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Investigating relationships between technological variability and ecology in the Middle Gravettian (*ca.* 32–28 ky cal. BP) in France

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A B S T R A C T

The French Middle Gravettian represents an interesting case study for attempting to identify mechanisms behind the typo-technological variability observed in the archaeological record. Associated with the relatively cold and dry environments of GS.5.2 and 5.1, this phase of the Gravettian is characterized by two lithic typo-technical entities (*faciès* in French): the Noaillian (defined by the presence of Noailles burins) and the Rayssian (identified by the Raysse method of bladelet production).

The two *faciès* have partially overlapping geographic distributions, with the Rayssian having a more northern and restricted geographic extension than the Noaillian. Their chronological relationship, however, is still unclear, and interpretations of their dual presence at many sites within the region of overlap are not yet consensual. Nonetheless, the absence of the Raysse method south of the Garonne River suggests that this valley may have separated two different cultural trajectories for which the Rayssian represents an adaptation to environmental conditions different from those associated with Noaillian assemblages south of the Garonne River. The aim of this study is to test this hypothesis quantitatively using ecological niche modeling (ENM) methods. First, we critically evaluate published data to construct inventories of Noaillian and Rayssian archaeological sites. Next, using ENM methods, we estimate the ecological niches associated with the Middle Gravettian north (Noaillian + Rayssian) and south (Pyrenees Noaillian) of the Garonne River, which are then quantitatively evaluated and compared. Results demonstrate that, despite a relatively large degree of similarity, the niches differ significantly from one another in both geographic and environmental dimensions and that the niche associated with the northern Middle Gravettian is broader than that of the Pyrenees Noaillian. We propose that this pattern reflects different technological, subsistence and mobility strategies linked to the development of the Raysse method in the North, which was likely more advantageous in its environmental contexts than technologies employed by contemporaneous populations in the Pyrenees.

1. Introduction

The Gravettian is an Upper Paleolithic techno-complex (*sensu* Clarke, 1968) that has been the subject of extensive research since its recognition (e.g. Klima, 1983; Roebroeks et al., 1999; Rigaud, 2008, 2009b; de las Heras et al., 2013; Otte, 2013; Wojtal et al., 2015). Spanning ca. 34,000–26,000 calibrated years before present (y. cal. BP), its main unifying characteristics are Gravette-style backed blades and bladelets (Pesesse, 2013), diagnostic graphic expressions (Féruglio et al., 2011), as well as a high frequency of burials (Henry-Gambier, 2008) compared to preceding and subsequent archaeological cultures. These common characteristics are observed in sites across Europe, from Portugal to the Don Valley in western Russia (Otte, 2013). However, the term "Gravettian" groups together a wide variety of cultural traditions, especially concerning lithic and osseous technology (de la Peña-Alonso, 2009; Pesesse,

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2013; Noiret, 2013; Goutas, 2013a). This diversity is challenging to explain since it is characterized by disparate data, many of which were obtained with non-modern excavation methods decades ago or differing analytical approaches (de la Peña-Alonso, 2011; Pesesse, 2017). Moreover, sites that date to the same chronological interval but that lack typical Gravettian features (i.e. Gravette-style points) serve to challenge the definition of this techno-complex (e.g. Morala, 2011; Klaric et al., 2011, 2018). In Western Europe, various hypotheses have been proposed to explain this diversity, such as differences in site activities (e.g. Laville and Rigaud, 1973; Rigaud, 1988), the nature of our archaeological definitions (e.g. Touzé, 2013; Pesesse, 2017), regionally differentiated populations that did not share the same technological knowledge or traditions (e.g. Klaric et al., 2009), or differential environmental influences (e.g. David, 1985; Djindjian et al., 1999). Efforts to identify and evaluate the mechanisms—defined as “a constellation of factors and components that through the process of their interaction with one another stimulates the trajectory of a system” (d’Errico and Banks, 2013, p. 374)—that influenced these cultural traditions can aid in assessing these various hypotheses.

1.1. The French Middle Gravettian

In France, the Middle Gravettian occurs between ca. 32–28.5 ky cal. BP and is defined by two *faciès*, termed the “Noaillian” and the “Rayssian” that are characterized principally on the basis of their lithic industries (Touzé, 2013). The term “*faciès*” (in French) is used to describe an archaeological entity according to “the nature of the considered remains and the method employed to study them” (Touzé, 2013, p. 397). This neutral term is especially useful in the case of the Middle Gravettian, since the two *faciès* are not defined equally. The Noaillian is a typological *faciès*, defined solely by the presence of Noailles burins (Bardon and Bouyssonies, 1903; Tixier, 1958) and sometimes by the presence of bone or antler points called “Isturitz points”, although this point type’s precise chrono-cultural status remains uncertain (Goutas, 2013b). On the other hand, the Rayssian is a typo-technological *faciès*, defined by a reduction method aimed at removing, from Raysse burins, bladelets that were used as implements on projectiles (Fig. 1, Movius and David, 1970; Klaric et al., 2002; Lucas, 2002; Pottier, 2006; Klaric, 2017). Furthermore, Rayssian bladelet and blade reduction sequences show strong conceptual parallels and technical similarities (Klaric, 2003, 2008).

The chronological relationship between the Noaillian and the Rayssian has yet to be determined with precision. This is due to the fact that very few contextually reliable ^{14}C ages are associated with these two *faciès*, and for regions north of the Garonne River the low number of available ages renders any chronological comparison between the two phases uninformative at present (Banks et al., 2019). This situation is complicated by the fact that Noailles burins and the Raysse method are frequently found together within the same archaeological layer in the region of overlap. Past and ongoing studies suggest that, at many sites, this association is not culturally meaningful due to imprecise excavation methods and/or disturbed stratigraphic contexts (e.g. Klaric, 2003; 2007; Vignoles et al., 2019). However, in a few stratified contexts, the development of the Raysse method is always stratigraphically younger than the Noaillian (e.g., Abri Pataud and Flageolet I sites; David, 1985; Rigaud, 1982; Klaric, 2003). An exception to this statement is found at Les Jambes, a site where Noailles burins are described as being stratigraphically *above* the Raysse burins (Célérier, 1967). This configuration, though, remains to be verified. First, the two levels identified by Célérier have been described as part of a slope deposit which raises doubts as to the integrity of the levels. Moreover, stratigraphic projections of artifacts show that the levels defined by Célérier correspond to a single archaeological layer. Finally, an ongoing reexamination (conducted by A.V) of the site’s assemblage demonstrates that most of the “Noailles burins” do not correspond to the classic typological definition. In fact, only one artifact can be considered a typical Noailles burin, while all the others are highly atypical. Technological characterization of the blade/bladelet reduction sequences may provide new data with which to discuss the presence of Gravette points—a class of tool traditionally associated with the Noaillian rather that the Rayssian—at Les Jambes.

Numerous hypotheses have been proposed to explain the co-occurrence of Noaillian and Rayssian materials in the same archaeological level, such as a gradual replacement of the Noaillian by the Rayssian (David, 1985; Pottier, 2005), differing site activities (Laville and Rigaud, 1973; Rigaud, 2008, 2011), the use of different typo-technological traditions within a broad regional population (Touzé, 2013) or the result of post-depositional mixing or the inability of old excavation methods to differentiate between

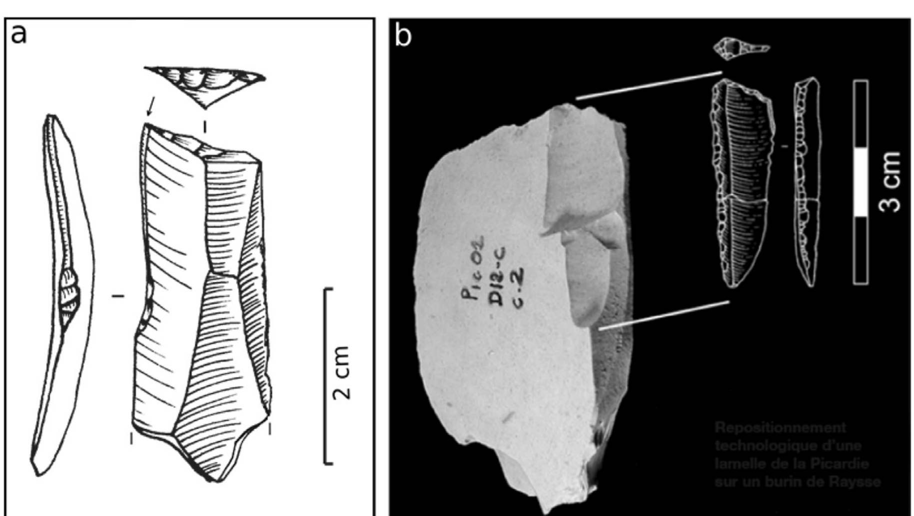

Fig. 1. Diagnostic Middle Gravettian artifact types. a. Noailles burin from Fourneau du Diable, Dordogne, France (drawing: A.Vignoles). b. Technological position of a “Picardie” bladelet on a Raysse burin-core from La Picardie, Indre-et-Loire, France (from Klaric, 2008).

discrete occupations (Klaric, 2003, 2007; Vignoles et al., 2019). Unfortunately, taphonomic evaluations of individual sites are not yet sufficiently numerous to evaluate these hypotheses adequately (Klaric, 2003, 2007; Pottier, 2005; Agsous, 2008; Michel, 2010; Gottardi, 2011).

With respect to geography, these two archaeological traditions have only partially overlapping distributions (Fig. 2). The Noaillian is observed in regions south of the Loire River, as well as a very isolated presence in the Vosges region, with extensions into Cantabrian Spain and the Italian Peninsula. The Rayssian is restricted to a smaller geographic area situated between the Garonne River and the southern portion of the Paris Basin, with extensions into Burgundy and Brittany (Klaric, 2003, 2017; Touzé, 2013). Despite mentions of the presence of Raysse burins at the sites of La Carane-3, Isturitz and Tuto de Camalhot by David (1985), the presence of the Raysse method south of the Garonne River has not been unequivocally demonstrated: none of these artifacts have been described or pictured, nor do recent technological studies (e.g. Simonet, 2009a) mention them. The demonstration of the Raysse method relies on precise technical criteria and more specifically on the identification of the bladelet component associated with Raysse burin-cores, and David (1985) did not use such criteria to describe the Late Noaillian (i.e. Rayssian) in these southern contexts. It is also important to point out that look-alike artifacts (*faux-amis*) have been described at Brassempouy (Klaric, 2006). The exemples reported by David could therefore be misleading in the same way.

