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Complexity in the Middle to Upper Paleolithic Transition in Peninsular Southern Europe and application of refugium concepts

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ABSTRACT: During the Middle to Upper Paleolithic transition in the Balkan, Italian and Iberian peninsulas of southern Europe, late Neanderthal and early Anatomically Modern Human (AMH) populations may have overlapped in some capacity. Many of the hypotheses and models for the transition interval suggest that Neanderthal populations remained in, or migrated to, refugial zones while AMHs colonized areas not suitable for, or abandoned by, Neanderthals. However, many hypotheses and models have not been conclusively tested due to general issues impeding a clear understanding of the relevant archeological record and because of a lack of specificity in defining and applying the term 'refugium'. This paper briefly summarizes what is known about the Middle to Upper Paleolithic transition in southern European Peninsulas and discusses some new directions in the use of refugium concepts in the study of Neanderthal extinction and AMH dispersal. We highlight the complexity of the archeological record in each region and in the studies of refugia more generally. Finally, we make an appeal for generating local, multi-proxy paleoenvironmental and paleoclimatic records to address these complexities so that hypotheses and models integrating refugial concepts in explanations of the Middle to Upper Paleolithic transition can be properly formulated and tested. © 2021 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Anatomically Modern Humans; Neanderthals; paleoecology; refugium; Southern Europe

Introduction

Neanderthal and Anatomically Modern Human (AMH) adaptation to the rapid and dramatic climatic oscillations of the late Pleistocene is a widely discussed topic in paleoanthropology and archaeology (e.g. Finlayson and Giles-Pacheco, 2000; Stewart, 2005, 2007; Finlayson and Carrión, 2007; Sepulchre *et al.*, 2007; Bradtmöller *et al.*, 2012; Bicho *et al.*, 2017; Staubwasser *et al.*, 2018), particularly in the context of their extinction. Various environmental hypotheses and models link the disappearance of Neanderthals to the extremely cold and dry conditions in Heinrich Events 5 and 4 that may have reduced Neanderthal populations below survival thresholds (Finlayson and Giles-Pacheco, 2000; d'Errico and Sánchez Goñi, 2003; Stewart *et al.*, 2003; Stewart, 2004a,b; Van Meerbeeck *et al.*, 2009; Müller *et al.*, 2011). Simultaneously, AMH populations were rapidly dispersing westward through Europe. Though genetic evidence points to interaction (Sankararaman *et al.*, 2014; Vernot and Akey, 2014; Fu *et al.*, 2015; Villanea and Schraiber, 2019), whether AMHs occupied territories already devoid of Neanderthal populations (e.g. Wood *et al.*, 2013) or the two groups occupied the same territories and possibly interacted (e.g. Marín-Arroyo and Mihailović, 2017; Marín-Arroyo *et al.*, 2018; Haws *et al.*, 2020; Marciani *et al.*, 2020; Bergström *et al.*, 2021) is still unclear.

In the southern European peninsulas, the Balkans, Italy and Iberia, Neanderthal and early AMH populations may have occupied the peninsulas simultaneously on a peninsular (Riel-Salvatore, 2010; Marín-Arroyo and Mihailović, 2017; Marciani *et al.*, 2020) or potentially regional scale (Marín-Arroyo *et al.*, 2018; Haws *et al.*, 2020). All three southern European peninsulas have long been considered a refugium – an environment whose favorable conditions supported animals and people during periods of adverse circumstances (Jochim, 1987) – for biota during the Pleistocene (e.g. Hewitt, 2000; Gómez and Lunt, 2007; Previšić *et al.*, 2009; Carrión and Leroy, 2010; González-Sampériz *et al.*, 2010; Rodríguez-Sánchez *et al.*, 2010). The refugium concept has been incorporated into many Middle to Upper Paleolithic transition scenarios in southern Europe, particularly in the context of late Neanderthal survival (e.g. Finlayson *et al.*, 2006; Zilhão *et al.*, 2017). The definition of the term 'refugium' has been, however, problematic (e.g. Ashcroft, 2010; Feliner, 2011; Jones, 2021/this Special Issue).

Despite their status as a refugium and similarities in their archeological records during the transition interval, some areas, such as the Balkans and westernmost Iberia, have been largely left out of model-building until relatively recently. The lack of specificity in the application of concepts of refugia in the context of Neanderthal extinction and AMH dispersal, limited archeological records, chronological uncertainty, limited number of local multi-proxy paleoenvironmental records, and lack of human fossils dating to the transitional phase that would clarify the makers of each technocomplex, results in a theoretical framework where the role of climate, environment and refugia in Neanderthal extinction and emergence of AMH is still not well understood.

The purpose of this paper is to outline what we consider future directions of research incorporating concepts of refugia, particularly in the context of Neanderthal extinction and AMH dispersal in the three peninsulas of southern Europe. First, we briefly review the current state of knowledge about the Middle to Upper Paleolithic transition in each peninsula. This is by no

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means a comprehensive summary of what is known about the massive research endeavors on the transition in each peninsula, but we provide enough context to elucidate some similarities and complexities in the archeological record. Second, we outline some approaches we think are useful in moving this line of research forward.

Neanderthal Extinction and AMH dispersal in the Balkans, Italy and Iberia

Paleolithic research in the Balkans, Italy and Iberia has yielded a rich archeological record that showcases regional variations in the timing, spatial patterning and technological industries involved in the Middle to Upper Paleolithic transition. The transition is complex and mosaic-like, with chronological overlap observed between transitional industries and few direct associations between human fossils and late Mousterian, transitional and Initial Upper Paleolithic assemblages (e.g. Davies, 2007; Straus, 2020/this Special Issue), though in this paper, we use the associations assumed in the literature (e.g. Benazzi *et al.*, 2011; Hublin, 2015; Hublin *et al.*, 2020). As cul-de-sacs for human populations, these geographically circumscribed areas provided barriers and corridors for the movement of human and animal populations during times of harsh glacial conditions and retained rich biodiversity that eventually populated the once-abandoned uninhabitable areas in more northern latitudes, once conditions ameliorated. All three peninsulas have heterogenous geography that form microhabitats and microclimates. In addition, current (though often contested) evidence points to simultaneous occupation of each peninsula by both Neanderthals and AMHs, with enclaves of Neanderthal populations potentially contracting into refugia as AMH populations expanded.

