodland)
Larch forest - steppe (parkland)
Continental timberline
Stable Fan (I) / Short Grass Steppe
Stable Lake Deposits / Steppe
Riverside forest-steppe (larch)
Stable Fan (II) / Short Grass Steppe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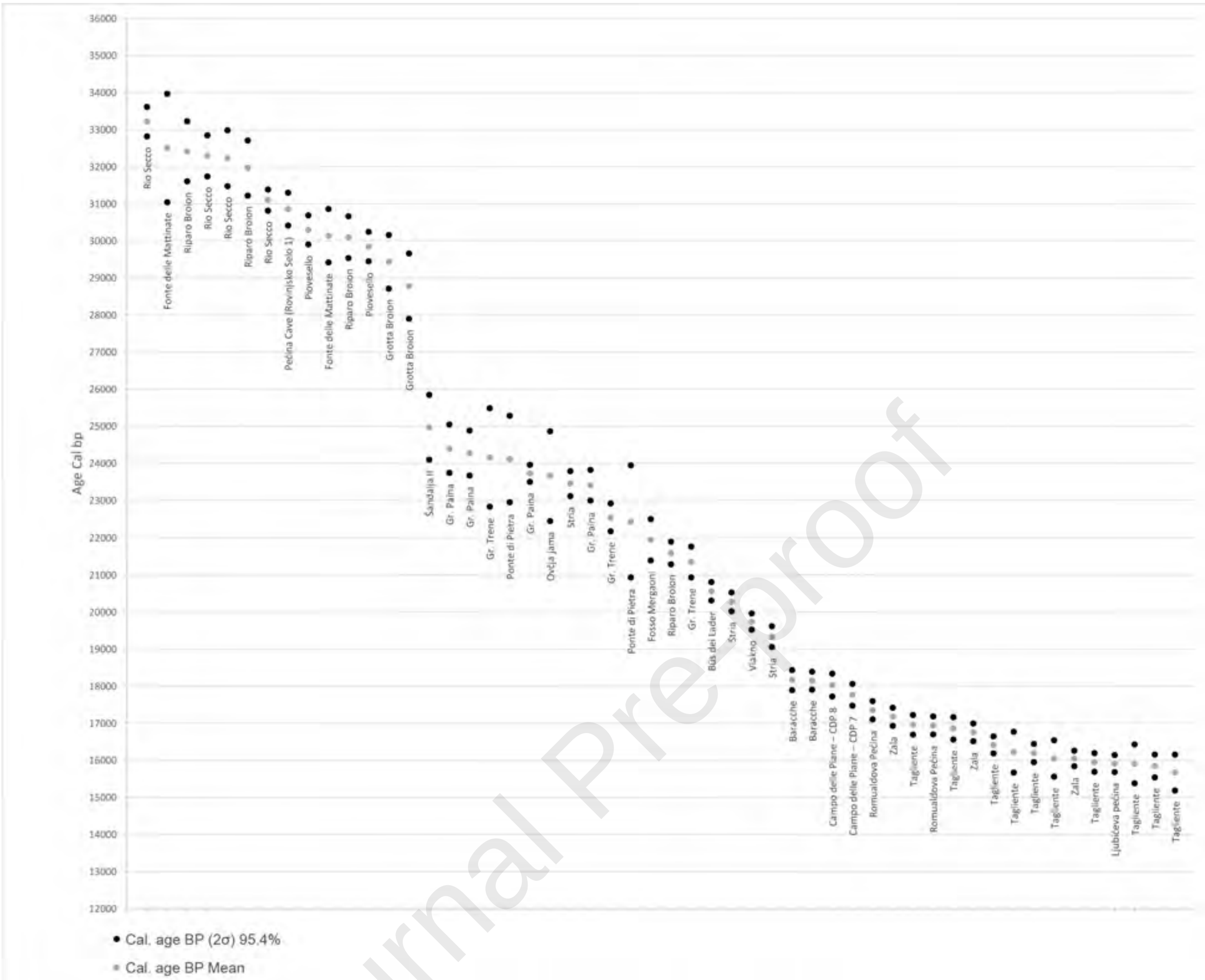

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Age Cal bp
Rio Secco
Fonte delle Mattinate
Riparo Broion