The absence of the Raysse method south of the Garonne River suggests that this valley may have played a role in the separation of the two different technological trajectories. This is also paired with the fact that the Noaillian in the Pyrenees appears to have lasted as long as the entire Middle Gravettian phase (Noaillian and subsequent Rayssian) present north of the Garonne River (Touzé, 2013; Klaric, 2017; Banks et al., 2019). This pattern suggests that the environment may have played a role in the development of the cultural adaptation that serve to define the Rayssian *faciès* (David, 1985; Djindjian et al., 1999).

1.2. Research question and approach

Here, we test the hypothesis that the typo-technological differences observed on either side of the Garonne River valley during the Middle Gravettian reflect the exploitation of different environmental conditions via different technological (i.e. cultural) adaptations. The application of Ecological Niche Modeling (ENM) methods to the archaeological record is one means with which to conduct such a test (Banks, 2017; d'Errico and Banks, 2013). ENM (the terminology employed in this study, cf. Peterson and Soberón, 2012; Warren, 2012) provides a means for estimating the ecological niches of past hunter-gatherer populations, employing archaeological sites as occurrence data and environmental variables derived from high-resolution paleoclimatic simulations. These data are then used by predictive modeling algorithms to identify sets of environmental parameters associated with known archaeological sites and create an estimation of the presence of suitable environmental conditions (i.e. the ecological niche) across the study area. Niche estimations can be compared with one another in order to characterize and evaluate potential differences between niches (e.g. Warren et al., 2008). The use of these tools has been demonstrated to be a valuable approach for assessing culture-environment relationships of past hunter-gatherer populations, both synchronically and diachronically (e.g. Banks et al., 2008, 2009, 2011, 2013; d'Errico et al., 2017). Research focused on

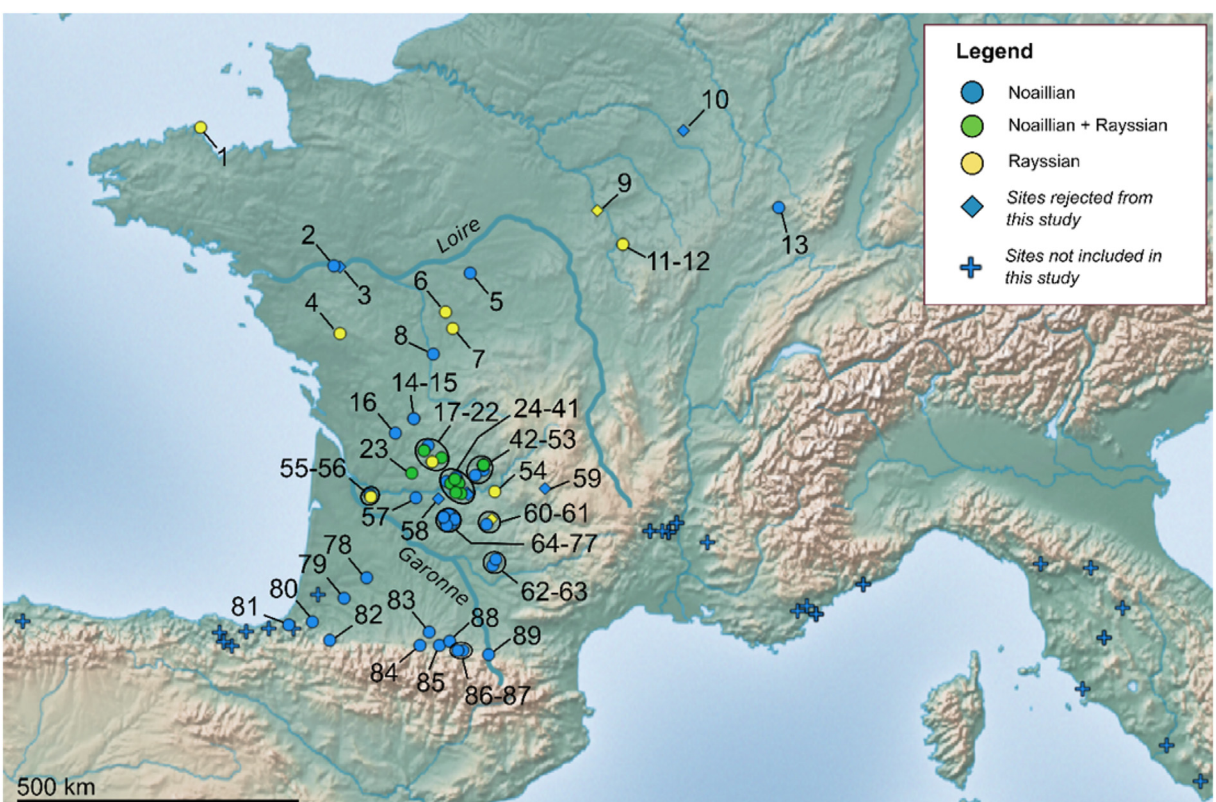

Fig. 2. Sites where Noailles burins and/or Raysse burins have been found (after Touzé, 2013; Klaric, 2017; the present study). Sites are labeled according to their number presented in Table 1 (cf. 2.2.1). Topographic background: http://www.naturalearthdata.com.

material culture variability observed in the archaeological record is often polarized between two sets of explanations, cultural *vs.* functional, mirroring the well-known Bordes-Binford debate concerning Mousterian lithic industries. An advantage of ENM is that it allows one to approach evaluations of such variability from a different angle by taking into account the ecological niches exploited by archaeological hunter-gatherer populations. For example, comparisons of the ecological niches associated with two archaeological cultures or lithic industries allow one to evaluate to what extent cultural (i.e. technological) differences have an ecological basis. In such scenario, one would expect their ecological niches to differ from one another significantly due to the fact that the different typo-techno-complexes represent adaptations to distinct ecological niches more than purely social factors. If their niches are highly similar, one could interpret technological variability to be more the result of internal cultural dynamics that led to the development of two cultural trajectories. As stated earlier, multiple hypotheses have been proposed to explain the typo-technological variability observed within the French Middle Gravettian and no consensus has been reached. The objective of this study is to provide new data on the ecological niches of these hunter-gatherer populations in order to evaluate to what extent ecological factors may have played a role in the observed material culture variability.

2. Materials and methods

2.1. Conceptual framework of ecological niche modelling

The conceptual framework of ENM is based on Hutchinson's (1957) definition of the fundamental niche ($\mathbf{N}_F$): an *n*-dimensional hypervolume whose dimensions are the non-interactive environmental variables (i.e. scenopoetic variables) necessary for a species to maintain populations indefinitely without immigrational subsidy. Following Peterson and Soberón (2005, 2012), we consider the Biotic-Abiotic-Mobility framework (**BAM**, Fig. 3) to describe factors constraining geographic distribution of species. The projection of $\mathbf{N_F}$ in geographic space (**G**), i.e. the geographic localities corresponding to $\mathbf{N}_F$, identifies areas with conditions favorable to the species (**A**). However, the geographic distribution of a species can be constrained by at least two other types of factors: biotic interactions (**B**), i.e. the species' positive or negative interactions with other species or resources that are present, and the areas that have been physically accessible to the species over a relevant period of time (**M**). The intersection of **A** and **B** is the potential distributional area ($\mathbf{G}_P$), which is the geographic expression of the realized niche ($\mathbf{N}_R$) defined by Hutchinson (1957). In this study, we focus on $\mathbf{N}_F$, defined solely on the basis of non-interactive variables, following the Eltonian-noise hypothesis, which argues that biotic interactions may often be manifested at fine spatial resolutions and thus may not have a significant or limiting effect on a species' distribution at broad geographic scales (Soberón, 2007). Finally, the intersection of $\mathbf{G}_P$ with **M** defines the occupied distributional area ($\mathbf{G}_O$). In environmental space, the intersection between $\mathbf{N_F}$ and the environments associated with **M** define the existing fundamental niche ($\mathbf{N}_F$*), which is the portion of the fundamental niche that is actually observable in nature (Peterson and Soberón, 2012).

When applied to the archaeological record, the goal is to identify the sets of environmental conditions associated with a cultural trait or with a techno-complex, and evaluate their eventual co-variability through time (Banks, 2017). Furthermore, with respect to examinations of culture-environment relationships and cultural adaptations, it is pertinent to evaluate to what extent an archaeological typo-technological complex (archaeological culture) occupied its existing niche (i.e. $\mathbf{G}_O$ vs. observed distribution).

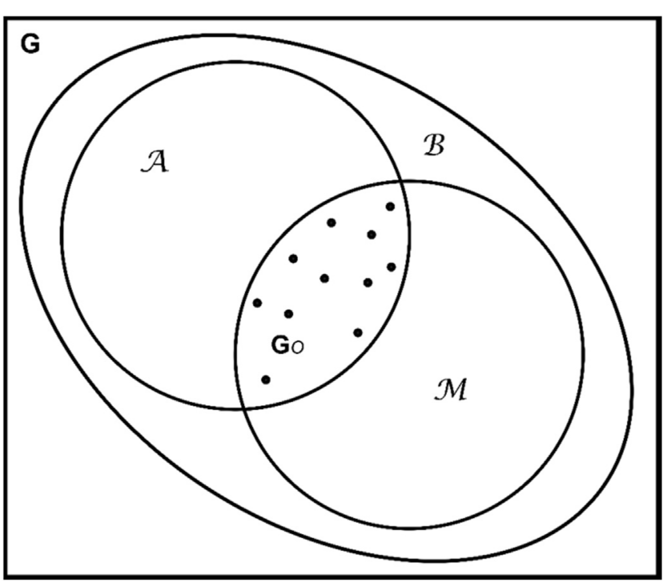

Fig. 3. BAM diagram representing the factors that constrain the geographic distribution of a species at broad geographic scales, if the Eltonian-noise hypothesis holds true (after Soberón and Peterson, 2005, 2012; modified). Circles represent the different factors and black dots represent the observed distribution of the species. **G**: geographic space; **A**: non-interactive variables; **B**: biotic interactions; **M**: areas accessible to the species; $\mathbf{G}_O$: occupied distributional area.

2.2. Data

2.2.1. Archaeological data

Occurrence data consist of the geographic coordinates of archaeological sites where Noaillian and/or Rayssian material culture assemblages have been identified (Fig. 4). These data were assembled through a critical examination of the literature, although one must keep in mind that this approach has certain limitations. First, most sites were excavated and studied in the late 19th and first half of the 20th century, sometimes in an expeditious manner. Due to the fact that excavated sediments were rarely sieved and often only large, diagnostic tools were kept, many assemblages are biased and do not necessarily contain artifacts that allow the two typo-technological *faciès* to be reliably recognized, since their diagnostic artifacts are of small size (e.g., Raysse and Picardie bladelets, some Noailles burins, Noailles burins spalls), and/or correspond to flint knapping by-products (e.g., Raysse bladelets, blades with oblique lateralized faceted platforms). As a result, there are numerous sites where one or both of these Middle Gravettian *faciès* was not initially recognized (e.g., Fourneau du Diable, Laussel or Combe-Saunière I; Klaric, 2017; Vignoles et al., 2019) and this is likely the case for many others. Therefore, the corpus of sites associated with these two archaeological *faciès* should be considered incomplete at present. Furthermore, many assemblages, even those that were rather well-excavated (piece-plotted artifacts, sieved archaeological sediments, collection of unretouched artifacts) often have not been subjected to recent contextual examinations or typo-technological re-evaluations (e.g., Les Jambes, Le Facteur). This is especially a problem for the bibliographic identification of the Raysse method. Although the Raysse burin type was first described in the 1950s (Pradel, 1953; Couchard and de Sonneville-Bordes, 1960; Movius and David, 1970), its function as a core for producing standardized projectile point implements was

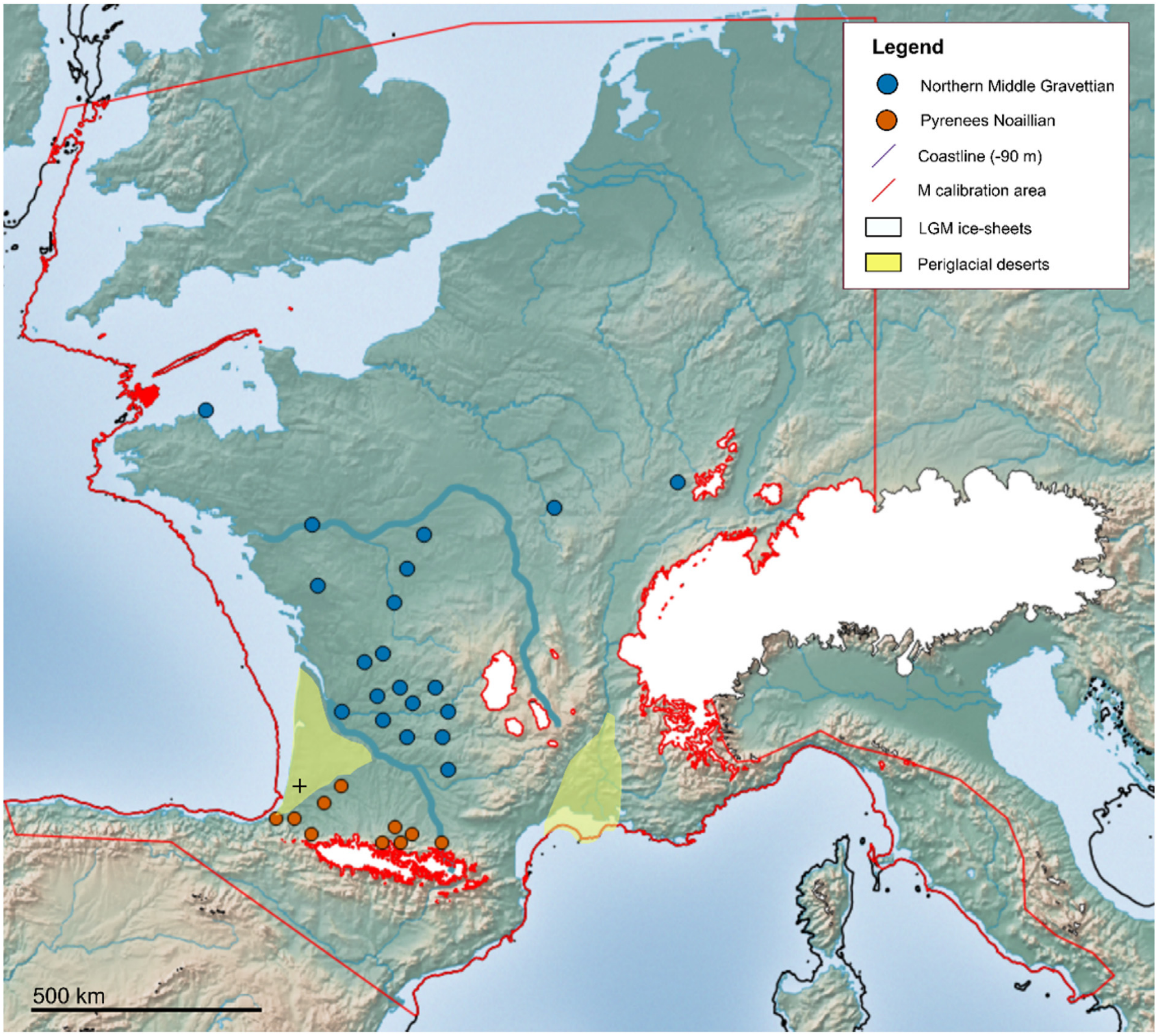

Fig. 4. Noaillian and Rayssian site locations used for calibration and the study's defined accessible area (**M**) hypothesis. Topographic background: http://www.naturalearthdata.com; Coastlines: Siddall et al. (2003); Glacier extent: Ehlers and Gibbard (2004); Periglacial cold deserts: Bertran et al. (2013); Bosq et al. (2018)..

only demonstrated in the early 2000s (Klaric et al., 2002; Lucas, 2002). It is therefore necessary to reconsider, from a technological standpoint, all previously identified Raysse burins and to identify the presence of the associated bladelet component in order to avoid attributing archaeological levels to this *faciès* on the basis of look-alike (*faux-amis*) artifacts (Klaric, 2003, 2006).

Another problem is the unequal definition of the Noaillian (i.e. sole presence of Noailles burins in an assemblage) and the Rayssian (Touzé, 2013). The latter's technical system is relatively well-described across its area of expression (Lucas, 2000, 2002; Klaric, 2003, 2017; Pottier, 2005, 2006; Guillermin, 2006; Touzé, 2011, 2013; Gottardi, 2011; Sarrazin, 2017, 2018). Variability in the use of the Raysse method has been attributed mainly to blank selection, the availability of suitable lithic raw materials, levels of technological expertise and contingencies of the reduction sequence (Klaric et al., 2009; Klaric, 2017, 2018). To the contrary, the technical system associated with Noailles burins has only been the subject of isolated studies in the Landes (e.g. Klaric, 2003; Simonet, 2009a; 2011a; Lacarrière et al., 2011), the Pyrenees piedmont and plateau (e.g. Foucher, 2004; Simonet, 2009a), and to lesser extents the Perigord region (Lucas, 2000; Pottier, 2005) and the southern Paris Basin (Kildea and Lang, 2011), thus rendering evaluations of its homogeneity difficult. Typo-technological studies conducted on assemblages from Cantabrian Spain (e.g. de la Peña-Alonso, 2011), the French Mediterranean coast (e.g. Onoratini, 1982; Santaniello, 2016), and the Italian peninsula (e.g. Onoratini, 1982; Aranguren et al., 2006; 2015; Simonet, 2010; Santaniello, 2016; Santaniello and Grimaldi, 2019) have employed different methodological approaches for characterizing reduction sequences (i.e. *chaînes opératoires*) and typologies, with a few exceptions (e.g. Simonet, 2010), thus making comparisons to sites studied via the methods traditionally used in France difficult. An additional obstacle is related to this record's chronology. Noailles burins have been recovered from Cantabrian contexts that are contemporaneous with the Late Aurignacian in southwestern France, as well as contexts that extend into the Solutrean (de la Peña-Alonso, 2011, p. 681). Noailles burin contexts in Italy are also interpreted as being younger than those in France (Touzé, 2013), but the majority of their associated radiocarbon ages were produced decades ago (non-AMS) and evaluations of their archaeological association are lacking, thus rendering any comparison to the French archaeological record unreliable at present.

Taking into account these limitations, we constrain our analysis to the comparison of two adjacent regions that are thought to represent coherent territories during the Middle Gravettian: 1) the Pyrenees piedmont and plateau, based on assemblages that are regionally coherent with respect of lithic typo-technology (i.e. contexts that contain Noailles burins and in which the Raysse method is absent) and raw material circulation for the entirety of the Middle Gravettian (Foucher et al., 2008; Foucher, 2013; Simonet, 2009a, 2017; Banks et al., 2019), and 2) the area constrained along its southern margin by the Garonne River Valley and by the most northerly sites where the "Raysse method" has been observed (Klaric, 2017). The latter territory is characterized by both the Noaillian and the Rayssian *faciès*, and the lack of precision, at present, concerning their chronological relationship required that we group them together, mirroring the approach employed by Banks et al. (2019).

In an effort to retain only sites for which a reliable techno-typological attribution could be made, published studies were carefully evaluated with respect to the pertinence of the data they contained (see Appendix). A source was considered pertinent if it provided precise counts of tool types based on the most recent typo-technological definitions (e.g. for the "Noailles burin" type: Bardon and Bouyssonies, 1903; Tixier, 1958; for "Picardie bladelet" type and "Raysse burin-core": Klaric et al., 2002; Klaric, 2003; Klaric, 2017), preferably supplemented with artifact drawings or photos. We also included personal observations made during the course of on-going and yet-to-be-published studies (L. K. and A. V.). We, thus, did not retain sites for which one or both *faciès* were only suspected to be present in order to avoid potentially aberrant attributions based on look-alike artifacts. For example, "Raysse burins" reported in Brassempouy or Le Gratadis have been shown to not be actual Raysse burin-cores aimed at the production of La Picardie bladelets (Klaric, 2003, 2006). Bearing this in mind, we did not retain sites where Raysse burins were only mentioned with no demonstration of the presence of the Raysse method (e.g. Abri André Ragout; David, 1985). Also, sites where Raysse burins are depicted in published drawings (Klaric, 2003) but that have not been confirmed by us via direct observation and where the presence of the associated bladelet component has not yet been evaluated, such as the site of Roc de Gavaudun in Lot-et-Garonne or Lespaux shelter in Gironde (Monméjean et al., 1964; Krtolitza and Lenoir, 1998), were not included. Finally, we also eliminated sites for which the presence of Raysse burin cores is not consensual, such as Chamvres in Yonne (Klaric, 2003 vs. Sarrazin, 2018). In the same vein, we did not retain sites where reported "Noailles burins" have been demonstrated to be look-alike artifacts, such as the site of Les Jambes (ongoing examination by A.V.). Moreover, sites where Noailles burins are all atypical, such as Peutille in Lot-et-Garonne (Morala, 1984), or sites where only one or two Noailles burins are reported and their presence is not supported by published drawings, such as La Verpillière I cave in Saône-et-Loire (Floss et al., 2013), were eliminated from consideration. In the end, we retained 74 sites for our analysis. North of the Garonne River, there are 9 Rayssian sites, 40 Noaillian sites, as well as 13 additional sites that yield both *faciès*. In the Pyrenees piedmont and plateau, 12 Noaillian sites were retained (Fig. 4; Table 1).

2.2.2. Environmental predictors

In order to employ the appropriate environmental data, it is paramount to determine accurately the precise chronology of the target archaeological culture so that it can be correlated to the appropriate climatic event or events (Banks, 2015; Banks et al., 2019). Based on the results presented by Banks et al. (2019), the Middle Gravettian begins between the latter part of Greenland Interstadial 5.2 (GI 5.2) and Greenland Stadial 5.2 (GS 5.2) and ends between the latter part of GS 5.1 and GI 4. It was thus present during GS 5.2 and 5.1, during which occurred Heinrich Event 3 (HE3), as well as GI 5.1. Considering the lack of chronological resolution facing this portion of the Upper Paleolithic, two important assumptions were made for the choice of the best possible environmental data. First, since most Middle Gravettian occupations have not been dated or are not associated with reliable dates, we must assume that all sites date to some point between *ca.* 32 and 28.5 ky cal. BP (after Banks et al., 2019). Second, the chronological resolution of individual radiocarbon measurements does not allow us to determine whether a specific dated occupation is associated with a specific Interstadial or Stadial (GI 5.1 or GS 5.1 for example). This limitation makes it impossible to create separate occurrence data sets such that correspond to specific Stadial or Interstadial events. Therefore, we choose environmental data such that correspond to stadial conditions since those were present during the majority of the period concerned by this study (*ca.* 2.5 ky for GS 5.2 and 5.1 combined *vs. ca.* 0.5 ky for GI 5.1).

We employed as environmental background climatic variables derived from a high-resolution paleoclimatic simulation obtained with the Atmospheric Global Circulation Model (AGCM) LMDZ5A (Hourdin et al., 2013). It was run with a zoomed grid permitting a spatial resolution of *ca.* 50 km over Europe, following Sima et al. (2009, 2013). We used the same coastlines and ice-sheet configuration as Sima et al. (2009, 2013), i.e. those corresponding to the Last Glacial Maximum (LGM; Fig. 4). Atmospheric greenhouse gas concentrations were also left at their LGM values ($CO2 = 185$ ppm, $CH4 = 350$ ppb, $N2O = 200$ ppb). The orbital parameters are set to 32 ky cal. BP (Berger et al., 1978), which correspond to the beginning of GS 5.2. Initial boundary conditions for prescribed sea surface temperatures (SSTs) and sea ice cover were computed with the coupled atmosphere-ocean general circulation model IPSLCM4 (Marti et al., 2010). This model was obtained by setting forcing and boundary conditions of the PMIP3 LGM experiment described in Alkama et al. (2008) and Kageyama et al. (2013) to 32 ky cal. BP, thus producing an enhanced seasonal cycle of incoming insolation and surface temperatures in the Northern hemisphere.

Results were further downscaled to a spatial resolution of 11.5 km via the spline interpolation available in ArcMap 10.7.1. The simulated variables employed in this analysis are mean annual precipitation, warmest month temperature and coldest month temperature. We did not use elevation as a covariate in this process. Elevation is usually considered to be a proxy for temperature, because these two variables are highly correlated. Moreover, elevation is also taken into account during the paleoclimatic simulation process. These reasons make it a redundant and non-informative variable for the niche analyses presented here.

2.3. Ecological niche modeling

2.3.1. Modeling preparation

Prior to estimating niches, we analyzed and filtered the occurrence datasets to reduce potential spatial biases. First, we trimmed duplicate site occurrences from each grid-cell, so that a grid-cell contained only a single occurrence point, thus ensuring that the training and testing occurrence datasets would be spatially unique (i.e., no shared occurrences). Next, we thinned the occurrence datasets to eliminate clusters of sites, thereby preventing over-sampling of environmental conditions from certain areas (e.g., the northern Aquitaine area) and reducing potential spatial autocorrelation (Anderson and Gonzalez, 2011; Boria et al., 2014). This consisted of eliminating occurrences such that the minimum distance between any pair of occurrence points was twice the grid resolution, i.e. *ca.* 23 km. This step was performed manually using

Table 1
Sites retained or rejected based on a critical review of the literature, along with their geographic coordinates and references. A site was assigned to a specific data set or rejected based on criteria detailed in the Appendix. Geographic coordinates correspond to the commune (i.e. town administrative territory) in which the site is localized. Although these coordinates do not necessarily correspond to the site itself, their resolution is more than adequate considering the 11.5 km-grid resolution of the environmental data.

N°	Site	Lat. (N)	Long. (E)	Noailles burins	Raysse method	Data set	References
1	Plasenn-al-Lomm	−3,00	48,85	absence	presence	Northern Middle Gravettian	Le Mignot (2000); Klaric (2003); Sarrazin (2018)
2	La Martinière	−0,86	47,36	presence	suspected	Northern Middle Gravettian	Allard (1986)
3	Roc-en-Pail	2,29	48,86	insufficient	absence	*rejected*	Allard and Gruet (1976); Gruet (1984); Hinguant and Monnier (2013)
4	Le Taillis des Coteaux	−0,77	46,62	absence	presence	Northern Middle Gravettian	Klaric (2017)
5	La Croix-de-Bagneux	1,33	47,29	presence	absence	Northern Middle Gravettian	Kildea and Lang (2011, 2013)
6	La Picardie	0,93	46,86	absence	presence	Northern Middle Gravettian	Klaric (2003); Klaric et al. (2011); Klaric et al. (2018)
7	Abri Charbonnier	1,04	46,68	absence	presence	Northern Middle Gravettian	Aubry et al. (2013); Klaric, pers. obs.
8	Abri Laraux	0,73	46,40	presence	suspected	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985)
9	Chamvres	3,36	47,96	absence	controversial	*rejected*	Klaric (2003, 2013); Sarrazin (2018)
10	Grotte de la Verpillère I	4,73	48,81	insufficient	absence	*rejected*	Floss et al. (2013)
11	Grotte du Renne	3,76	47,60	absence	presence	Northern Middle Gravettian	Klaric (2003)
12	Grotte du Trilobite	3,76	47,60	absence	presence	Northern Middle Gravettian	Klaric (2003); David (1985)
13	Hautmougey	6,26	48,00	presence	absence	Northern Middle Gravettian	Hans (1997)
14	Abri André Ragout	0,42	45,68	presence	Insufficient	Northern Middle Gravettian	Tixier (1958); David (1985)
15	Abri du Chasseur	0,42	45,68	presence	absence	Northern Middle Gravettian	Tixier (1958); David (1985)
16	Les Vachons	0,12	45,51	presence	suspected	Northern Middle Gravettian	David (1985); Fontaine (2006)
17	Le Petit-Puyrousseau	0,72	45,19	presence	insufficient	Northern Middle Gravettian	de Sonneville-Bordes (1960); Daniel (1967); David (1985)
18	Abri Durand-Ruel	0,65	45,37	presence	suspected	Northern Middle Gravettian	de Sonneville-Bordes (1960); Daniel and Schmider (1972); David (1985)
19	Gisement de la Chèvre	0,59	45,32	presence	insufficient	Northern Middle Gravettian	David (1985); Arambourou and Jude (1964)
20	Combe Saunière	0,87	45,24	presence	presence	Northern Middle Gravettian	Klaric (2017); Klaric, pers. obs.
21	Le Fourneau du Diable	0,59	45,32	presence	presence	Northern Middle Gravettian	David (1985); Klaric (2003), 2017; Vignoles et al. (2019)
22	Les Jambes	0,72	45,19	unlikely	presence	Northern Middle Gravettian	Célérier (1967); Vignoles, pers.obs.
23	Solvieux	0,39	45,06	presence	presence	Northern Middle Gravettian	David (1985); Sackett (1999); Klaric (2003)
24	Abri Sous-le-Roc	1,09	45,01	insufficient	absence	*rejected*	de Sonneville-Bordes (1960); David (1985)
25	Abri de Fongal	1,08	44,99	insufficient	insufficient	*rejected*	de Sonneville-Bordes (1960), p.97; David (1985)
26	Abri des Merveilles	1,11	45,00	suspected	absence	*rejected*	Delage (1936); de Sonneville-Bordes (1960); David (1985)
27	La Rochette	1,09	45,01	presence	suspected	Northern Middle Gravettian	de Sonneville-Bordes (1960); Schmider (1969); David (1985); Klaric (2003), p.220
28	Abri Labattut	1,11	45,00	Presence	insufficient	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985)
29	Masnaigre	1,14	44,94	Presence	suspected	Northern Middle Gravettian	David (1985)
30	Abri Pagès	1,04	44,97	presence	absence	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985)
31	Abri du Poisson	1,01	44,94	presence	absence	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985)
32	Grotte d'Oreille d'Enfer	1,01	44,94	presence	absence	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985); Pradel (1959)
33	La Ferrassie	0,95	44,97	presence	absence	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985)
34	Abri Pataud	1,01	44,94	presence	presence	Northern Middle Gravettian	David (1985); Bricker, 1995; Pottier (2005, 2006); Nespoulet (2008)
35	La Roque Saint-Christophe	1,08	44,99	presence	presence	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985); Vignoles, pers. obs.
36	Abri du Facteur	1,04	44,97	presence	presence	Northern Middle Gravettian	Delporte (1968); David (1985); Vignoles, pers. obs.
37	Grand-abri de Laussel	1,14	44,94	presence	presence	Northern Middle Gravettian	Roussot (1985); David (1985); Klaric (2017); Klaric, pers. obs.
38	Grotte Maldidier	1,18	44,83	presence	presence		Klaric (2017); Caux, 2012

(*continued on next page*)

Table 1 (*continued*)

N°	Site	Lat. (N)	Long. (E)	Noailles burins	Raysse method	Data set	References
						Northern Middle Gravettian	
39	Le Flageolet I	1,09	44,84	presence	presence	Northern Middle Gravettian	Rigaud (1982); David (1985); Lucas (2000); Gottardi (2011)
40	Cantelouve	1,28	44,84	insufficient	absence	*rejected*	Tixier (1958); David (1985)
41	Grotte de Péchialet	1,29	44,82	suspected	absence	*rejected*	David (1985); Breuil (1927)
42	Grotte du Bos-del-Ser	1,54	45,16	insufficient	insufficient	*rejected*	David (1985)
43	Grotte "Chez Serre"	1,53	45,10	presence	absence	Northern Middle Gravettian	David (1985)
44	Roc de Combe	1,40	45,04	presence	absence	Northern Middle Gravettian	David (1985)
45	Grotte Lacoste	1,54	45,16	presence	absence	Northern Middle Gravettian	David (1985)
46	Grotte de Champ	1,53	45,16	presence	insufficient	Northern Middle Gravettian	David (1985); Daniel (1969)
47	Grotte Thévénard	1,54	45,16	presence	insufficient	Northern Middle Gravettian	David (1985)
48	La Font-Robert	1,54	45,16	presence	insufficient	Northern Middle Gravettian	de Sonneville-Bordes (1960); David (1985)
49	Pré-Aubert	1,54	45,16	presence	suspected	Northern Middle Gravettian	David (1985); Demars (1977)
50	Grotte Bouyssonie	1,54	45,16	presence	presence	Northern Middle Gravettian	Touzé (2011); Klaric (2017); Klaric, pers. obs.
51	Bassaler-Nord	1,54	45,16	presence	presence	Northern Middle Gravettian	David (1985); Touzé (2011)
52	Abri du Raysse	1,54	45,16	presence	presence	Northern Middle Gravettian	David (1985); Touzé (2011)
53	Les Morts	1,54	45,16	presence	presence	Northern Middle Gravettian	David (1985); Sarrazin (2017)
54	Les Fieux	1,71	44,85	absence	presence	Northern Middle Gravettian	Guillermin (2006), 2008
55	Les Artigaux	−0,27	44,79	unlikely	presence	Northern Middle Gravettian	Lenoir (1977); Klaric (2003); Vignoles, pers. obs.
56	Abri Lespaux	−0,29	44,82	presence	suspected	Northern Middle Gravettian	David (1985); Krtoliza and Lenoir (1998)
57	Le Caillou	0,45	44,78	presence	absence	Northern Middle Gravettian	Boyer et al. (1984)
58	Roc de Combe-Capelle	0,82	44,77	insufficient	absence	*rejected*	de Sonneville-Bordes (1960); David (1985)
59	Grotte du Roc de Vézac	2,52	44,89	insufficient	absence	*rejected*	Rigaud (1982), p.262; Aujoulat *in* Leroi-Gourhan (1984)
60	Abri des Peyrugues	1,67	44,54	absence	insufficient	*rejected*	Guillermin (2011)
61	Abri de la Bergerie	1,58	44,48	presence	absence	Northern Middle Gravettian	Clottes et al. (1990)
62	Les Battuts	1,73	44,08	presence	suspected	Northern Middle Gravettian	Alaux (1967); Alaux (1971); David (1985)
63	Grotte de Rouzet	1,69	44,00	presence	absence	Northern Middle Gravettian	Foucher et al. (2008)
64	Abri du Couvert	1,02	44,49	presence	absence	Northern Middle Gravettian	Morala (1984)
65	Abri Peyrony	0,89	44,56	presence	absence	Northern Middle Gravettian	Le Tensorer (1981); David (1985)
66	Guiraudel	0,95	44,54	presence	absence	Northern Middle Gravettian	Morala (1984)
67	Las Pélénos	0,93	44,50	presence	absence	Northern Middle Gravettian	Morala (1984)
68	Le Callan	0,97	44,60	presence	absence	Northern Middle Gravettian	Morala (2011)
69	Le Roc de Cavart	1,07	44,54	presence	absence	Northern Middle Gravettian	Le Tensorer (1981); David (1985)
70	Station du Fresquet	0,94	44,47	presence	absence	Northern Middle Gravettian	Morala (1984)
71	Gisement du château	1,01	44,59	suspected	absence	*rejected*	Le Tensorer (1974), p.467
72	Peutille	0,97	44,58	suspected	absence	*rejected*	Morala (1984)
73	Termo-Pialat	0,82	44,77	suspected	absence	*rejected*	de Sonneville-Bordes (1960); David (1985)
74	Métayer	0,89	44,56	presence	insufficient	Northern Middle Gravettian	Le Tensorer (1981); David (1985)
75	Plateau Baillard	0,89	44,56	presence	absence	Northern Middle Gravettian	Le Tensorer (1981); David (1985)
76	Roquecave	0,89	44,56	presence	absence	Northern Middle Gravettian	Le Tensorer (1974); Le Tensorer (1981)
77	Le Roc de Gavaudun	0,89	44,56	presence	suspected	Northern Middle Gravettian	de Sonneville-Bordes (1960); Monméjean et al. (1964); Le Tensorer (1981); David (1985)
78	Hin-de-Diou	−0,33	43,86	presence	absence	Pyrenees Noaillian	Briand et al. (2010)
79	Brassempouy	−0,69	43,63	presence	absence	Pyrenees Noaillian	Klaric (2003); Foucher et al. (2008); Simonet (2009a)

Table 1 (*continued*)

N°	Site	Lat. (N)	Long. (E)	Noailles burins	Raysse method	Data set	References
80	Isturitz	−1,20	43,35	presence	insufficient	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a); Lacarrière et al. (2011)
81	Lézia	−1,58	43,31	presence	absence	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a)
82	Gatzarria	−0,92	43,14	presence	absence	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a)
83	Grotte des Rideaux	0,67	43,23	presence	absence	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a)
84	Gargas	0,52	43,07	presence	absence	Pyrenees Noaillian	David (1985); Foucher et al. (2008, 2012)
85	Bois de Touaa	0,83	43,07	presence	absence	Pyrenees Noaillian	Foucher et al. (2008); Clottes (1985), p. 346
86	Tuto de Camalhot	1,13	43,01	presence	absence	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a)
87	Grotte d'Enlène	1,20	43,02	presence	absence	Pyrenees Noaillian	Foucher et al. (2008); Simonet (2009a)
88	Tarté	0,99	43,12	presence	absence	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a)
89	La Carane-3	1,61	42,96	presence	insufficient	Pyrenees Noaillian	David (1985); Foucher et al. (2008); Simonet (2009a)

the "Measure line" tool in QGIS 2.18.28. The final datasets consisted of 10 occurrence points for the Noaillian in the Pyrenees piedmont and plateau, and 20 occurrences for the Middle Gravettian north of the Garonne River (Noaillian and Rayssian combined).

The definition of a calibration area (**M**) relies on biogeographic assumptions (Peterson et al., 2011 p. 135; Barve et al., 2011). To define (**M**) for Middle Gravettian hunter-gatherers in our region of study (Fig. 4), we assume that these populations could not live in regions in close proximity to ice sheets, and that they could have occupied areas exposed by the period's lower sea levels. We therefore masked the environmental variables with coast lines 90 m below present day sea level (Waelbroeck et al., 2002; Siddall et al., 2003), as well as with LGM ice sheet coverage reconstructions in the Alps, Pyrenees and the Massif Central (Ehlers and Gibbard, 2004). While these reconstructions slightly over-estimate ice coverage for *ca.* 32 ky cal. BP, they still serve as an adequate proxy since the areas in question would have been characterized by cold and dry, if not periglacial, conditions during the corresponding stadials and HE. Furthermore, based on the nature of raw material (flint) circulation in the Pyrenees region (Foucher et al., 2008; Simonet, 2017), we allowed the predictive modeling architecture to extrapolate into the regions of Cantabria and Catalonia. Finally, the Rhône River Valley in the East may have served to limit the movements of hunter-gatherer populations (no raw material circulation across the valley, cf. Santaniello, 2016). Furthermore, recent geomorphological studies show that the lower and middle Rhône Valley, as well as the Mediterranean continental shelf, likely consisted of a desert, with deflation-related landforms (e.g., yardangs, pans, desert pavements) and sand deposits (dunes, sand ramps) surrounded by loess accumulations during the coldest events of the Last Glacial period (Bosq et al., 2018). However, the presence of Noailles burins and Gravette points to the east indicates that they were permeable barriers. Thus, we included in our (**M**) coastal regions of Liguria, Tuscany, Lazio and Campania in present-day Italy where Noailles burins are observed in the archaeological record (Palma di Cesnola, 1991; Touzé, 2013). This step was performed with QGIS 2.18.28.

2.3.2. Model calibration and selection

Model calibration and selection were performed using the kuenm R package (Cobos et al., 2019a), which employs Maxent 3.4 (Phillips et al., 2006, 2017). In R 3.6.1 (R Core Team, 2019), we created a total of 448 candidate models for each occurrence dataset using distinct parameter settings resulting from the combination of 16 regularization multiplier values, 7 response types representing all possible combinations of the three feature classes (linear, quadratic and product), and four sets of environmental predictors derived from all possible combinations of the three paleoclimatic variables, following Cobos et al. (2019b). Threshold and hinge feature classes were not used in order to reduce model complexity and overfitting. The kuenm package allows the evaluation of statistical significance via partial ROC measures (Peterson et al., 2008), omission rates based on a maximum allowed error ($E = 5\%$, user defined; Anderson et al., 2003; Peterson et al., 2008), and model complexity by means of the Akaike information criterion corrected for small sample sizes (AICc; Warren and Seifert, 2011). For the retention of the best performing models among those that were statistically significant, we selected those with omission rates lower than E and of those we retained only the models with Δ_{AICc} values lower than two (i.e. $\Delta_{AICc} = AICc_i - AICc_{min}$, where $AICc_i$ is the AICc of the ith model and $AICc_{min}$ is the lowest AICc among all significant models for which omission rates are below 5%).

2.3.3. Creation of final models and model comparisons

Using kuenm, we created final models within (**M**) using the parameter settings selected after model calibration (Table 2). As more than one "best parameter" setting was used to create the final models for the Pyrenees Noaillian, we created a consensus model of all results across all parameterizations by calculating a median model, following Cobos et al. (2019c). We also calculated the range from these final models as a variability index.

Consensus niche estimations were thresholded by reclassifying as non-suitable all grid cells with suitability scores that fell within the bottom 5% of all values from grid cells that contained an occurrence point (Peterson et al., 2008). Subsequently, the remaining range of suitability scores were classified as low, medium or high suitability using equal intervals in QGIS 2.18.28.

Model comparisons were performed in both geographic and environmental dimensions. To compare the geographic projections of the niches, we used the background similarity and identity tests (Warren et al., 2008, 2017), which quantify the similarity/identity between two predictions by measuring their geographic overlap and then comparing the result to a null distribution. The two metrics recommended for such comparisons are Schoener (1968)'s statistic D for niche overlap and the similarity statistic I. They range from 0 (no similarity/not identical) to 1 (total similarity/identical) and are obtained via the comparison of the two empirical niche predictions. These measured metrics are then compared to those obtained from 1000 sets of null niche predictions produced using occurrences randomly sampled from the environmental background available in the calibration area. The difference between the two predictions is deemed to be significant if the empirical value falls below the 5% limits of the null distribution. To compare niches in environmental space, we used NicheA (Qiao et al., 2016). We employed a three-dimensional environmental background using the three paleoclimatic variables to develop minimum volume ellipsoid (MVE) niche estimations, with a precision of 0.01, for the Pyrenees Noaillian and the northern Middle Gravettian (Fig. 4). We measured the volume of each ellipsoid and calculated the level of environmental overlap between them using the Jaccard index (Qiao

Table 2
Models calibration results. Only one set of parameters was retained for the northern Middle Gravettian model, whereas 45 sets of parameters were relevant to the Pyrenees Noaillian model. Parameters corresponding to the models compared via the background similarity and identity tests are indicated in bold. L: linear; Q: quadratic; P: product; ctemp: temperature of the coldest month; wtemp: temperature of the warmest month; mprec: mean annual precipitation.

Parameters			Evaluation results				
Regularization multiplier	Features	Environmental variables	Partial ROC	Omission rates below 5%	AICc	Δ_{AICc}	Number of parameters
Northern Middle Gravettian							
0.3	**LQP**	**All**	**0**	**0**	**311.258**	**0**	**4**
Pyrenees Noaillian							
0.9	QP	ctemp, mprec	0	0	170.583	0	1
1	QP	ctemp, mprec	0	0	170.680	0.098	1
2	Q	ctemp, mprec	0	0	170.680	0.098	1
3	Q	ctemp, mprec	0	0	171.206	0.623	1
3	LQ	ctemp, mprec	0	0	171.206	0.623	1
2	QP	ctemp, mprec	0	0	171.758	1.175	1
2	LQP	ctemp, mprec	0	0	171.758	1.175	1
4	Q	ctemp, mprec	0	0	171.758	1.175	1
4	LQ	ctemp, mprec	0	0	171.758	1.175	1
0.1	Q	ctemp, wtemp	0	0	172.045	1.463	2
0.2	Q	ctemp, wtemp	0	0	172.056	1.473	2
0.3	Q	ctemp, wtemp	0	0	172.072	1.489	2
0.2	QP	ctemp, wtemp	0	0	172.093	1.510	2
0.4	Q	ctemp, wtemp	0	0	172.093	1.510	2
0.4	Q	All	0	0	172.093	1.510	2
0.5	Q	ctemp, wtemp	0	0	172.119	1.536	2
0.5	Q	All	0	0	172.119	1.536	2
0.3	QP	ctemp, wtemp	0	0	172.148	1.566	2
0.6	Q	ctemp, wtemp	0	0	172.148	1.566	2
0.6	Q	All	0	0	172.148	1.566	2
0.5	LQ	ctemp, mprec	0	0	172.153	1.570	2
0.7	Q	ctemp, wtemp	0	0	172.183	1.600	2
0.7	Q	All	0	0	172.183	1.600	2
0.3	LQP	ctemp, mprec	0	0	172.197	1.614	2
0.6	LQ	ctemp, mprec	0	0	172.197	1.614	2
0.4	QP	ctemp, wtemp	0	0	172.220	1.638	2
0.8	Q	All	0	0	172.220	1.638	2
0.7	LQ	ctemp, mprec	0	0	172.247	1.664	2
0.9	Q	ctemp, wtemp	0	0	172.262	1.679	2
0.9	Q	All	0	0	172.262	1.679	2
0.4	LQP	ctemp, mprec	0	0	172.303	1.721	2
0.8	LQ	ctemp, mprec	0	0	172.303	1.721	2
0.5	**QP**	**ctemp, wtemp**	**0**	**0**	**172.306**	**1.724**	**2**
1	Q	All	0	0	172.306	1.724	2
1	Q	ctemp, wtemp	0	0	172.306	1.724	2
5	Q	ctemp, mprec	0	0	172.311	1.729	1
5	LQ	ctemp, mprec	0	0	172.311	1.729	1
0.9	LQ	ctemp, mprec	0	0	172.366	1.783	2
0.6	QP	ctemp, wtemp	0	0	172.404	1.822	2
0.6	LQP	ctemp, wtemp	0	0	172.404	1.822	2
0.5	LQP	ctemp, mprec	0	0	172.433	1.851	2
1	LQ	ctemp, mprec	0	0	172.433	1.851	2
0.7	QP	ctemp, wtemp	0	0	172.513	1.930	2
0.7	LQP	ctemp, wtemp	0	0	172.513	1.930	2

et al., 2016, 2017).

3. Results

3.1. Niche predictions

The northern Middle Gravettian niche estimation (Fig. 5a) displays high suitability scores in the northern Aquitaine Basin, the southern Paris Basin, and low-to-medium suitability for the western Italian coast, northwestern Alps piedmont, southern Landes and Western Pyrenees, Brittany, and southern Britain. The site of Hautmougey has the lowest suitability score of all the occurrence points, and this is likely because it is situated in the northeastern portion of the study region and is isolated from the other sites. This is likely the result of less intensive archaeological research in this region relative to others (e.g., Southwestern France, southern Paris Basin; Angevin et al., 2018). The Garonne River Valley is characterized by a low level of suitability with the exception of a narrow corridor that connects the high suitability areas in northern Aquitaine to the regions of medium suitability situated in the southern Landes and Western Pyrenees. Finally, the geographic extent of the northern Middle Gravettian niche prediction corresponds closely to the geographic distribution of the occurrence data.

The Pyrenees Noaillian niche prediction (Fig. 5b) is geographically extensive and is significantly larger than the distribution of archaeological occurrence data. The estimated niche displays continuous high suitability scores from the coast of Cantabrian Spain up to southern Britain. The lowest predicted occurrence point is that of the site of La Carane-3, and all other sites from the central Pyrenees are located in areas with low to medium suitability scores.

Variability maps indicate that the northern Middle Gravettian model is probably more reliable than that of the Pyrenees Noaillian (Fig. 5c and d). The northern Middle Gravettian variability map

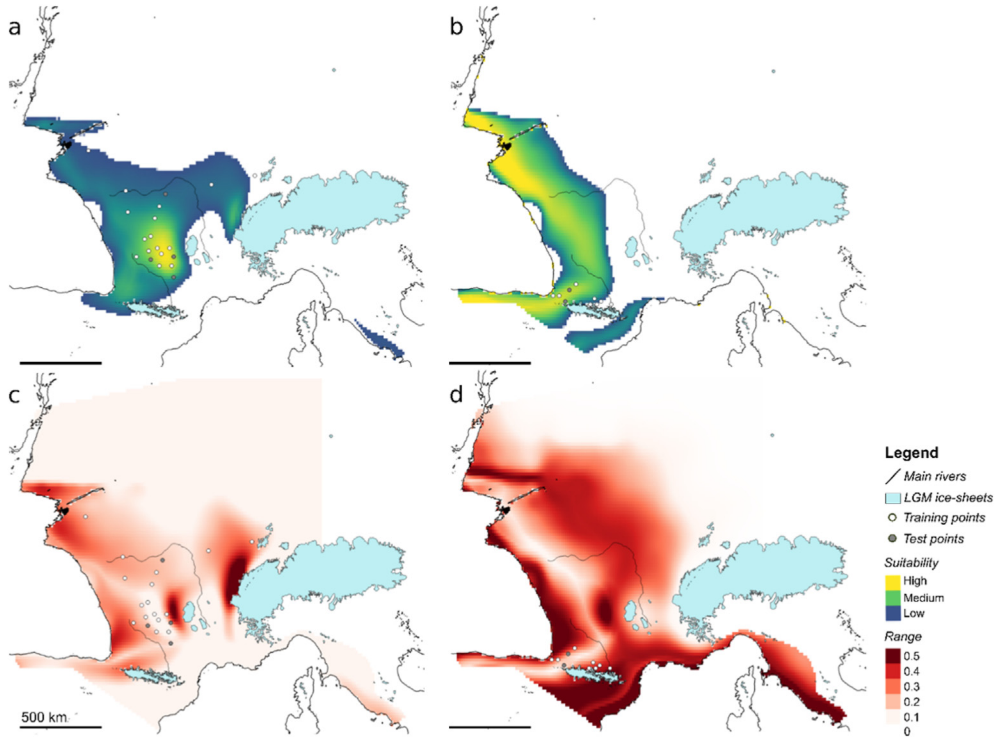

Fig. 5. Geographic projections of Maxent-produced median niche estimations. **a.** Northern Middle Gravettian. **b.** Pyrenees Noaillian. **c.** Variability map for the northern Middle Gravettian prediction showing the suitability range of 10 models produced with the same data. **d.** Variability map for the Pyrenees Noaillian prediction showing the suitability range of all 45 significant models.

displays few and relatively small areas with a range higher than 0.3. The highest suitability ranges occur in Brittany and southern Britain, the Landes platform area, the Massif Central as well as the northern Alps. The Pyrenees Noaillian variability map, however, shows variability ranges higher than 0.3 in areas along the Mediterranean coasts, the Eastern side of the Pyrenees, the Massif Central, as well as along the Atlantic coast and in the Landes periglacial desert area. The suitability estimates in these areas should therefore be considered less reliable since they can vary substantially between models.

3.2. Niche comparisons

The Pyrenees Noaillian and the northern Middle Gravettian niches are highly similar in geographic space (Fig. 6). However, their differences are significant and they are significantly less similar than would be expected by chance (D metric: North *vs.* Pyrenees: $p = 0.03$; Pyrenees *vs.* North: $p = 0.006$; I metric: North *vs.* Pyrenees: $p = 0.029$; Pyrenees *vs.* North: $p = 0.007$; for a statistical significance achieved if $p < 0.05$; Fig. 6). With respect to environmental dimensions, our analysis shows that the niches overlap significantly (MVE overlap volume = 1.110, which corresponds to 97% of the Pyrenees Noaillian ellipsoid volume and 7% of the Northern Middle Gravettian ellipsoid volume; Fig. 7). Comparisons demonstrate that the Pyrenees Noaillian niche is smaller and less broad than that of the northern Middle Gravettian, and is primarily contained within the latter (Fig. 7). It is worth noting, however, that a small portion of the Pyrenees Noaillian ellipsoid falls outside of the northern Middle Gravettian ellipsoid, thus occupying a subset of environmental conditions not present in the latter's niche estimation.

4. Discussion

The fact that the northern Middle Gravettian niche is significantly broader than that of the Pyrenees Noaillian suggests that the development of the Raysse method is linked to the exploitation of a significantly expanded niche composed of colder, drier conditions that correspond to more open landscapes and associated large mammal prey species. Available archaeological data support this hypothesis.

The Raysse method is a highly standardized reduction process that can be applied to a wide variety of blanks, from blades to thick flakes produced during various stages of the blade reduction sequences or other less standardized reduction sequences (e.g., production of flakes or blade-like flakes). The bladelets produced with the Raysse method did not require further intensive modification due to their standardized morphology. Furthermore, if a problem was encountered during the final stages of their production, only minimal investment was needed to produce a new or replacement bladelet (Klaric et al., 2002, 2009; Klaric, 2003, 2008, 2017). This highly standardized bladelet production system served to create end-products that could be easily transformed into *armatures* (a French term commonly used in technological and functional studies to designate either the lithic point hafted on the tip/head of a projectile or the lithic implements hafted laterally on a projectile's foreshaft) that were likely part of a composite and readily maintainable hunting weaponry toolkit. Such a technological adaptation is commonly observed in highly mobile hunter-gatherers that operate in landscapes where access to resources needed to maintain weaponry is unpredictable (Binford 1977; Bleed, 1986). The importance placed on producing highly standardized components for a maintainable and curated hunting toolkit is further supported by the emphasis that appears to have been placed on transmitting

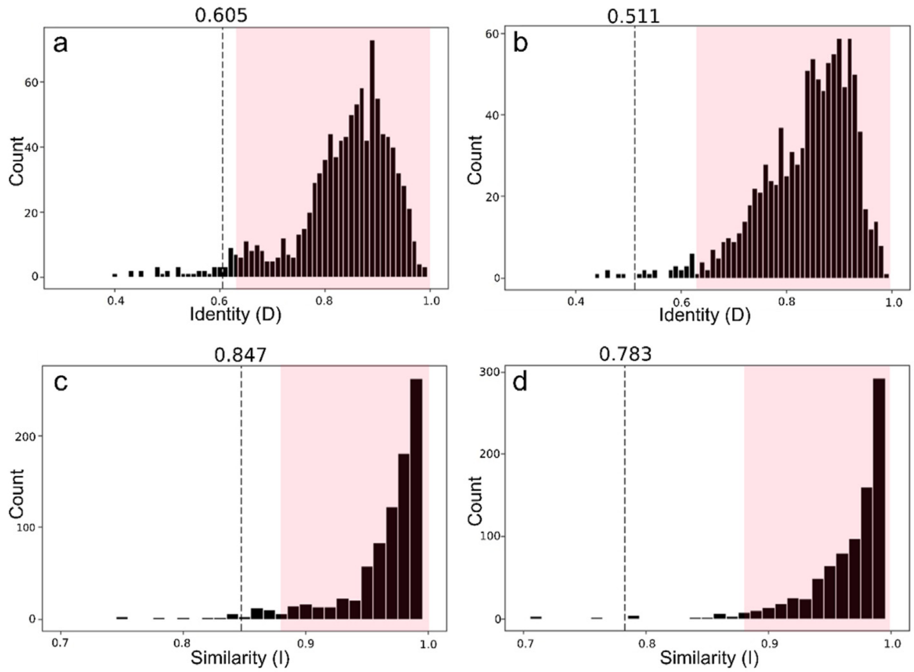

Fig. 6. Background similarity and identity tests results for comparisons between the northern Middle Gravettian vs. the Pyrenees Noaillian (**a.** and **c.**), and the Pyrenees Noaillian vs. the northern Middle Gravettian (**b.** and **d.**). Dashed lines represent measures between the empirical models and the histograms depict measures from 1000 background-derived comparisons. The colored areas represent the non-significance range above the 5th percentile of the distribution.

and maintaining this technique (Klaric, 2017, 2018). This has been inferred from the numerous technical details that one must take into account when using the Raysse method to replicate La Picardie bladelet blanks, and this is further supported by the frequent presence of unretouched flint knapping debris and retouched objects that appear to have been produced by apprentices or individuals who did not completely master the intricacies of the method (Klaric, 2017, 2018).

The opposite appears to have been the case in the Pyrenees, where *armature* forms are more diverse: Gravette points, microgravettes points, bi-truncated backed bladelets, and simple backed implements made from blades or bladelets (Klaric, 2003; Simonet, 2009a, 2011b, 2017). While these *armature* types were made from straight blade or bladelet blanks, the latter do not need to be highly standardized and can be obtained from a variety of reduction methods. Intensive retouch is all that is necessary to transform an initial blank into one of these *armature* types (e.g., Gravettes points broken during fabrication indicate that the blank's width can be reduced up to 50%; Klaric, 2003, p. 257; Simonet, 2009a, Fig. 21). The higher typological diversity of *armatures* in the Pyrenees may reflect a higher degree of variability in how these points were integrated into weapon systems (e.g., axial points *vs.* laterally mounted elements) used by these populations. These different technological strategies for producing hunting equipment between the northern Middle Gravettian and the Pyrenees Noaillian archaeological records are likely related to differences in targeted medium to large prey species and, in turn, the subsistence strategies and mobility patterns employed to exploit them.

Faunal data indicate that populations in the Pyrenees hunted a variety of animals, such as reindeer, bovids, horse, chamois, bison, deer and fox, whereas northern groups relied principally on reindeer (Lacarrière, 2015). This fact does not necessarily indicate that the availability of prey species was different between these two regions (Lacarrière, 2015, p. 347), but it is worth noting that the smaller Pyrenees niche is associated with a more diverse spectrum of prey species. Thus, it would appear that the Pyrenees piedmont plateau and plains, with its more reduced range of environmental conditions, contained a wide variety of prey species that, as indicated by seasonality data (Lacarrière, 2015), were present throughout the year. These data are consistent with inferred Gravettian occupation of the region, which is dominated by small, specialized sites (e.g., Tercis, Gatzarria) situated some distance from larger aggregation sites (e.g., Isturitz, Brassempouy), as well as an exploitation of predominantly local lithic raw materials (Simonet, 2017). Pyrenees populations, thus, were likely logistically mobile with a well-organized exploitation of resources within a relatively restricted region and narrow ecological niche. The high prey species diversity could therefore be the result of a more generalized hunting strategy within a reduced territory. In this framework, *armature* diversity could be interpreted as an adaptation to the exploitation of a more diverse prey species spectrum within a smaller and more rugged territory, allowing hunters to easily adapt to different situations by changing their hunting weaponry (e.g. prey type, topography etc.).

To the north, in contrast, the wider range of environmental conditions (i.e., broader ecological niche) exploited by the northern Middle Gravettian populations would suggest a higher degree of mobility than is observed in the Pyrenees since the main prey species identified in northern archaeological assemblages is reindeer (Lacarrière, 2015). Higher mobility is supported by technological data. For example, the Grotte du Renne site is located some distance from high quality lithic raw material sources (35–120 km according to Klaric et al., 2009), and its Middle Gravettian assemblage shows a high degree of curation, in contrast to other sites that are situated at or near raw material sources, such as the site of La Picardie (although a small percentage of artifacts at La Picardie are made from raw materials coming from sources located in the Charente region, some 200 km away; Delvigne et al., 2020). With respect to curation, Raysse burins (i.e. bladelet cores) from the Grotte du Renne often have double bladelet production platforms,

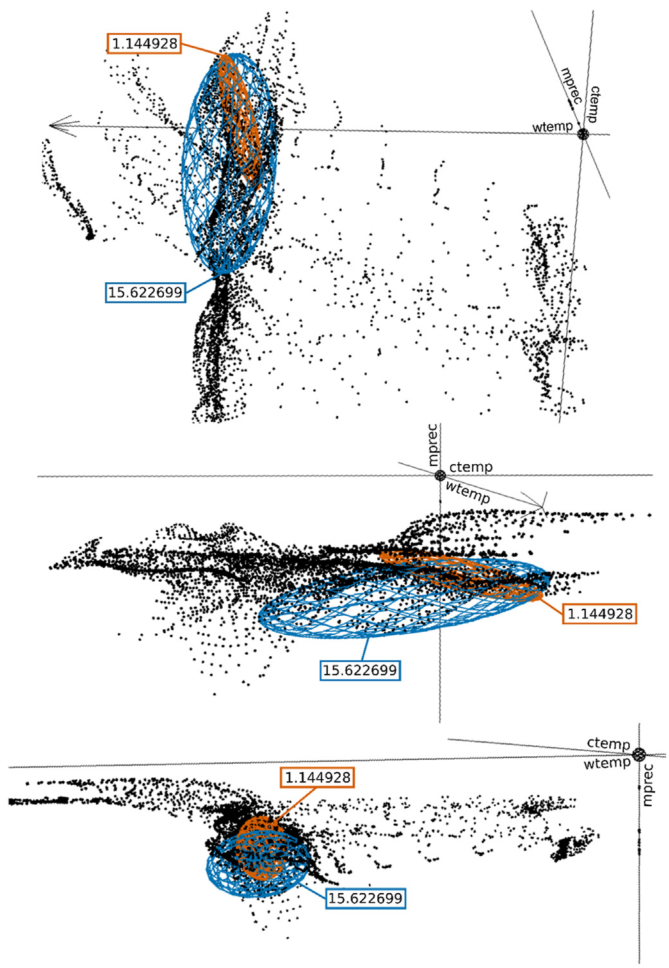

Fig. 7. NicheA Minimum Volume Ellipsoids (MVE) for the northern Middle Gravettian (blue) and the Pyrenees Noaillian (red) in environmental space during GS.5 (black points) according to different orientations of the axes. The environmental dimensions are temperature of the coldest month (ctemp), temperature of the warmest month (wtemp) and mean annual precipitation (mprec). The MVE volumes are displayed in the corresponding colored boxes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

are smaller than those recovered from La Picardie, and the blanks selected to make La Picardie bladelets are generally smaller and are not always typical: many bladelets are more twisted and do not always have a *pan-revers* and/or a pointed distal end (Klaric, 2006, 2017; Klaric et al., 2009). In this scenario, the Raysse method could reflect a technological specialization directed at producing *armatures* for hunting reindeer. It does not mean that reindeer was the only available species in the environment; in fact, other species are always present to a lesser extent in faunal assemblages (Lacarrière, 2015). This could therefore be the result of a cultural choice of northern populations focusing on reindeer (Klaric et al., in press)—a choice that would require higher mobility. Nevertheless, one must be careful to not generalize this pattern, since it relies on only a handful of studies, and numerous sites have assemblages that contain both by-products of the Raysse method and Gravette points, two conceptually different *chaînes opératoires* (i.e. reduction sequences), and thus different kinds of composite hunting weapons. However, we must bear in mind that occurrences of Picardie bladelets and Gravette points together are observed almost exclusively within cave or rock shelter deposits, where archaeological levels represent palimpsests of multiple occupations that often were subject to complex post-depositional processes that can homogenize initially distinct occupations. The co-occurrence of the two *armature* types is also observed at two open-air sites: the site of Solvieux in Dordogne (Sackett, 1999), where the stratigraphic setting is extremely complex, and Sackett's analysis has raised doubts concerning the integrity of its archaeological assemblages; and the site of Les Jambes in Dordogne (Célérier, 1967), where slope depositional processes influenced the site's formation (Klaric, 2003, p. 222), thus raising doubts as to whether the distinct archaeological levels defined by Célérier are valid. Whether these two types of *armatures*—la Picardie bladelets and Gravette/microgravette points—were associated with the same hunting tool-kit or whether their association in the same archaeological level is the result of post-depositional processes or palimpsest deposits, is a subject that requires further study.

At present, the site of Callan represents the only known location of specialized occupations or activities north of the Garonne River (Morala, 2011). Its lithic assemblage is dominated by Noailles burins and no *armatures* have been recovered. This general absence of specialized sites suggests that groups in these higher latitude regions had a higher level of residential mobility than those in the Pyrenees. Such a pattern of highly mobile groups using highly standardized and curated toolkits to exploit large territories via a residential system of mobility is in sharp contradiction with the pattern observed during the same period in the Pyrenees. This pattern, though, may be influenced by the lack of chronological resolution for this time-period, which is the result of reduced stratigraphic resolution due to imprecise excavation methods, to post-depositional mixing of levels, palimpsest deposits and the standard errors associated with radiocarbon ages for this period. Such factors make determinations of discrete activity episodes difficult, if not impossible, and the potential homogenization of archaeological levels renders making inferences of how human activities were organized across the landscape difficult.

With respect to the geographic expressions of the estimated niches and the technological differentiation observed between the two regions, what factors potentially influenced these patterns? We propose that the cold desert of the Landes region (Bertran et al., 2013) and the Garonne River Valley corridor (Bruxelles & Jarry, 2011, 2012) served as an ecological barrier that played a role in the territories exploited by Middle Gravettian hunter-gatherer populations. The presence of this barrier would have been a factor in limiting the diffusion of the Raysse method to the Pyrenees area. This idea is supported by the fact that this region is associated with low suitability measures (Fig. 5), and these suitability scores are even likely to be overestimated since the climatic variables used for this study insufficiently capture the particular conditions of a cold desert whose existence was the result of specific geographic and geomorphic factors (Bertran et al., 2013). The presence of this ecological barrier likely influenced the territories exploited by different Middle Gravettian hunter-gatherer populations and thus in term served to create a cultural barrier between the Pyrenees and regions to the north. This hypothesis is supported by the fact that the Pyrenees Noaillian's existing niche is more geographically extensive than the distribution of sites used to reconstruct it, whereas the northern Middle Gravettian niche more closely corresponds to its occurrence data. Thus, the presence of populations in these northern habitats that were characterized by different technological systems and mobility strategies, from which one could infer other cultural differences, could have prevented the Pyrenees populations from occupying their entire existing fundamental niche.

Another observation concerns the northern model's predictions for regions beyond the borders of present-day France—regions in which Noailles burins are present in archaeological assemblages

(Touzé, 2013). There exists a small area of low suitability along the western Italian coast for the northern Middle Gravettian prediction, but the region between this area and the main suitable area in France is predicted as unsuitable. As for the niche associated with the Pyrenees Noaillian, regions east of the French Massif Central are predicted as unsuitable. One possible interpretation is that the Rhône River Valley functioned as a barrier during GS.5. This interpretation, however, is contradicted by the presence of Noailles burins in the lower Rhône River Valley and along the Italian Mediterranean coast (Palma di Cesnola, 1993; Onoratini et al., 2010; Touzé, 2013). Moreover, these areas are characterized by a high degree of variability depending on model parametrization, thus indicating that their corresponding suitability estimates are less reliable (Fig. 5d). Additional niche predictions, comparisons, and tests that take into account Italian sites, in conjunction with detailed examinations of their lithic industries and comparisons to assemblages to the west, would be necessary to further evaluate this issue. To the west, the Cantabrian region is characterized by high suitability scores for the Pyrenees Noaillian niche, whereas it is not suitable in the northern Middle Gravettian niche prediction, except for a small portion along the Western Pyrenees. This pattern supports the idea that the Cantabrian region was part of the Pyrenees Noaillian territory—a pattern supported by the presence of Noailles burins in this region (Foucher et al., 2008; Simonet, 2009a, 2017; de la Peña-Alonso, 2011). This pattern should be further evaluated with detailed studies of the archaeological assemblages and new niche predictions that include the presence of these sites. It is also paramount to couple such analyses with critical evaluations of existing chronological data (cf. Banks et al., 2019), as well as with efforts to obtain new ^{14}C ages from reliable archaeological contexts.

5. Conclusions

Comparisons of the reconstructed niches for the two Middle Gravettian typo-technological *faciès*, the Noaillian and the Rayssian, in both geographic and environmental dimensions, indicate that their respective niches were significantly different, despite a large degree of overlap in environmental space, due to the fact that the northern Middle Gravettian niche was significantly broader than that of the Pyrenees Noaillian. We interpret this pattern as indicating that the appearance of the Raysse method is related to the exploitation of a significantly broader ecological niche. As opposed to what is observed in areas south of the Garonne River, the Raysse method appears to be associated with particular mobility and settlement strategies contained within a larger exploited territory or territories. Furthermore, this observed pattern suggests that La Picardie bladelets (products of the Raysse method) represented a technological specialization directly associated with a hunting strategy focused on reindeer. Picardie bladelets may have been considered—at least by some hunter-gatherer populations—to be more appropriate within this context than backed points and abrupt backed bladelet *armatures* (such as Gravette and microgravette points), although this hypothesis warrants further testing in the archaeological record. Furthermore, the Raysse method would have been advantageous in such contexts because it would have been more easily maintainable and adapted to hunting activities organized within territories such that access to raw material resources was less predictable or available. Conversely, we interpret *armature* diversity of the Pyrenees Noaillian as reflecting an adaptation to the organization of subsistence activities within smaller territories and the use of specialized weapon systems adapted to a variety of prey species and/or situations (e.g. topography). Furthermore, the need for a highly maintainable hunting toolkit was probably not as paramount, since access to raw material resources would have been more predictable or available.

These niche results further support the hypothesis that the Landes cold desert and Garonne River Valley corridor served to limit the homogenization of technological traditions between the Pyrenees and regions to the north. The nature of this barrier (i.e. environmental and/or cultural) warrants further evaluation incorporating other potentially relevant variables (distribution of cold deserts etc.) in future ecological niche modeling analyses that target the concerned archaeological populations. Furthermore, continued investigations centered on identifying Middle Gravettian sites and the typo-technological attributes of their archaeological assemblages are needed. In turn, the niche modeling results presented here will provide important context and details for research addressing issues of chronology, settlement and subsistence strategies, lithic raw material exploitation, lithic and bone technologies, and site function pertaining to the Middle Gravettian archaeological record.

Authorship statement

Anaïs Vignoles: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Visualization. William E. Banks: Conceptualization, Methodology, Writing – original draft (English proof-reading) and review & editing, Funding acquisition. Laurent Klaric: Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition. Masa Kageyama: Resources, Writing – original draft (paleoclimatic simulations description) and review & editing. Marlon E. Cobos: Methodology, Writing – original draft (ENM methodology) and review & editing. Daniel Romero-Alvarez: Methodology, Writing – review & editing

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106766.

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