The Balkans

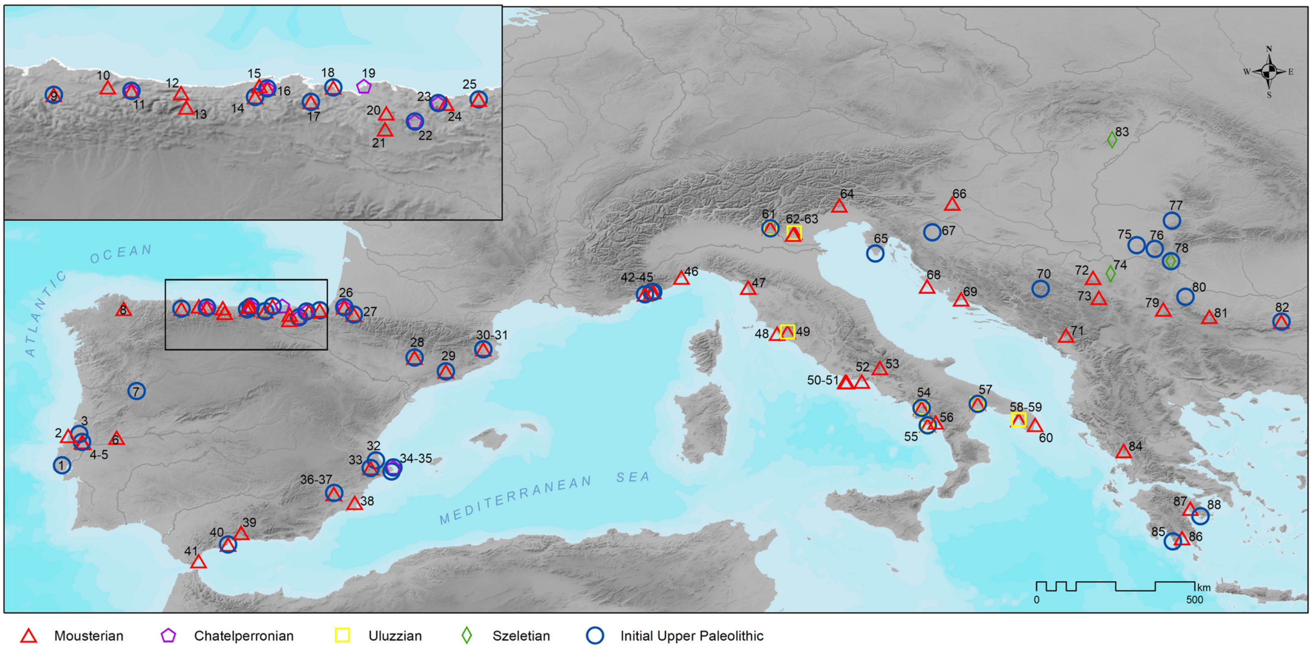
The Balkan Peninsula is located in a pivotal area for the dispersal of hominids and is, in addition to a cul-de-sac (Kozlowski, 1998), often called 'the gateway to Europe'. Topography and orography seem to be key variables to better understand both human settlement and migration. The Balkans are dominated by mainly mountainous zones, and coastal areas and major river systems formed corridors, such as the Danube and along the Mediterranean, that were important for the movement of AMHs (Conard, 2002; Van Andel *et al.*, 2003; Mellars, 2011; Mihailović *et al.*, 2011). In terms of the Paleolithic archeological record, although relatively rich for other time periods, there is a limited record that corresponds to the Middle to Upper Paleolithic transition, particularly in the central part of the peninsula (e.g. Mihailović *et al.*, 2011; Mihailović, 2014). However, there has been a significant increase in the research from various Balkan countries that have provided valuable information for this transitional period, occurring roughly between 47 and 38k cal a BP (Rink *et al.*, 2002; Miracle, 2005; Hublin *et al.*, 2020; Fewlass *et al.*, 2020; Mihailović *et al.*, 2011; Dogandžić *et al.*, 2014; Marín-Arroyo and Mihailović, 2017; Boric *et al.*, 2012; Kuhn *et al.*, 2014; Mihailović and Mihailović, 2014; Alex *et al.*, 2019; Vujević *et al.*, 2017; Karavanić *et al.*, 2018; Tourloukis *et al.*, 2016; Dogandžić and Đuričić, 2017; Mihailović and Whallon, 2017; Whallon, 2017; Tourloukis and Harvati, 2018; Mihailović, 2020; Karavanić, this Special Issue).

Middle Paleolithic sites are concentrated in the Lower and Middle Danube basins as well as the Adriatic, Ionian and Aegian coastal regions (Fig. 1) (see Tourloukis and Harvati, 2018; Mihailović, 2020 and references therein) in areas of lowland steppe and hilly terrain (Marín-Arroyo and Mihailović, 2017; Hauck *et al.*, 2018). It has been observed that during glacial conditions, the frequency of northern Balkan sites decrease, while sites located in the southern parts of the peninsula have continuous records of Neanderthal occupation, indicating that southern latitudes of the Balkans could have been a refugium that sustained Neanderthal populations (Stewart, 2005; Hublin and Roebroeks, 2009; Roebroeks *et al.*, 2011; Mihailović, 2017; Karavanić *et al.*, 2018). Chronological issues plague many of the Balkan late Mousterian sites, but redating efforts (e.g. Devièse *et al.*, 2017), evaluations of reliable radiocarbon dates (Mihailović, 2017) and new radiocarbon dates (Alex *et al.*, 2019) suggest that for the most part, the late Mousterian in the peninsula does not continue past 44–43k cal a BP, with the exception of late dates from Mousterian deposits at Velika Pećina (41.9–36.3k cal a BP) (Karavanić *et al.*, 2018) and Šalitrena Cave (42.8–39.2k cal a BP) (Marín-Arroyo and Mihailović, 2017). If the late dates are accurate, Late Neanderthal survival could be possible in central and south-western portions of the peninsula.

The transitional industries in this region are the Szeletian and the Uluzzian. The Szeletian industry is a transitional technocomplex encountered from roughly 45 to 40k cal a BP in the Balkans that is still not clearly typologically defined (despite a century of study), potentially associated with Neanderthals (although this is questioned) and encountered in many parts of northern and central Europe (Svoboda and Simán, 1989; Valoch, 1990; Svoboda, 2001, 2006; Nigst, 2006; Mester, 2014, 2018). In the Balkans, Szeletian occupations can be found in the peri-Pannonian area and re-evaluations of dates in Szeleta Cave produced date ranges of 41.5–44k cal a BP (Hauck *et al.*, 2016).

While the Uluzzian is a transitional industry typically encountered in the Italian Peninsula, it also has been identified in Klissoura Cave in Greece (Kaczanowska *et al.*, 2010) and is probably dated to before 40k cal a BP, as Uluzzian artifacts typically lie below cryptotephrae that correspond to the Campanian Ignimbrite eruption at *c.* 39k cal a BP (Kuhn *et al.*, 2010; Lowe *et al.*, 2012; Douka *et al.*, 2014; Tourloukis and Harvati, 2018). It has also been identified at Crevena Stijena (Mihailović, 2017; Mihailović and Whallon, 2017), where no signs of intermixing have occurred with the local Mousterian occupations. The relationship between the Uluzzian of the Italian Peninsula, where deciduous teeth belonging to AMHs have been associated with Uluzzian assemblages (Benazzi *et al.*, 2011 – but see Zilhão *et al.*, 2015 for an opposite interpretation), and how the Uluzzian of the Balkans compares to the Italian record is unknown.

Current data support an AMH dispersal in an east–west direction beginning at *c.* 46k cal a BP in the Balkan Peninsula at Bacho Kiro (Fewlass *et al.*, 2020; Hublin *et al.*, 2020). The 'Bachokirian', first identified there, was once considered its own transitional assemblage but its recent association with modern human remains (Fewlass *et al.*, 2020; Hublin *et al.*, 2020) means it is now argued to be a variant of the earliest Upper Paleolithic (Tsanova and Bordes, 2003), which has been dated to 47–45k cal a BP. The Proto-Aurignacian and Aurignacian, typically associated with AMHs, are found throughout the peninsula with the exception of some areas such as the central peninsula and immediately south of the Balkan Mountains (Mihailović, 2020). While there have been debates over designations of lithic assemblages as Proto-Aurignacian and Aurignacian, some argue that there is not enough data to be able to distinguish between the two technocomplexes in the region (e.g. Dogandžić *et al.*, 2014). However, these assemblages appear in the Balkans before 40k cal a BP, perhaps as early as 44k cal a BP (Mihailović, 2020). For discussions of other



1	Pego do Diabo
2	Mira Nascente
3	Lagar Velho
4	Lapa do Picareiro
5	Gruta da Oliveira
6	Foz do Enxarrique
7	Cardina-Salto do Boi
8	Valiña
9	La Viña
10	El Sidrón
11	Abrigo de la Güelga
12	Llonín
13	Esquilleu
14	El Castillo
15	Covalejos
16	Morín
17	El Mirón
18	El Abrigo de El Cuco
19	Aranbaltza
20	Axlor
21	Arrillor
22	Labeko Koba
23	Ekain
24	Amalda
25	Aitzbitarte III
26	Isturitz
27	Gatzarria
28	Cova Gran
29	Abric Romaní
30	Arbreda
31	Reclau Viver
32	Les Mallaetes
33	Cova Beneito
34	Les Cendres
35	Foradada
36	La Boja
37	Anton
38	Sima de las Palomas
39	Zafarraya
40	Bajondillo
41	Gorham's Cave
42	Observatoire
43	Grotta del Principe
44	Riparo Mochi
45	Riparo Bombrini
46	Arma Manie
47	Buca della Iena
48	Santi
49	La Fabbrica
50	Breuil
51	Fossellone
52	S. Agostino
53	Reali
54	Castelcivita
55	Grotta della Cala
56	Riparo del Poggio
57	Riparo l'Oscurusciuto
58	Cavallo
59	Uluzzo
60	Romanelli
61	Fumane
62	San Bernardino
63	Riparo Broion
64	Rio Secco
65	Šandalja II
66	Vindija
67	Luščić
68	Velika Pećina
69	Mujina Pećina
70	Orlovača
71	Bioče
72	Šalitrena Pećina
73	Hadži Prodanova Pećina
74	Risovača
75	Crvenka-At
76	Pestera cu Oase
77	Româneşti-Dumbrăviţa
78	Tabula Traiana
79	Pešturina
80	Kozarnika
81	Temnata Dupka
82	Bacho Kiro
83	Szeleta
84	Asprochaliko
85	Kolominitsa
86	Lakonis
87	Klissoura
88	Franchthi

Figure 1. Map showing the distribution of selected Mousterian, transitional and Initial Upper Paleolithic (Aurignacian and Proto-Aurignacian) sites in the three southern European peninsulas, including sites mentioned in the text. Map made by Célia Gonçalves. [Color figure can be viewed at wileyonlinelibrary.com]

regional traditions of early Upper Paleolithic cultures, we refer the reader to Mihailović (2020) and Alex *et al.* (2019).

As it has been proposed for other parts of Europe, there may have been a chronological overlap of thousands of years between late Middle and Initial Upper Paleolithic populations in the Balkans, presumably Neanderthals and AMHs (Marín-Arroyo and Mihailović, 2017; Alex *et al.*, 2019; Marín-Arroyo *et al.*, in press), although others suggest this overlap could have been short-lived (Marín-Arroyo and Mihailović, 2017). A number of scenarios have been proposed for this population turnover or assimilation (*sensu* Hublin, 2015) in the Balkans. One explanation is that Neanderthals disappeared at the onset of Heinrich Event 4, triggered by the Campanian Ignimbrite around 39 ka BP, leaving behind empty space for AMHs to colonize (Fitzsimmons *et al.*, 2013). Others, however, suggested Neanderthal depopulation of the Balkans may have occurred earlier as cooler and drier conditions prevailed with Heinrich Event 5, again leaving open unoccupied landscapes for AMH to recolonize (Müller *et al.*, 2011). In some places where Neanderthals may have survived until relatively late, like the eastern Adriatic, the Campanian Ignimbrite may not have strongly affected Neanderthal populations as this moisture-rich area (Tzedakis and Bennett, 1995; Griffiths *et al.*, 2004; Tzedakis, 2004; Weiss and Ferrand, 2007) could be considered a Neanderthal refugium (Vishneskiy *et al.*, 2019). Another scenario is that the southern coastal belt, which fostered continuous Neanderthal occupation, was a core refugium, and the mountainous areas in the Central Balkans saw local Neanderthal extinctions (Dogandžić *et al.*, 2014). The opposite has also been proposed as a possibility, wherein central mountainous areas may have been key refugial zones that had continuous Neanderthal occupations (Dogandžić *et al.*, 2014) or a mountainous refugium for Neanderthals as AMH populations rapidly dispersed around them (Marín-Arroyo and Mihailović, 2017; Marín-Arroyo *et al.*, in press).

Unfortunately, these scenarios remain untested not only because of the limited archeological record, but due to the paucity of local paleoenvironmental records that could help clarify what areas in such a heterogenous landscape could have acted as a refugium. Regardless, it is notable that there may not have been a hiatus between the last Neanderthal and first AMH occupations in parts of the Balkans.

Italy

The Italian Peninsula shares some characteristics with the Balkans. Areas in the northern portion of the peninsula such as the Po Valley and Mediterranean and Adriatic coasts possibly acted as corridors for AMH dispersal. Simultaneously, the Alps and Apennines acted as geographical barriers, influenced by the cyclical submersion of the North Adriatic platform due to fluctuating sea levels (Sala, 1990; Sala and Marchetti, 2006), and climatically and ecologically segregated the Mediterranean zone from Eastern Europe. The diverse ecological and climatic conditions heterogeneously distributed throughout the peninsula mean that Italy, too, has been considered a refugium for human populations as well as an interesting backdrop for the replacement or absorption of Neanderthal populations by AMHs (e.g. Benazzi *et al.*, 2011; Higham *et al.*, 2011; Riel-Salvatore, 2010; Moroni *et al.*, 2018; Peresani *et al.*, 2019; Romandini *et al.*, 2020a). Italy has a rich Middle and Upper Paleolithic record and a relatively long (10–12 ka) transition between the late Middle Paleolithic and Initial Upper Paleolithic, from ~42.7 to 30.7k cal a BP (Romandini *et al.*, 2020a; Riel-Salvatore, 2007, 2009; Higham *et al.*, 2009; Riel-Salvatore *et al.*, this Special Issue).

Concentrations or clusters of Middle Paleolithic sites are located in the Ligurian Arch, north-east Italy, along the Tyrrhenian Coast, and in the Ionian region in the south–east (Fig. 1) (see also fig. 1 in Marciani *et al.*, 2018; and fig. 1 in Romandini *et al.*, 2020a). There is the common misconception that Middle Paleolithic sites are located in mostly caves and rockshelters found along the coasts and lowlands of the peninsula, but open-air sites are, in fact, more abundant (Milliken, 2001). The lack of reliable contextual information that open-air sites often offer in comparison to caves and rockshelters results in the fact that, in general, open-air sites are less studied, generally published less and usually in mostly local journals, and often left out of syntheses and model-building. Late Middle Paleolithic sites disappear in most of the peninsula by 41k cal a BP (Higham *et al.*, 2009), with the exception of Riparo Bombrini (Liguria), Grotta Breuil and Grotta Reali (central Italy) whose dates for the last Middle Paleolithic are 40.9, 39.4–38.7 and 40.7k cal a BP, respectively (Peretto, 2012; Grimaldi and Santaniello, 2014; Holt *et al.*, 2018; Negrino and Riel Salvatore, 2018; Riel-Salvatore and Negrino, 2018; Peretto *et al.*, 2020).

The two post-Middle Paleolithic industries most commonly encountered in the Italian Peninsula are the Uluzzian and the Proto-Aurignacian. The Uluzzian, considered a transitional complex, was first identified in the 1960s at Grotta del Cavallo (Apulia) (Palma di Cesnola, 1963, 1964). It is a technocomplex that displays both Middle and Upper Paleolithic characteristics (Riel-Salvatore, 2009). Originally identified only in southern Italy, in recent decades, the Uluzzian also has been found in the northern parts of the peninsula at Grotta di Fumane and Riparo del Broion (Peresani, 2008; Peresani *et al.*, 2016, 2019), and at one site in the center of the peninsula: La Fabbrica in Tuscany (Pitti *et al.*, 1976). Current radiocarbon dates for the Uluzzian in Italy place it at ~46–33k cal a BP (Gambassini, 1997; Hedges *et al.*, 1998; Riel-Salvatore, 2009; Benazzi *et al.*, 2011; Peresani, 2012; Wood *et al.*, 2012; Fabbri *et al.*, 2016; Villa *et al.*, 2018; Zanchetta *et al.*, 2018; Peresani *et al.*, 2019). The Uluzzian has been associated with AMHs as their makers after the discovery of two AMH deciduous teeth associated with an Uluzzian assemblage (Benazzi *et al.*, 2011). However, as we mentioned before, the association of the lithic assemblage with AMH remains has been contested (Zilhão *et al.*, 2015).

The Proto-Aurignacian is considered one of the first manifestations of AMHs into Europe (Bailey and Hublin, 2005; Mellars, 2006; Nigst *et al.*, 2014; Benazzi *et al.*, 2015). This Upper Paleolithic industry was first identified in northern Italy and has characteristics of typical Initial Upper Paleolithic assemblages such as manufacture of blades and small implements, personal adornments and ochre and bone tools, including awls and needles (Broglio *et al.*, 2006; Mellars, 2006; Teyssandier, 2008). Proto-Aurignacian sites are present in various geographical regions of Italy (Fig. 1) (e.g. Riel-Salvatore, 2010; see also fig. 1 in Marciani *et al.*, 2020; Romandini *et al.*, 2020). Proto-Aurignacian and Uluzzian occupations are contemporaneous, with available radiocarbon dates for Proto-Aurignacian occupations ranging from 41.7 to 30.3k cal a BP (Hedges *et al.*, 1998; Higham *et al.*, 2009, 2014; Peresani, 2012; Wood *et al.*, 2012; Douka *et al.*, 2014). The Proto-Aurignacian is thought to be associated with AMHs in Europe (Broglio *et al.*, 2006; Mellars, 2006; Teyssandier, 2008) and in Italy this in association with AMH remains has been confirmed at Riparo Mochi dating to 42k cal a BP (Douka *et al.*, 2012; Benazzi *et al.*, 2015; Falcucci *et al.*, 2017; Falcucci and Peresani, 2018).

Like the Balkans, there seems to be evidence of both Neanderthals and AMHs occupying the Italian peninsula contemporaneously, with Neanderthal and AMH populations occupying areas both near and distant to each other. While the Uluzzian and the Proto-Aurignacian are encountered in the northern and southern thirds of the peninsula, the latest Mousterian industries cluster in the west-central and northern portions of the Peninsula (Riel-Salvatore, 2009), meaning that west-central Neanderthal populations may have remained there while AMHs colonized the north and south (Riel-Salvatore, 2010) and northern Neanderthal populations of Neanderthals may have lived in close proximity to AMHs (Peresani, 2011; Benazzi *et al.*, 2014; Romandini *et al.*, 2020b).

The ecological changes associated with the Campanian Ignimbrite tephra in a vast portion of Eurasia around 39k cal a BP have been linked to both the disappearance of Neanderthals (Golovanova *et al.*, 2010) as well as the Proto-Aurignacian (Fedele *et al.*, 2002, 2008; Giaccio *et al.*, 2008, 2017) in various parts of Europe. However, the explosion probably did not uniformly impact the continent ecologically (Lowe *et al.*, 2012; Fitzsimmons *et al.*, 2013; Davies *et al.*, 2015). It is possible that the Campanian Ignimbrite eruption is related to, or even triggered, the onset of Heinrich Event 4 (Giaccio *et al.*, 2017), which in Italy coincides with the end of the Uluzzian and Proto-Aurignacian, confirming some past studies (Fedele *et al.*, 2002, 2008; Giaccio *et al.*, 2006, 2008). Others have shown, however, through the observation of new dates, that the Proto-Aurignacian in Italy (Riel-Salvatore, 2007; Douka *et al.*, 2012; Higham *et al.*, 2014; Benazzi *et al.*, 2015) as well as Neanderthals (Lowe *et al.*, 2012) survived thousands of years after this volcanic event.

Here, as in the Balkans and elsewhere, it could be that Neanderthals were not able to successfully adapt to the unstable and dramatically fluctuating conditions of Marine Isotope Stage (MIS) 3, failing to recover from Heinrich Events 4 (Fitzsimmons *et al.*, 2013) or 5 (Müller *et al.*, 2011) although in southern Italy, Heinrich Event 5 conditions were relatively mild and the region may have acted as a refugium (Columbu *et al.*, 2020). Another explanation for the Middle to Upper Paleolithic transition is that regions such as central Italy served as a dependable refugium (Blondel and Aronson, 1999), and that Neanderthal populations were able to survive there for longer while the Uluzzian and Proto-Aurignacian are first identified in regions of Italy where climatic conditions may have been more unstable and paleoenvironmental changes more severe (Riel-Salvatore, 2007). The severity of Heinrich Event 3 in parts of Italy such as the north-east, however, has recently been brought into question (Badino *et al.*, 2020). Similar situations have been observed in one of the Balzi Rossi caves, Riparo Bombrini, although not contemporaneous with the previous scenario (Riel-Salvatore *et al.*, 2021/this Special Issue). Here, it has been argued that a Neanderthal enclave represented through the latest Mousterian of Liguria was surrounded by thriving Proto-Aurignacian and Early Aurignacian populations to the north and west of the alps with Uluzzian populations expanding to the south and east (Barshay-Szmidt *et al.*, 2018, 2020; Villa *et al.*, 2018). The ephemeral Neanderthal occupations in two of the Balzi Rossi caves, Riparo Bombrini and Riparo Mochi, as hypothesized by Riel-Salvatore *et al.*, (2021/this Special issue), could be representative of small Neanderthal populations contracting into an ecologically stable, *in situ* micro-refugium with suitable conditions until they were ultimately replaced or absorbed (Hublin, 2015) by AMH populations.

Once again, in Italy, these scenarios remain largely unevaluated due to issues of association between technocomplexes and their makers and but also a large number of sites were excavated before the employment of modern methods and chronological issues. In a similar vein, significant portions of the archeological record, namely sites with limited contextual information (e.g. open-air sites) and sites with low artifact densities, are often missing from analyses, potentially resulting in skewed interpretations. In addition, given the diversity in the topography, climate and ecology of the Italian Peninsula, there is a general lack of local paleoenvironmental records that could identify other small-scale refugia that affected small human populations on local scales as exemplified by Riel-Salvatore *et al.* (this Special Issue) in Liguria.

Iberia

The Iberian Peninsula was the last southern peninsula in Europe to be colonized by AMHs, the last place where Neanderthals disappeared, and potentially the location of late Neanderthal survival (*c.* 37k cal a BP) (e.g. Straus *et al.*, 1993; Straus, 1996; Finlayson et al, 2006; Bicho and Haws, 2008; Zilhão *et al.*, 2010, 2017; Bicho *et al.*, 2015). The peninsula is barricaded by the Pyrenees, limiting the dispersal routes of animals and humans alike and has a climate that was and is heavily regulated by both the Mediterranean Sea and Atlantic Ocean. Iberia has long been considered a refugium for humans (e.g. Finlayson *et al.*, 2006), with glaciers only occurring in its northern mountain ranges during stadials, and has a long list of endemic species (e.g. Abellán and Svenning, 2014). Paleolithic site distribution favors coasts and river valleys with the middle of the peninsula relatively empty during the transition interval (e.g. Straus *et al.*, 2000; Bicho, 2004; Wolf *et al.*, 2018). Based on current available dates, the Middle to Upper Paleolithic transition may have occurred somewhere over 8000–12 000 years, spanning roughly 45–37k cal a BP but perhaps even into ~30k cal a BP in areas such as Gibraltar (Finlayson et al, 2006).

Late Middle Paleolithic sites in Iberia tend to cluster in specific regions (Fig. 1) such as the Portuguese Estremadura and Douro Valley, south-eastern coast of Andalucía, the Mediterranean coasts of Valencia, Murcia and Catalonia, and along the northern strip of the peninsula, also known as Vasco-Cantabria (Fig. 1; see also fig. 1 in Haws *et al.*, 2020). In Iberia, the disappearance of Neanderthals was a spatially and regionally variable phenomenon. While for a time southern Iberia was thought to have supported Neanderthal populations for several millennia later than elsewhere in Europe, evidence seems to indicate that Late Mousterian sites disappear in Iberia by ~42k cal a BP. Possible exceptions are sites in the Vasco-Cantabrian region, where the Mousterian disappeared earlier, between 47.9 and 45k cal a BP. In southern Iberia, the sites of Gorham's Cave (Gibraltar) and Cueva Antón (Murcia) produced dates suggesting a persistence of the Mousterian until 37k cal a BP or later (Finlayson *et al.*, 2006; Zilhão *et al.*, 2017). Late Neanderthal survival has been attributed to the southern rim of Iberia being a refugium (and, in some cases, a biodiversity hotspot) that supported Neanderthals who were well adapted to temperate and forested conditions (Finlayson and Giles-Pacheco, 2000; Finlayson *et al.*, 2006; Finlayson and Carrión, 2007; Jennings *et al.*, 2011). The idea of a Neanderthal refugium in the southern half of the peninsula pedestaled models such as the Ebro Frontier Model (Zilhão, 2000), whose validity has been challenged due to new dating and re-evaluations of old dates (Wood *et al.*, 2013; Higham *et al.*, 2014; Haws *et al.*, 2020; Zilhão *et al.*, 2021).

The Châtelperronian is the only transitional industry identified in Iberia, and it is limited to Vasco-Cantabria (Altuna and Merino, 1984; Marín-Arroyo *et al.*, 2018; see also Marín-Arroyo and Sanz-Royo, 2021/this Special Issue). While this technocomplex, which is characterized by Middle and Upper Paleolithic lithic components, temporally coincides with late Mousterian assemblages in south-western France (Maroto *et al.*, 2012), in the Cantabrian region there seems to be a hiatus of around three millennia between the late Mousterian and the Chatelperronian, the latter of which lasted between 42.6 and 41.5k cal a BP (Marín-Arroyo *et al.*, 2018). This industry's presence in Iberia is brief and seems to disappear by 41.5k cal a BP (Marín-Arroyo *et al.*, 2018). Although there has been considerable debate in the past, Neanderthals are generally accepted to be the makers of this industry (Hublin et al, 2012), though there is still some debate (e.g. Bar-Yosef and Bordes, 2010; Gravina *et al.*, 2018).

The early Aurignacian, considered one of the first true Upper Paleolithic industries in Eurasia, is present in northern Iberia somewhere between 43.3 and 40.5k cal a BP. This implies that in northern Iberia, makers of the Châtelperronian (presumably Neanderthals) and the Aurignacian (presumably AMHs) may have overlapped for a short period, no more than 1000 years (Marín-Arroyo *et al.*, 2018). The situation in central and southern Iberia is quite different. For a long time, the earliest Upper Paleolithic and, by proxy, AMH appearance in southern Iberia was attributed to the Evolved/Late Aurignacian at Cova de les Cendres on the Mediterranean coast, La Boja in southern Spain and Pego do Diabo in Central Portugal, which yielded earliest dates of ~35 (Villaverde *et al.*, 2019), ~36.5 and ~34.5k cal a BP (Zilhão *et al.*, 2017 – but see Bicho *et al.*, 2015 for an opposite view), respectively. However, recent discoveries at Bajondillo Cave, Lapa do Picareiro and Cardina-Salto do Boi, suggest an earlier presence of an Aurignacian, with dates of 45–43 (Cortés-Sánchez *et al.*, 2019), 41–38 (Haws *et al.*, 2020) and 35.6–31.6 k a BP (Aubry *et al.*, 2020), respectively, although the stratigraphic integrity of Bajondillo Cave has been questioned (Anderson *et al.*, 2019; de la Peña, 2019). Complicating the matter further, unfortunately, is the fact that Iberia (particularly Portugal) has very limited archeological records that force models and hypotheses for the Middle to Upper Paleolithic transition to be based upon a handful of sites. In addition, the lack of human fossils associated with Late Mousterian, Châtelperronian and Aurignacian industries leaves open the question about their makers, as there are no human fossils associated with these lithic assemblages (Straus, 2018, 2020/this Special Issue).

The data discussed here imply that the chronology of Neanderthal and AMH occupations overlapped in Iberia at the peninsular and possibly even regional scale, although whether these populations interacted remains unknown – still, there has been strong arguments for genetic mixing between the two populations due to the presence of a hybrid AMH skeleton at Lagar Velho, central Portugal (Duarte et al, 1999). In Cantabria, central Portugal and possibly south-east Spain, Neanderthals and AMHs had territories that were in close proximity but why these areas were possible Neanderthal holdouts is still not clear. Many of the explanations proposed for the Middle to Upper Paleolithic transition in the Balkans and Italy are also proposed for Iberia. The effects of Heinrich Events 5 and 4 on late Neanderthals and early AMHs could have reduced Neanderthal populations while expanding habitats to which AMHs were adapted (Finlayson and Giles-Pacheco, 2000; d'Errico and Sánchez Goñi, 2003; Stewart *et al.*, 2003; Stewart, 2004a,b; Van Meerbeeck *et al.*, 2009; Müller *et al.*, 2011). The Ebro Frontier Model suggested Neanderthal populations retreated as the extent of the temperate Mediterranean woodland habitats shrank while AMHs expanded their range as the open-steppe they dispersed through in their colonization of Europe expanded southward in Iberia (Zilhão, 2000; Zilhão *et al.*, 2010), but this has been challenged (Wood *et al.*, 2013; Higham *et al.*, 2014; Haws *et al.*, 2020). The two sites whose dates still support very late Neanderthal survival, Gorham's and Anton, if dated accurately, suggest that enclaves of Neanderthal populations survived longer in refugia (e.g. Finlayson *et al.*, 2006; Zilhão *et al.*, 2017) while going locally extinct in other areas (Wolf *et al.*, 2018). Should these dates be inaccurate, there could have been a hiatus between Neanderthal and AMH populations in southern Iberia (Wood *et al.*, 2013).

Unfortunately, these scenarios remain unevaluated due to the same issues described for the Balkans and Italy: chronological issues, a paucity of human fossils in association with transitional industries, or in the case of Iberia, early Upper Paleolithic industries, limited local paleoenvironmental records and small number of sites with deposits spanning the Middle to Upper Paleolithic transition, the latter of which might be due to stratigraphic discontinuities (see Aubry *et al.*, 2011; Mallol *et al.*, 2012). While in some regions, such as southernmost and south-east Iberia, the role of a refugium in late Neanderthal survival has been tested (Ochando *et al.*, this Special Issue; Finlayson *et al.*, 2006; Jennings *et al.*, 2011) this is not true for other parts of the peninsula, and contention over the accuracy of dates supporting late Neanderthal survival is a particularly difficult issue to tackle.

The archeological records in the Balkans, Italy and Iberia all demonstrate the complexity in the spatial patterning and timing of the Middle to Upper Paleolithic transition, reinforcing the idea that Neanderthal populations disappeared at different times in different areas The record clearly displays a mosaic (Straus, 2005). We want to emphasize that all three peninsulas have chronological issues, a paucity of human remains, debates over makers of certain technocomplexes, limited local paleoenvironmental records and various areas that have been loosely considered refugia, and have had various hypotheses and models proposed that relate to human adaptation to climate change. Adding to this list of issues that hinder our understanding of this critical time in our human history are misconceptions of archeological trends due to problematic syntheses that lack information on open-air and lesser-known sites or information published in other languages, usually in local journals. However, the state of evidence in the three peninsulas suggests that on a peninsular and sometimes regional scale, Neanderthals and AMHs coexisted, and Neanderthal populations seem to have persisted in patches with favorable environmental conditions, or refugia, before their disappearance. Many of these hypotheses have not been conclusively tested. While the aforementioned list describes many of the reasons for this, the lack of specificity and inconsistency in the application of refugium concepts, an underappreciation for the complexity of southern European refugia and a general lack of local multi-proxy environmental records mean that evaluating refugia concepts in the context of Neanderthal extinction and AMH dispersal is only possible through loose or conservative interpretations about the paleoecology of transitional populations. Below, we describe some issues that must be considered in studying the concept of late Neanderthal refugia to sidestep some of these issues.

Refugia: problems and solutions

The refugium concept is widely used in paleoecology for a variety of purposes (Bennett and Provan, 2008) and is key for understanding the persistence of species over time through changing climates (Tzedakis *et al.*, 2002). Since its inception, the term 'refugium' has been loosely defined, resulting in inconsistencies in how the term is applied and the methods used to study or identify it (e.g. Ashcroft, 2010; Feliner, 2011). In addition, the study of refugia is sometimes gleaned from *ad hoc* descriptive data sources, making comparisons or observations of patterns difficult (e.g. Feliner, 2011). The ambiguity of refugia has been discussed in depth over the past few decades, and even though there is no consensus on how the term should be applied, recent perspectives provide approaches that prove to be useful for studying refugia in the Middle to Upper Paleolithic transition in southern Europe.

The term refugium was used initially in the biological sciences to describe areas that are spatially limited to which organisms reacted, in which they survived stadial phases during the Last Glacial Maximum, and from which organisms eventually expanded into surrounding areas (Dahl, 1946; Bennett and Provan, 2008; Keppel *et al.*, 2012). In other words, according to Keppel *et al.* (2012) 'refugia are habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions'. Out of the increasing number of studies on European refugia published in the last three decades, the most well-understood refugium systems are mostly from northern latitudes, and this is probably because observed patterns of the expansion and extraction of an organism's distributions were simpler relative to the more southern portions of Europe, since the focus was on major losses of biodiversity during periods of adverse climate change (Feliner, 2011). Refugia in southern Europe, however, are more complex because they retained genetic diversity due to preservation of genotypes, experienced relatively less biodiversity loss, and are the product of the amalgamation of various biological processes taking place over hundreds of thousands of years in a topographically varied, heterogeneous landscape (Feliner, 2011). The difference between the characterization of an area as a refugium for different organisms that are typically part of the same ecological community can therefore be subtle, and more difficult to identify.

Extensive reviews about the current and past uses of the term 'refugium' demonstrate that the methods involved in studying or identifying refugia are founded by the term's definition (Bennett and Provan, 2008; Feliner, 2011; Birks, 2015). While there is no right or wrong definition of refugium, a few components should be defined that render the term a much more useful concept. While we do not summarize the various areas of definition for its concept here (see Bennett and Provan, 2008; Ashcroft, 2010; Feliner, 2011; Birks, 2015) we highlight Jones' (2021/this Special Issue) ideas about the definable characteristics of the term 'refugium' in Paleolithic studies pulled from the work of Ashcroft (2010). Jones (2021/this Special Issue) demonstrates that considering a set of variables, briefly listed below, in the study of refugia in Paleolithic Europe can sidestep some ambiguity issues.

For the Middle to Upper Paleolithic transition, we often use single-species concepts in studying late Neanderthals and early AMHs with the goal of finding their geographical range (Jones, 2021/this Special Issue). However, when it comes to reconstructing human paleoecology, the focus is on more than one species and in the context of Pleistocene climate change, the characteristics of temperate or steppe–tundra communities. This is often a measure of biodiversity at any given location during stadials and Heinrich Events (Keppel *et al.*, 2012). Jones (2021/this Special Issue) argues for using single-taxon approaches for studying human populations since different species respond differently to climate change and measures of biodiversity are already encapsulated in the term 'hotspot' (Ashcroft, 2010). While there will probably be overlap between single-taxon and multiple-taxa approaches, focusing on the differences between the two removes one level of ambiguity from the concept of refugium. An example of this overlap is evident in research in southern Spain, considered a hotspot or multi-species refugium (e.g. Ochando *et al.*, 2020) but in the context of Neanderthal extinction, a single-species concept is implied (Finlayson *et al.*, 2006; Jones, 2021/this Special Issue). Both perspectives can be useful, but the differentiation or separation between the two is a step towards addressing the complexities of the biological and environmental systems at play.

Different methods are used to identify different scales of refugia (macro-refugia, micro-refugia, refugia-within-refugia or sub-refugia) and this is important because refugia function differently at different scales (Bennett and Provan, 2008). An approach identifying refugium at the peninsular scale (i.e. macro-refugium) is often too simplistic and therefore unadvised, unless it makes sense to do so (Gómez and Lunt, 2007). Given the heterogeneity of the environments found within the three southern European peninsulas, and the notion that the Middle to Upper Paleolithic transition was a temporal and spatial mosaic, focusing on micro-refugia may be more useful (Gómez and Lunt, 2007; Jones, 2021/this Special Issue). In Riel-Salvatore *et al.*'s (this Special Issue) discussion of the Sterile Mousterian in some of the Balzi Rossi caves, the definition of micro-refugia made sense because the Neanderthal populations that were surrounded by AMH populations were hypothesized to be enclaves. Macro-refugia, however, could be applied to the scenario of Neanderthals in central Italy occupying a refugial zone while surrounded by AMH populations to the north and the south.

The distinction between *in situ*, or locations where environmental conditions continue to be favorable for any given taxon, and *ex situ*, or locations to which a single-taxon or multiple species migrate, is particularly useful for climate-driven environmental change. Thinking about Neanderthal refugia in an *in situ* context carries the assumption that populations were contracting while for AMH dispersal, if influenced by the expansion of steppe conditions to which they were well adapted, their endpoint could be considered *ex situ*. As Jones points out, this is rarely explicitly done in Paleolithic archeology (see Glantz *et al.*, 2018 for an exception) but examples of these concepts being used are present in models such as the Ebro Frontier Model (Zilhão *et al.*, 2010). Discerning *in situ* from *ex situ* refugia is particularly important because it incorporates the direction of movement and migration of populations and would be particularly useful for evaluating the Middle to Upper Paleolithic transition.

The last definable characteristic concerns ecological stability, an oft-cited element for why any given region may be attractive for human occupation (Carrión *et al.*, 2008; Jones, 2012; Jones *et al.*, 2020). Ecological stability can be defined by either climate (i.e. areas where climates remain relatively unaffected by cyclical climate change) or habitat (i.e. an area occupied by any given species and its characteristics). In the context of archaeology, however, distinguishing between the two may be impossible (see Carrión *et al.*, 2018 for an exception) because archeological and paleoenvironmental information from the Paleolithic is often time-averaged, available in different scales and of coarse-grained resolution (Jones, 2021/this Special Issue). Generally, however, new methods, such as stable isotope analysis of zooarcheological assemblages, could provide the tools with which ecological stability can be evaluated for human populations on a more general level (Jones *et al.*, 2018, 2020; Dombrosky *et al.*, 2020). Assessing environmental stability can also generate the opportunity to formulate hypotheses about *in situ* vs *ex situ* refugia, where stable environments could indicate an *in situ* refugium while unstable environments could suggest the existence of an *ex situ* refugium (Jones, 2021/this Special Issue). Furthermore, the attributes of a stable or unstable environment can provide information for understanding the 'push' or 'pull' factors that would elicit migration (e.g. Mihailović, 2020).

The identification of refugia generally requires two components, reconstructions of the spatial and temporal distributions of a single species or a number of species, and paleoclimatic or paleoenvironmental reconstructions. However, some scientists have questioned the validity of identifying refugia at all in this way. Feliner (2011), describes the search for refugia as being like 'looking for the holy grail of evolution from the last three million years'. Instead of focusing on the identification of refugia, Feliner (2011) argues, the focus should be on formulating specific testable hypotheses about observed changes in the distribution of animals on modestly limited temporal and spatial scales, how these changes were motivated by climate change and how we can predict expected patterns.

However, the two are not necessarily mutually exclusive. We believe that the study of refugia in the context of Neanderthal extinction and AMH dispersal in southern peninsular Europe would benefit by adopting these two approaches wherever possible:

1. Specificity in defining various characteristics of the term refugia (*sensu* Jones, 2021/this Special Issue);
2. Focusing on formulating specific testable refugium hypotheses that are temporally and spatially limited (Feliner, 2011).

As we have demonstrated above, the Middle to Upper Paleolithic transition in the Balkans, Italy and Iberia involves complex, asynchronous processes, and local population replacements or absorptions differ in their timing, spatial patterning, paleoclimatic context and causes. The same is true for the processes that formed and maintained refugia for different taxa. This mosaic of change that is the Middle to Upper Paleolithic transition (Straus, 2005) in the patchy landscape of the southern European peninsulas therefore requires rebuilding of individual 'tesserae' and processes therein. While the analogy of a mosaic is not novel for the Middle to Upper Paleolithic transition or other processes that caused cultural transitions, the study of two already complex processes (Middle to Upper Paleolithic transition and refugia) must be approached with attention to detail and specificity, starting from the smallest temporal and spatial scale possible and then expanding to regional or even peninsular levels, if appropriate. To reconstruct the tesserae of this analogous mosaic, we believe we must place more importance on comprehensive syntheses of pertinent archeological information as well as on the creation of *local, multi-proxy* environmental records in archeological endeavors.

The misconception mentioned above that most Mousterian sites in Italy are located in caves and rockshelters when, in reality, open-air sites are more abundant (Milliken, 2001) is an example of the dangers that a lack of detail and specificity when building local and regional hypotheses and models can have. Archeological sites contain varying levels of contextual information, and while having ample contextual information is ideal, this is often not the case. As a result, archeologists generally place tremendous importance on the rare magnificent 'star' sites with excellent preservation of contextual information and rich archeological records. Often, regional hypotheses and models are based on these 'star' sites, and these sites are sometimes considered the ultimate reference for what the Middle to Upper Paleolithic transition should look like in a specific area (e.g. Zilhão *et al.*, 2013). However, it only takes one new piece of information (e.g. new dates, new finds, new sites) to turn a model on its head. For example, recent developments at Gruta da Oliveira (central Portugal), a site once argued as *the* reference for modeling the Middle to Upper Paleolithic transition and late Neanderthal survival in southern Iberia (Zilhão *et al.*, 2013), is now believed to have Neanderthal occupations that do not continue past MIS 5 according to new dating assays, (Zilhão *et al.*, 2021), rendering the models proposed based on this site (e.g. Ebro Frontier Model) highly questionable. To adopt the approaches for studying the role of refugia on Neanderthal extinction and AMH dispersal outlined above, we must synthesize archeological information robustly and responsibly, taking into consideration the shortcomings and complexities of a region's entire archeological record. In other words, 'imperfect' sites (e.g. sites with limited quantities of archeological material or contextual information such as open-air sites) that are often less well-known and published in local journals should not be so easily discounted from syntheses and analyses, as so frequently happens.

'Imperfect' sites and even paleontological sites can also be a source of desperately needed paleoenvironmental information. Fortunately, we do not need sites with archeology to find proxies with which to build local paleoclimatic and paleoenvironmental records. Using records from hundreds of kilometers away, though they may be the only records available and are still fundamentally useful, is not adequate to account for the heterogeneity and complexity of the environmental systems of the southern European landscapes (e.g. Médail and Diadema, 2009). To use an Iberian example, though the Iberian Margin marine deep-sea sediment cores provide information on cyclical climate change on millennial and sometimes centennial scales, how these climatic changes manifest on land is still not well understood, though there are various efforts to do so (see Marín-Arroyo, 2019). While we have seen the successful identification of refugial zones through the synthesis of numerous local paleoenvironmental records which provide enough context to formulate specific hypotheses (see Ochando *et al.* and Real *et al.*, both in this Special Issue), a large portion of the Balkans, Italy and Iberia are not as fortunate to have large quantities of paleoenvironmental records in archeologically rich zones, and as a result, we are limited in the understanding of human–environment adaptations and the function of refugial zones as a whole.

The use of *numerous* local proxies is of utmost importance. The limitations of some paleoenvironmental/paleoclimatic proxies such as pollen have been detailed elsewhere (e.g. Jiménez-Espejo *et al.*, 2007; Carrión *et al.*, 2008), and these works show just how conservative we must be in the interpretation of these records. In some cases, different paleoenvironmental proxies from the same site may provide information on different components of an environment, and sometimes even contradict each other (e.g. Rofes *et al.*, 2015; Fernández-García *et al.*, 2018; Pederzani *et al.*, 2021; see fig. 3 in Jones *et al.* 2020). There are several reasons for this including differences in the geographical extent the proxy represents, its resolution, and the lag time between climate or environmental change and its manifestation in the proxy record, among others. With any given proxy, assumptions made in the interpretation of proxy records can mask the complicated processes that went into their formation (see discussion in Ochando, this Special Issue). This is especially important in light of the fact that different taxa have different tolerances and responses to climate change. The limitations and assumptions of the archeological and paleoenvironmental records are impossible to ignore. Regardless, with numerous, local, multi-proxy paleoenvironmental records, testable hypotheses that are spatially and temporally limited on the role of refugia in the Middle to Upper Paleolithic transition for any one location is one step towards addressing both the complexity of the archaeological record as well as the complexity of the biological processes that render a location a refugium.

With the number of different proxies and methods available (magnetic susceptibility, phytoliths, both micro- and macrofaunal composition, geoarcheological methods, micromorphology, palynology, lake and deep-sea sediment cores, stable isotope analysis of zooarcheological assemblages and sediments, among others), we find there are some, like stable isotopes analysis, that are particularly underused. The utility of stable isotope analysis on organic tissues, both human and zooarcheological, a relatively inexpensive method to generate paleoenvironmental and paleoclimatic information, is undeniable (Jones and Britton, 2019). Stable isotope analyses have been used to reconstruct animal and human niches (e.g. Newsome *et al.*, 2007; García García *et al.*, 2009; Feranec *et al.*, 2010; Naito *et al.*, 2016), seasonality (e.g. Balasse *et al.*, 2012; Drucker *et al.*, 2012), climates (e.g. Ambrose and DeNiro, 1989; Hedges *et al.*, 2004; Faith, 2018; Pederzani *et al.*, 2021), migration (e.g. Price *et al.*, 2004; Hobson and Wassenaar, 2018), diet (e.g. Schoeninger *et al.*, 1983; Richards *et al.*, 2000; Bocherens *et al.*, 2005), vegetation cover (e.g. Lee-Thorp *et al.*, 2007; Kohn, 2010) and environmental stability (Dombrosky *et al.*, 2020). Recent stable isotope studies have reconstructed the specific climate conditions of Neanderthal occupations that contradict other paleoclimatic indicators in southern France (Pederzani *et al.*, 2021), shown that Neanderthals and AMHs exploited a wide range of microenvironments that may have buffered against climate changes in Cantabria (Jones *et al.*, 2019), and demonstrated that conditions during Heinrich Events in westernmost Iberia may not have been any more severe than other stadials (Carvalho *et al.*, this Special Issue). If a majority of late Middle Paleolithic and Initial Upper Paleolithic sites in the three peninsulas conducted this type of analysis, the amount of paleoecological information for Neanderthals and AMHs would be astounding, and in conjunction with other records provide the detail with which paleoenvironments and paleoclimates should be reconstructed.

Another avenue is Ecological Niche Modeling, a useful tool that can help develop local and regional hypotheses or models for various processes by modeling the geographical distribution of an organism or phenomenon as well as the most influential niche parameters influencing its distribution (Peterson, 2003). While Ecological Niche Modeling is not new to archeology (Banks *et al.*, 2006, 2008; Banks, 2017), it provides a tool for identifying potential refugia through the analysis and modeling of more than one biological or environmental process. In addition to the identification of refugia, through the prediction of the distribution of various taxa or phenomena, Ecological Niche Modeling can produce models or generate hypotheses which we can test against the archeological record. Ecological Niche Modeling relies on comparable input data pertaining to the same time slice, and the longer the time period covered by the input data, the less accurate the model output becomes. This method is probably underused in Paleolithic archeology because it relies on various parameters (e.g. paleoclimatic simulations, paleoenvironmental records) to build robust models, and the current amount of temporally limited contemporaneous paleoenvironmental records specific to MIS 3 are generally lacking, and not distributed evenly across peninsulas.

Given that the overlap in Neanderthal and AMH occupations are mostly based on highly contentious dates, it may be that there was no or limited overlap between the two human populations, and refugia did not play as active a role in the Middle to Upper Paleolithic transition in southern Europe. Though Neanderthals faced climate change towards their demise as did AMHs during their dispersal, Neanderthals did not only adapt to climate change at the end of their evolutionary trajectory as a genetically distinct population, but as we know, lived through an incredible range of environmental and climatic conditions during hundreds of thousands of years' worth of glacial cycles (Finlayson, 2004), and refugia probably played a role in their adaptation. Kuhn (2020) emphasizes three important drawbacks in approaches to Paleolithic archeology that can limit our understanding of its archeological record and the evolution of the humans who made it: the fixation on transitions whose definitions are often arbitrary, the punctuation of evolution with technological development, and envisioning 'earlier hominins as unfinished or incomplete versions of contemporary modern humans (p. 13)'. We think the same notions apply to studying human–environmental adaptations more specifically. While transitions are important for understanding cultural change, these transitional periods represent a fragment of hundreds of thousands of years of human–environment adaptation. The focus on the role of refugia in the demise of Neanderthals overshadows its importance in the various glacial cycles Neanderthal populations endured. By also evaluating Neanderthal–environment adaptation throughout their 350 000–400 000 years of existence, we can understand more about their resilience and risk management strategies. This is especially important because we cannot assume that climate change is like the flipping of a switch, where environments oscillate back and forth from one set of conditions to the other but instead more closely resembles a positive feedback loop. In addition, a thorough understanding of the role of refugia in the adaptation of Neanderthals during their occupation of Eurasia on local and regional scales can be a source of hypotheses for their demise.

Conclusions

The archeological record of the Balkans, Italy and Iberia suggests that Neanderthal and AMH populations may have overlapped, and refugia could have played a role in the persistence of Neanderthal populations, as well as in the dispersal of AMHs. Here, we have described the complexities in the timing and spatial patterning of the Middle to Upper Paleolithic transition in the three peninsulas and in the application of the concept of refugia. Future endeavors in this area of research would benefit by defining refugium characteristics such as the number of species assessed, the scale of study, whether *in situ* or *ex situ*, and the function of ecological stability. It is equally as beneficial to focus on the formulation of testable hypotheses that are spatially and temporally limited and that are based on robust syntheses of information. This requires the creation of numerous local, multiproxy paleoenvironmental and paleoclimatic records that can be generated through the use of underutilized methods such as stable isotope analysis of organic tissues among others. An increase in the quantity of available paleoenvironmental and paleoclimatic records means that other analytical techniques, such as Ecological Niche Modeling, can also be utilized. Finally, a focus on the adaptations of Neanderthals to changing environments throughout their evolutionary history, and not just their demise, can be a source for generating hypotheses and provide a greater understanding for why a human population so similar to AMHs disappeared as a genetically distinct group.

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Abbreviations. AMH, Anatomically Modern Human; MIS, Marine Isotope Stage.

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