Rio Secco
Rio Secco
Riparo Broion
Rio Secco
Pećina Cave (Rovinjsko Selo 1)
Piovesello
Fonte delle Mattinate
Riparo Broion
Piovesello
Grotta Broion
Grotta Broion
Šandalja II
Gr. Paina
Gr. Paina
Gr. Trene
Ponte di Pietra
Gr. Paina
Ovčja jama
Stria
Gr. Paina
Gr. Trene
Ponte di Pietra
Fosso Mergaoni
Riparo Broion
Gr. Trene
Bus del Lader
Stria
Vlakno
Stria
Baracche
Baracche
Campo delle Piane – CDP 8
Campo delle Piane – CDP 7
Romualdova Pećina
Zala
Tagliente
Romualdova Pećina
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Ljubićeva pećina
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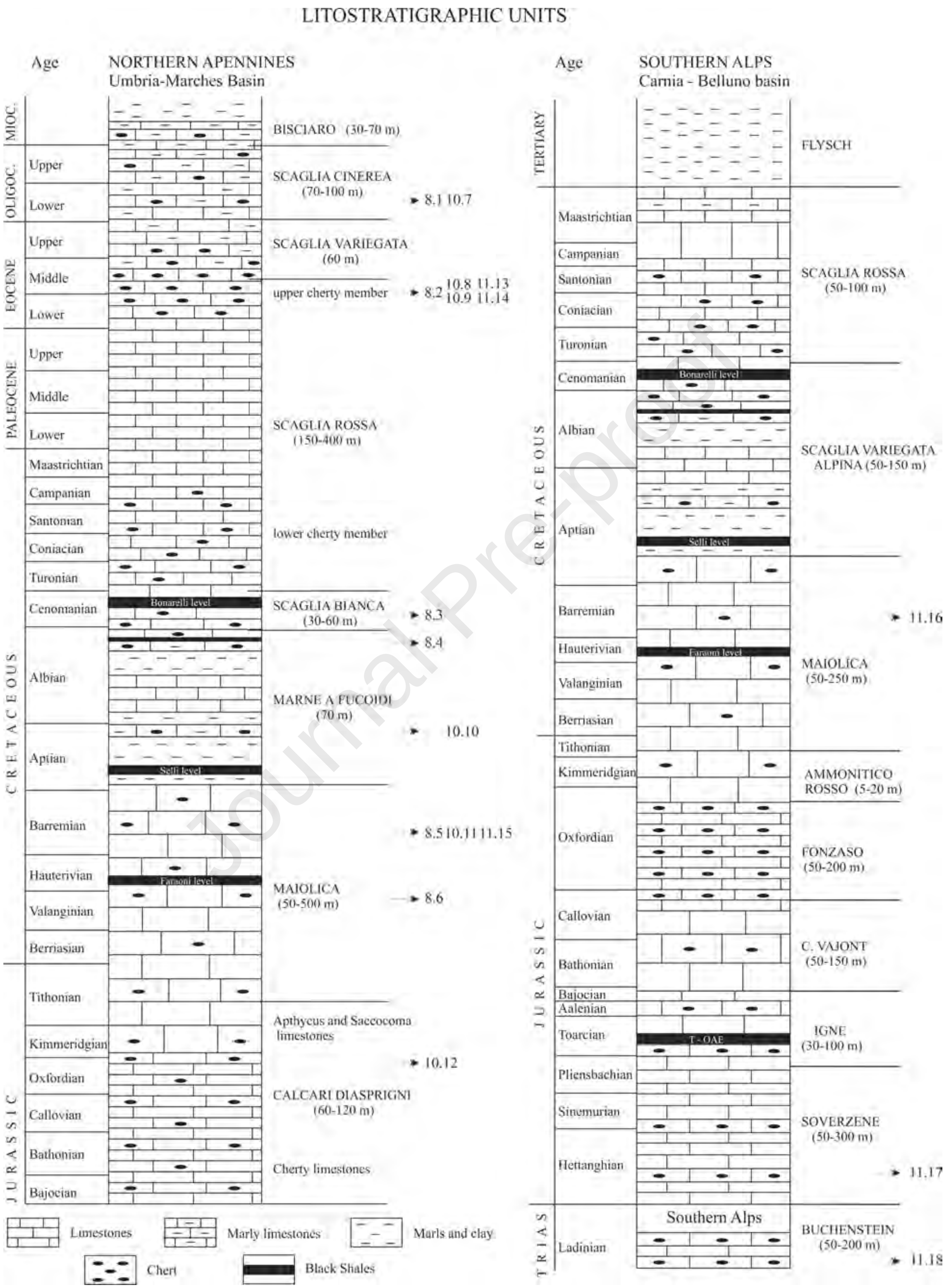
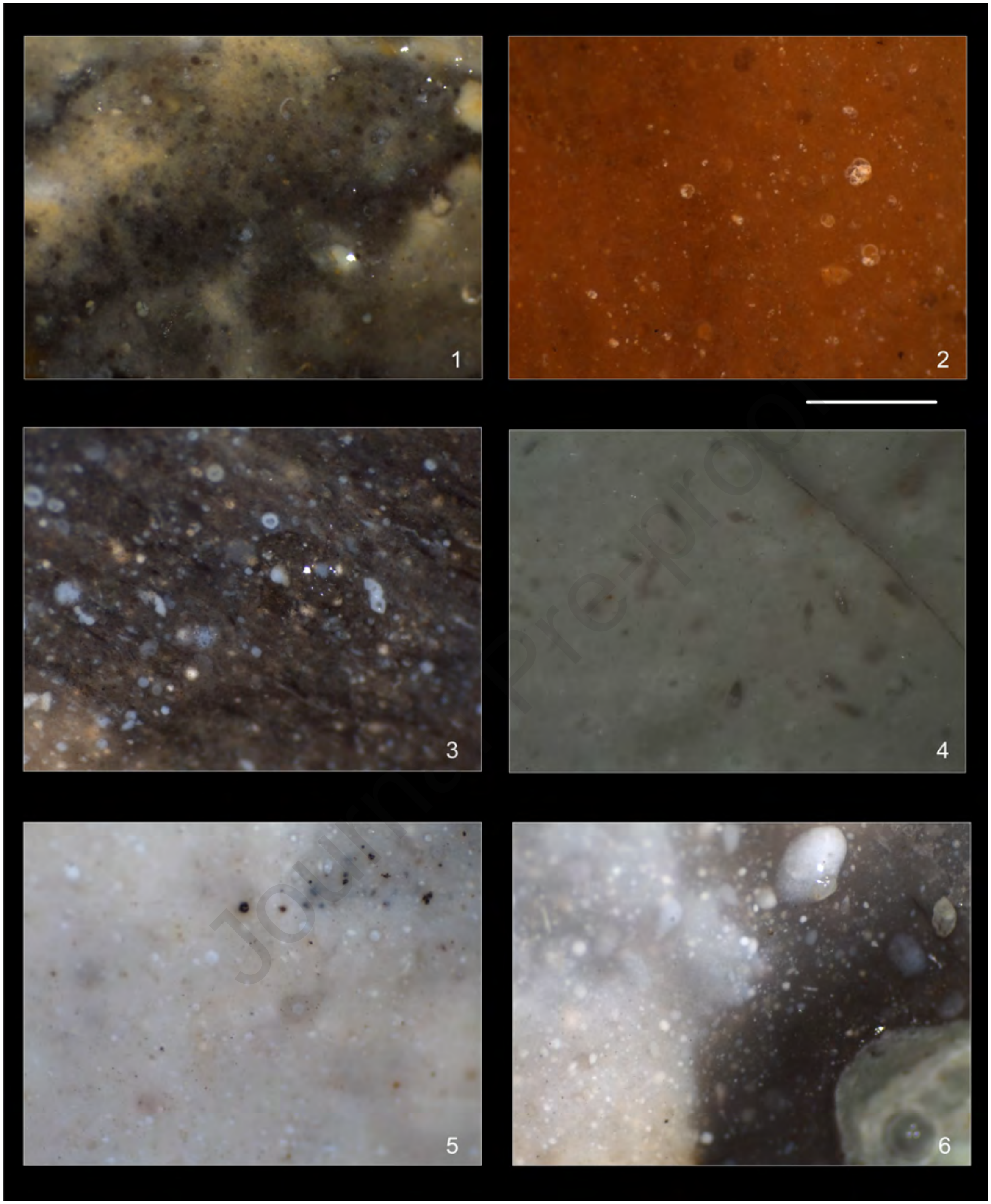
Cal. age BP (2σ) 95.4%
Cal. age BP Mean


LITOSTRATIGRAPHIC UNITS
Age
NORTHERN APENNINES
Umbria-Marches Basin
MIOC.
OLIGOC.
EOCENE
PALEOCENE
CRETACEOUS
JURASSIC
Upper
Lower
Upper
Middle
Lower
Upper
Middle
Lower
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Bonarelli level
Selli level
Faraoni level
BISCIARO (30-70 m)
SCAGLIA CINEREA
(70-100 m)
8.1 10.7
SCAGLIA VARIEGATA
(60 m)
upper cherty member
8.2 10.8 11.13
10.9 11.14
SCAGLIA ROSSA
(150-400 m)
lower cherty member
SCAGLIA BIANCA
(30-60 m)
8.3
8.4
MARNE A FUCOIDI
(70 m)
10.10
8.5 10.11 11.15
MAIOLICA
(50-500 m)
8.6
Apthycus and Saccocoma
limestones
10.12
CALCARI DIASPRIGNI
(60-120 m)
Cherty limestones
Age
SOUTHERN ALPS
Carnia - Belluno basin
TERTIARY
CRETACEOUS
JURASSIC
TRIAS
FLYSCH
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Aalenian
Toarcian
Pliensbachian
Sinemurian
Hettanghian
Ladinian
Bonarelli level
Selli level
Faraoni level
T - OAE
SCAGLIA ROSSA
(50-100 m)
SCAGLIA VARIEGATA
ALPINA (50-150 m)
11.16
MAIOLICA
(50-250 m)
AMMONITICO
ROSSO (5-20 m)
FONZASO
(50-200 m)
C. VAJONT
(50-150 m)
IGNE
(30-100 m)
SOVERZENE
(50-300 m)
11.17
Southern Alps
BUCHENSTEIN
(50-200 m)
11.18
Limestones
Marly limestones
Marls and clay
Chert
Black Shales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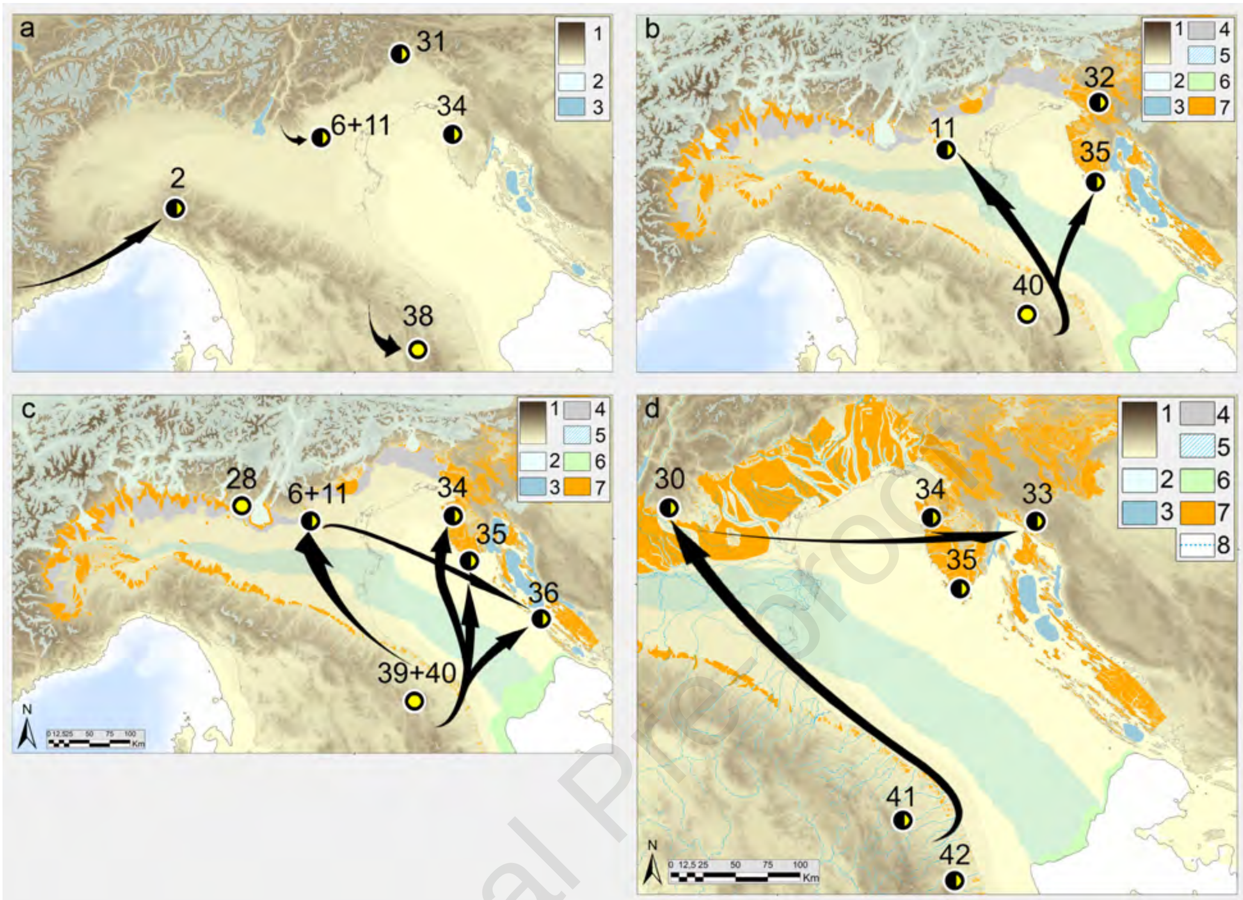
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Km

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: