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

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Declaration of interests

The authors of this article declare that they have no financial conflict of interest with the content of this article.

Authorship statement

Funding: WB, LK

Design of the study and methodology: WB, LK, AV.

Occurrence data gathering: AV, LK.

Paleoclimatic simulations: MK.

Niche analyses: AV with help from MC and DRA.

Writing: main author = AV, MK = simulations description, MC & DRA = ENM methodology and advice for figures and tables, LK = significant input for the archaeological context, occurrence data and interpretation, WB = significant input in writing the manuscript and English proofreading.

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Abstract

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

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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 the Noaillian assemblages south of the Garonne River. The aim of this study is to test this hypothesis quantitatively using ecological niche modeling (ENM) methods. We critically evaluate published data to construct inventories of Noaillian and Rayssian archaeological sites. Using ENM methods, we estimate the ecological niches associated with the Middle Gravettian north (Noaillian + Rayssian) and south (Pyrenees Noaillian) of the Garonne River, and these predicted niches 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 such environmental contexts than those employed by Pyrenees populations.

Keywords: Middle Gravettian, France, Noaillian, Rayssian, ecological niche modeling, culture-environment relationships

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. Klaric, 2003; de la Peña-Alonso, 2009, 2011; Noiret, 2013; Pesesse, 2013, 2017). 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 the preceding and following 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, 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). Various hypotheses have been proposed to explain this diversity, such as differences in site activities (e.g. Laville & 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 & 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*[1], termed the "Noaillian" and the "Rayssian" that are characterized principally on the basis of their lithic industries (Touzé, 2013). The Noaillian is a typological *faciès*, defined solely by the presence of Noailles burins[2] (Bardon & Bouyssonies, 1903; Tixier, 1958), whereas the Rayssian is a typo-technological *faciès*, defined by a reduction method aimed at removing, from Raysse burins, bladelets that were used as armatures (Figure 1, Movius & David, 1970; Klaric *et al.*, 2002; Lucas, 2002; Pottier, 2006; Klaric, 2017), as well as a strong conceptual parallel between both bladelet and blade reduction sequences (Klaric, 2003, 2008).

[1] 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.

[2] This determination is sometimes based on the presence of bone or antler points called "Isturitz points" although this point type's precise chrono-cultural status remains uncertain (cf. Goutas, 2013b).

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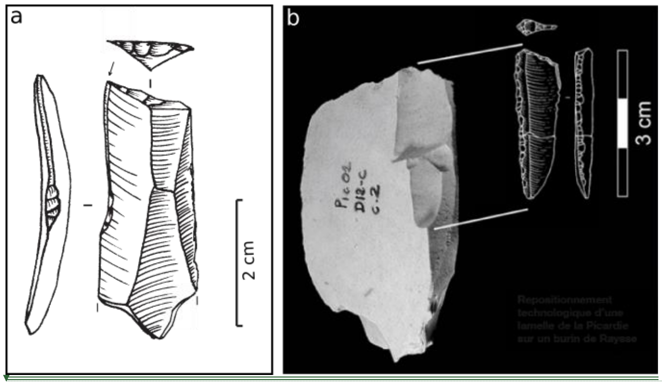

Figure 1: Middle Gravettian diagnostic artifact types. **a.** Noailles burin from Fourneau du Diable, Dordogne, France (drawing: A.Vignoles). **b.** Technological position of a "Picardie" bladelet on a Raysse burin-core from La Picardie, Indre-et-Loire, France (from Klaric, 2008).

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 on-going 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; A. Vignoles, PhD thesis on-going). However, in a few stratified contexts, the development of the Raysse method is always stratigraphically younger than the Noaillian[3] (e.g., Abri Pataud and Flageolet I sites; David, 1985; Rigaud, 1982; Klaric, 2003). 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 & Rigaud, 1973; Rigaud, 2008, 2011), the use of different typo-technological traditions within a broad regional population (Touzé, 2013) or the result of post-

[3] Except for Les Jambes site, where Noailles burins are described as being stratigraphically *above* the Raysse burins (Célérier, 1967). This configuration, though, remains to be validated. 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 in fact to a single archaeological layer. Finally, a recent reexamination of the site's assemblage has shown that most of the "Noailles burins" do not correspond to the classic typological definition (A. Vignoles, on-going study). 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 (A. Vignoles, on-going study) may provide new data with which to discuss the presence of Gravette projectile points–a class of tool traditionally associated with the Noaillian rather that the Rayssian–at Les Jambes.

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depositional mixing or the inability of old excavation methods to differentiate between 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 territories (Figure 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; Touzé, 2013; Klaric, 2017). The absence of the Raysse method south of the Garonne River[4] 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

The aim of this study is to test the hypothesis that the typo-technological differences observed on either side of the Garonne River valley during the Middle Gravettian may 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 test this hypothesis (Banks, 2017; d'Errico & Banks, 2013). ENM (the terminology employed in this study, cf. Peterson & 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 employed by

[4] Despite mentions of the presence of Raysse burins in La Carane-3, Isturitz and Tuto de Camalhot sites by David, 1985, the presence of the Raysse method is not consistently demonstrated: none of these artifacts has been described or pictured, and recent technological studies (e.g. Simonet, 2009a) do not mention them as well. The demonstration of the Raysse method relies on precise technical criteria and more specifically on the identification of the bladelet component associates with Raysse burin-cores, which was not the kind of criteria used by David to describe the Late Noaillian (i.e. Rayssian). It is also important to state that look-alike artifacts (*faux-amis*) have been described at Brassempouy (Klaric, 2006). The exemplars reported by David could therefore be misleading in the same way.

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predictive modeling algorithms to identify sets of environmental parameters associated with known archaeological sites and create, through an iterative process of training and testing using subsamples of occurrences, estimations for the presence of suitable environmental conditions 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).

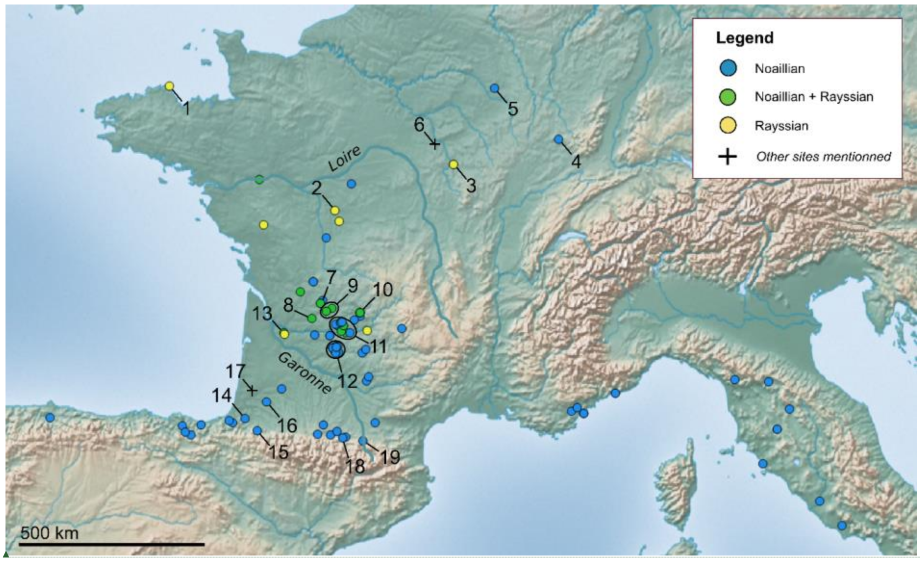

Figure 2: Sites where Noailles burins and / or Raysse burins have been found (after Touzé, 2013 ; Klaric, 2017). Main sites cited in the text : **1** – Plasenn al Lomm; **2** – La Picardie; **3** – Arcy-sur-Cure sites; **4** – Hautmougey; **5** – La Verpillère I cave; **6** – Chamvres; **7** – Fourneau du Diable; **8** – Solvieux; **9** – Combe Saunière I, Les Jambes; **10** – Bouyssonie cave; **11** – Le Flageolet I, Abri Pataud, Grand-Abri de Laussel, Abri du Facteur; **12** – Roc-de-Gavaudun, Peutille; **13** – Lespaux rockshelter; **14** – Isturitz cave; **15** – Gatzarria; **16** – Brassempouy; **17** – Tercis; **18** – Tuto de Camalhot; **19** – La Carane-3. Topographic background: http://www.naturalearthdata.com

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 (**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**, Figure 3) to

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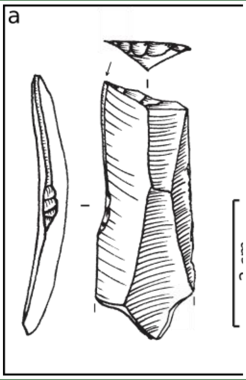

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Déplacé vers le haut [4]: Figure 1: Middle Gravettian's diagnostic artifacts types. **a.** Noailles burin from Fourneau du Diable, Dordogne, France (drawing: A.Vignoles). **b.** Technological position of a "Picardie" bladelet on a Raysse burin-core from La Picardie, Indre-et-Loire, France (from Klaric, 2008)¶

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The aim of this study is to test the hypothesis that the typo-technological differences observed on either side of the Garonne River valley during the Middle Gravettian may reflect the exploitation of two different ecological niches via different technological (i.e. cultural) adaptations. The application of Ecological Niche Modeling (ENM) methods to the archaeological record is one way to test this hypothesis (Banks, 2017; d'Errico & Banks, 2013). ENM (the terminology employed in this study, cf. Peterson & Soberón, 2012; Warren, 2012) provides a means by which to estimate the ecological niches of past hunter-gatherer populations, employing archaeological sites as occurrence data and high-resolution paleoclimatic simulations as the source of environmental variables. These data are then employed by predictive modeling algorithms to identify sets of environmental parameters associated with known archaeological sites and create, through an iterative process of training and testing based on subsamples of occurrences, ...

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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 & Soberón, 2012).

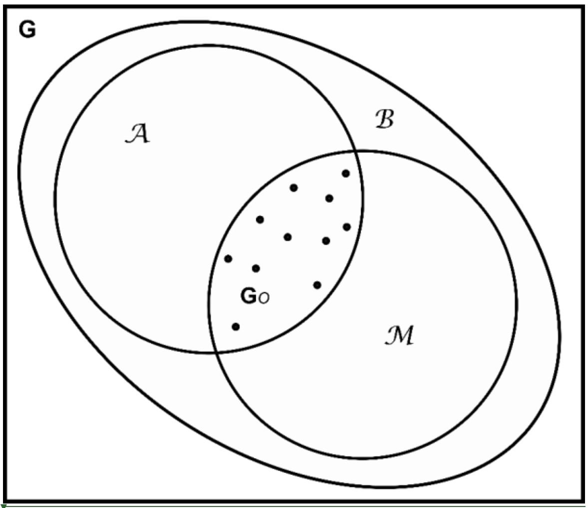

Figure 3: **BAM** diagram representing the factors that constrain the geographic distribution of a species at broad geographic scales, if the Eltonian-noise hypothesis holds true (after Soberón & Peterson, 2005, 2012; modified). Circles represent the different factors and black dots represent the observed 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.

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

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Mis en forme : Normal, Retrait : Première ligne : 1,25 cm 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).

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 (Figure 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 (screened) 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 (coordinated artifacts, screened 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 & de Sonneville-Bordes, 1960; Movius & David, 1970), its function as a core for producing standardized armature bladelets was 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).

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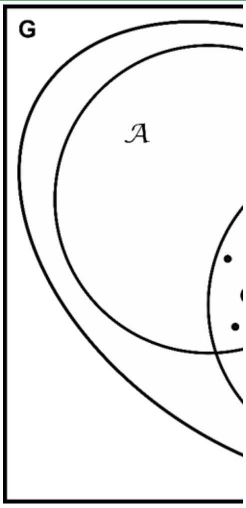

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Figure 3: **BAM** diagram representing the factors that constrain the geographic distribution of a species at broad

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Another problem is the inconsistent definition of the Noaillian (i.e. sole presence of Noailles burins in an assemblage) compared to 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, raw material types, 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; A. Vignoles, on-going study) and the southern Paris Basin (Kildea & 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 & Grimaldi, 2019) have employed different methodological approaches for characterizing reduction sequences (i.e. *chaîne opératoire*) and typologies, with a few exceptions (e.g. Simonet, 2010), thus rendering difficult comparisons to sites studied via the methods traditionally used in France. An additional difficulty 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 and extending 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 to the south by the Garonne River Valley and by the most northerly sites where the "Raysse method" has been observed (Klaric, 2017). The latter territory is

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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, which mirrors the approach employed by Banks *et al.* (2019).

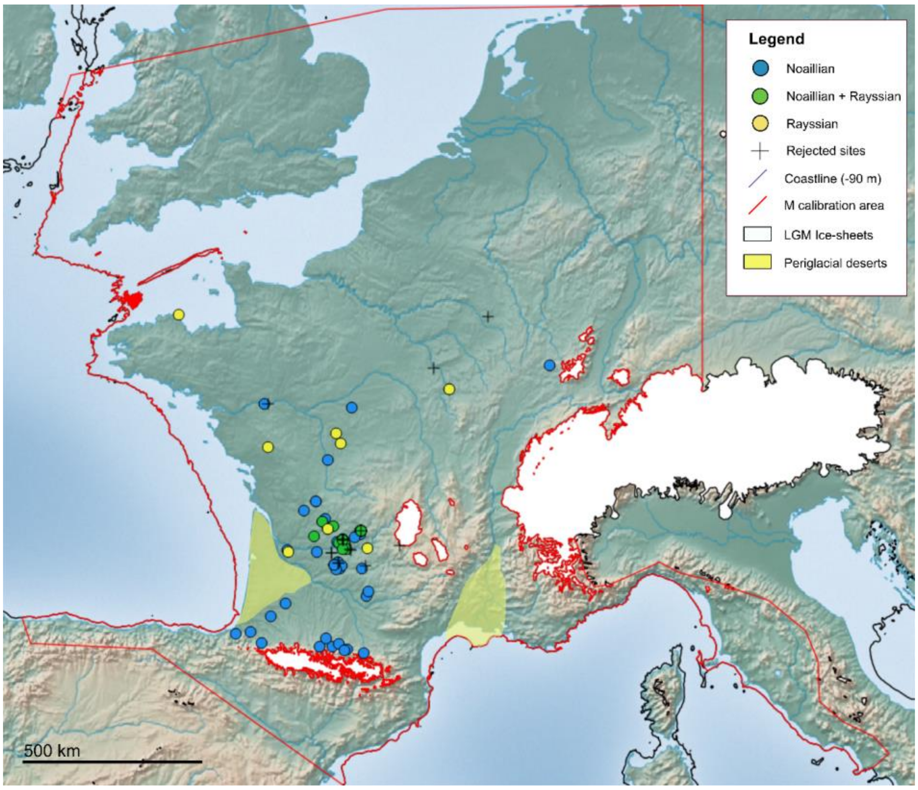

Figure 4: Noaillian and Rayssian sites location used for calibration and the study's defined accessible area (**M**) hypothesis. Topographic background: http://www.naturalearthdata.com; Coastlines: Siddall *et al.*, 2003; Glaciers cover: Ehlers & Gibbard, 2004; Periglacial cold deserts: Bertran *et al.*, 2013; Bosq *et al.*, 2018

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. A source was considered pertinent if it provided precise typological (tool type) counts and detailed descriptions of artifact characteristics based on the most recent definitions, 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. Klaric and A. Vignoles). We, thus, did not retain sites for which one or both phases were only suspected

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to be present[5] in order to avoid potentially aberrant attributions based on look-alike artifacts (such as for the "Raysse burins" from Brassempouy or Le Gratadis; Klaric, 2003, 2006; and for the "Noailles burins" from Les Jambes; A. Vignoles, on-going study). 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 end, 74 sites were retained 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 (Figure 4; *Table 1*). More sites will certainly be added to this corpus in the future as existing collections are reexamined, as new excavations are undertaken at known sites, and as new sites are excavated.

Table 1: Sites retained or rejected based on a critical review of the literature, along with their geographic coordinates and references. Geographic coordinates correspond to the commune 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.

Sites	Long. (E)	Lat. (N)	Noailles burins	Raysse method	References
Middle Gravettian North of the Garonne River occurrence dataset					
Abri André Ragout	0.42	45.68	presence	insufficient	Tixier, 1958; David, 1985
Abri Charbonnier	1.04	46.68	absence	presence	Aubry *et al.*, 2013; Klaric, pers. obs.
Abri de la Bergerie	1.58	44.48	presence	absence	Clottes *et al.*, 1990
Abri du Chasseur	0.42	45.68	presence	absence	Tixier, 1958; David, 1985
Abri du Couvert	1.02	44.49	presence	absence	Morala, 1984
Abri du Facteur	1.04	44.97	presence	presence	Delporte, 1968; David, 1985; Vignoles, pers. obs.
Abri du Poisson	1.01	44.94	presence	absence	de Sonneville-Bordes, 1960; David, 1985
Abri du Raysse	1.54	45.16	presence	presence	David, 1985; Touzé, 2011
Abri Durand-Ruel	0.65	45.37	presence	suspected	de Sonneville-Bordes, 1960; Daniel & Schmider, 1972; David, 1985
Abri Labattut	1.11	45.00	presence	insufficient	de Sonneville-Bordes, 1960; David, 1985
Abri Laraux	0.73	46.40	presence	suspected	de Sonneville-Bordes, 1960; David, 1985
Abri Lespaux	-0.29	44.82	presence	suspected	David, 1985; Krtoliza & Lenoir, 1998
Abri Pagès	1.04	44.97	presence	absence	de Sonneville-Bordes, 1960; David, 1985
Abri Pataud	1.01	44.94	presence	presence	David, 1985; Bricker (dir.), 1995; Pottier, 2005, 2006; Nespoulet, 2008

[5] e.g., 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 & Lenoir, 1998) ; also sites where Noailles burins are all atypical, such as at Peutille site 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).

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Table 1: Sites selected or rejected based on a critical review of the literature, geographic coordinates and references. Geographic coordinates correspond to the city or village within or nearby which the site is localized. Although these coordinates are not very precise, their resolution matches well the 11.5 km-grid resolution of the environmental data.
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Table 1 - continued

Sites	Long. (E)	Lat. (N)	Noailles burins	Raysse method	References
Abri Peyrony	0.89	44.56	presence	absence	Le Tensorer, 1981; David, 1985
Bassaler-Nord	1.54	45.16	presence	presence	David, 1985; Touzé, 2011
Combe Saunière	0.87	45.24	presence	presence	Klaric, 2017; Klaric, pers. obs.
Gisement de la Chèvre	0.59	45.32	presence	insufficient	David, 1985; Arambourou & Jude, 1964
Grand-abri de Laussel	1.14	44.94	presence	presence	Roussot, 1985; David, 1985; Klaric, 2017; Klaric, pers. obs.
Grotte "Chez Serre"	1.53	45.10	presence	absence	David, 1985
Grotte Bouyssonie	1.54	45.16	presence	presence	Touzé, 2011; Klaric, 2017; Klaric, pers. obs.
Grotte de Champ	1.53	45.16	presence	insufficient	David, 1985; Daniel, 1969
Grotte de Rouzet	1.69	44.00	presence	absence	Foucher *et al.*, 2008
Grotte d'Oreille d'Enfer	1.01	44.94	presence	absence	de Sonneville-Bordes, 1960; David, 1985; Pradel, 1959
Grotte du Renne	3.76	47.60	absence	presence	Klaric, 2003
Grotte du Trilobite	3.76	47.60	absence	presence	Klaric, 2003; David, 1985
Grotte Lacoste	1.54	45.16	presence	absence	David, 1985
Grotte Maldidier	1.18	44.83	presence	presence	Klaric, 2017; Caux *in* Boudadi-Maligne, 2012
Grotte Thévénard	1.54	45.16	presence	insufficient	David, 1985
Guiraudel	0.95	44.54	presence	absence	Morala, 1984
Hautmougey	6.26	48.00	presence	absence	Hans, 1997
La Croix-de-Bagneux	1.33	47.29	presence	absence	Kildea & Lang, 2011, 2013
La Ferrassie	0.95	44.97	presence	absence	de Sonneville-Bordes, 1960; David, 1985
La Font-Robert	1.54	45.16	presence	insufficient	de Sonneville-Bordes, 1960; David, 1985
La Martinière	-0.86	47.36	presence	suspected	Allard, 1986
La Picardie	0.93	46.86	absence	presence	Klaric, 2003; Klaric *et al.*, 2011; Klaric *et al.*, 2018
La Rochette	1.09	45.01	presence	suspected	de Sonneville-Bordes, 1960; Schmider, 1969; David, 1985; Klaric, 2003, p.220
La Roque Saint-Christophe	1.08	44.99	presence	presence	de Sonneville-Bordes, 1960; David, 1985; Vignoles, pers. obs.
Las Pélénos	0.93	44.50	presence	absence	Morala, 1984
Le Caillou	0.45	44.78	presence	absence	Boyer *et al.*, 1984
Le Callan	0.97	44.60	presence	absence	Morala, 2011
Le Flageolet I	1.09	44.84	presence	presence	Rigaud, 1982; David, 1985; Lucas, 2000; Gottardi, 2011
Le Fourneau du Diable	0.59	45.32	presence	presence	David, 1985; Klaric, 2003, 2017; Vignoles *et al.*, 2019
Le Petit-Puyrousseau	0.72	45.19	presence	insufficient	de Sonneville-Bordes, 1960; Daniel, 1967; David, 1985
Le Roc de Cavart	1.07	44.54	presence	absence	Le Tensorer, 1981; David, 1985

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Table 1 - continued

Sites	Long. (E)	Lat. (N)	Noailles burins	Raysse method	References
Le Roc de Gavaudun	0.89	44.56	presence	suspected	de Sonneville-Bordes, 1960; Monméjean *et al.*, 1964; Le Tensorer, 1981; David, 1985
Le Taillis des Coteaux	-0.77	46.62	absence	presence	Klaric, 2017
Les Artigaux	-0.27	44.79	unlikely	presence	Lenoir, 1977; Klaric, 2003; Vignoles, obs. pers
Les Battuts	1.73	44.08	presence	suspected	Alaux, 1967; Alaux 1971; David, 1985
Les Fieux	1.71	44.85	absence	presence	Guillermin, 2006, 2008
Les Jambes	0.72	45.19	unlikely	presence	Célérier, 1967; Vignoles, pers.obs.
Les Morts	1.54	45.16	presence	presence	David, 1985; Sarrazin 2017
Les Vachons	0.12	45.51	presence	suspected	David, 1985; Fontaine, 2006
Masnaigre	1.14	44.94	presence	suspected	David, 1985
Métayer	0.89	44.56	presence	insufficient	Le Tensorer, 1981; David, 1985
Plasenn-al-Lomm	-3.00	48.85	absence	presence	Le Mignot, 2000; Klaric, 2003; Sarrazin 2018
Plateau Baillard	0.89	44.56	presence	absence	Le Tensorer, 1981; David, 1985
Pré-Aubert	1.54	45.16	presence	suspected	David, 1985; Demars, 1977
Roc de Combe	1.40	45.04	presence	absence	David, 1985
Roquecave	0.89	44.56	presence	absence	Le Tensorer, 1974; Le Tensorer, 1981
Solvieux	0.39	45.06	presence	presence	David, 1985; Sackett, 1999; Klaric, 2003
Station du Fresquet	0.94	44.47	presence	absence	Morala, 1984
Pyrenees Noaillian occurrence datatset					
Bois de Touaa	0.83	43.07	presence	absence	Foucher *et al.*, 2008; Clottes, 1985, p. 346
Brassempouy	-0.69	43.63	presence	absence	Klaric, 2003; Foucher *et al.*, 2008; Simonet, 2009a
Gargas	0.52	43.07	presence	absence	David, 1985; Foucher *et al.*, 2008, 2012
Gatzarria	-0.92	43.14	presence	absence	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a
Grotte d'Enlène	1.20	43.02	presence	absence	Foucher *et al.*, 2008; Simonet, 2009a
Grotte des Rideaux	0.67	43.23	presence	absence	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a
Hin-de-Diou	-0.33	43.86	presence	absence	Briand *et al.*, 2010
Isturitz	-1.20	43.35	presence	insufficient	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a; Lacarrière *et al.*, 2011
La Carane-3	1.61	42.96	presence	insufficient	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a
Lézia	-1.58	43.31	presence	absence	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a
Tarté	0.99	43.12	presence	absence	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a
Tuto de Camalhot	1.13	43.01	presence	absence	David, 1985; Foucher *et al.*, 2008; Simonet, 2009a

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Sites	Long. (E)	Lat. (N)	Noailles burins	Raysse method	References
Sites considered insufficiently reliable from the litterature review					
Abri de Fongal	1.08	44.99	insufficient	insufficient	de Sonneville-Bordes, 1960, p.97; David, 1985
Abri des Merveilles	1.11	45.00	suspected	absence	Delage, 1936; de Sonneville-Bordes, 1960; David, 1985
Abri des Peyrugues	1.67	44.54	absence	insufficient	Guillermin, 2011
Abri Sous-le-Roc	1.09	45.01	insufficient	absence	de Sonneville-Bordes, 1960; David, 1985
Chamvres	3.36	47.96	absence	controversial	Klaric, 2003, 2013; Sarrazin, 2018
Gisement du château	1.01	44.59	suspected	absence	Le Tensorer, 1974, p.467
Grotte de la Verpillère I	4.73	48.81	insufficient	absence	Floss *et al.*, 2013
Grotte de Péchialet	1.29	44.82	suspected	absence	David, 1985; Breuil, 1927
Grotte du Bos-del-Ser	1.54	45.16	insufficient	insufficient	David, 1985
Grotte du Roc de Vézac	2.52	44.89	insufficient	absence	Rigaud, 1982, p.262; Aujoulat *in* Leroi-Gourhan, 1984
Peutille	0.97	44.58	suspected	absence	Morala, 1984
Roc de Combe-Capelle	0.82	44.77	insufficient	absence	de Sonneville-Bordes, 1960; David, 1985
Roc-en-Pail	2.29	48.86	insufficient	absence	Allard & Gruet, 1976; Gruet, 1984; Hinguant & Monnier, 2013
Tercis	-1.11	43.67	suspected	absence	Simonet, 2009a, b, 2013
Termo-Pialat	0.82	44.77	suspected	absence	de Sonneville-Bordes, 1960; David, 1985

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 was present during Greenland Stadial 5 (GS.5), during which occurred Heinrich Event 3 (HE3).

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

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the Last Glacial Maximum (LGM; Figure 4). Atmospheric greenhouse gas concentrations were also left at their LGM values (CO_2 = 185 ppm, CH_4 = 350 ppb, N_2O = 200 ppb). The orbital parameters are set to 32 ky cal. BP (Berger *et al.*, 1978). 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 considering its high correlation with temperature.

2.3. Ecological niche modeling

2.3.1. Modeling preparation

Prior to estimating niches, we analyzed and modified the occurrence datasets to reduce potential spatial biases. First, we trimmed duplicate site occurrences from each grid-cell, so that a grid-cell only contained a single occurrence point, thereby 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 thus preventing oversampling of environmental conditions from certain areas (e.g., the northern Aquitaine area) and reducing spatial autocorrelation (Anderson & Gonzalez, 2011; Boria *et al.*, 2014). This consisted of trimming the occurrence datasets such that the minimum distance between any pair of occurrence points was twice the grid resolution, i.e. *ca.* 23 km. This step was done manually using 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 the 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 (Figure 4), we hypothesize 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

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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 & Gibbard, 2004). While these reconstructions 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 stadial and HE. Furthermore, the nature of raw material (flint) circulation in the Pyrenees region (Foucher *et al.*, 2008; Simonet, 2017) led us to permit the predictive modeling architectures 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 between either sides of the Valley, cf. Santaniello, 2016). Indeed, 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 sands 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 in QGIS 2.18.28.

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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 & Seifert, 2011). For the retention of the best performing models among those that were statistically significant, we

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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. Δ_{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.

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

Table 2 - continued

Regularization multiplier	Features	Environmental variables	Partial ROC	Omission rates below 5%	AICc	ΔAICc	Number of parameters
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	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
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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

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 spaces. To compare the geographic projections of the niches, we used the background similarity and identity tests (Warren *et al.*, 2008, 2017) which quantifies 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 /

identity) to 1 (total similarity / identity) and are obtained via the comparison of the two empirical niche predictions. The measurement is then compared to those obtained from 1000 sets of null niche predictions produced using occurrences randomly sampled from the environmental background of the calibration area. The difference between the two predictions is deemed to be significant if the empirical value fall below the 95% limits of the null distribution, respectively. To compare niches in environmental space, we used NicheA (Qiao *et al.*, 2016). We employed a three-dimensional environmental background using the three retained 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 (Figure 4). The volume of each ellipsoid was measured, and their level of environmental overlap was calculated using the Jaccard index (Qiao *et al.*, 2016; Qiao *et al.*, 2017).

3. Results

3.1. Niche predictions

The northern Middle Gravettian niche estimation (Figure 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 (Figure 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.

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Variability maps indicate that the northern Middle Gravettian model is probably more reliable than that of the Pyrenees Noaillian (Figure 5c and 5d). The northern Middle Gravettian variability map displays 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 ranges higher than 0.3 in areas along the Mediterranean coasts, the Eastern side of the Pyrenees, as well as in the Parisian basin. The suitability estimates in these areas should therefore be considered as less reliable, since they can vary substantially between models.

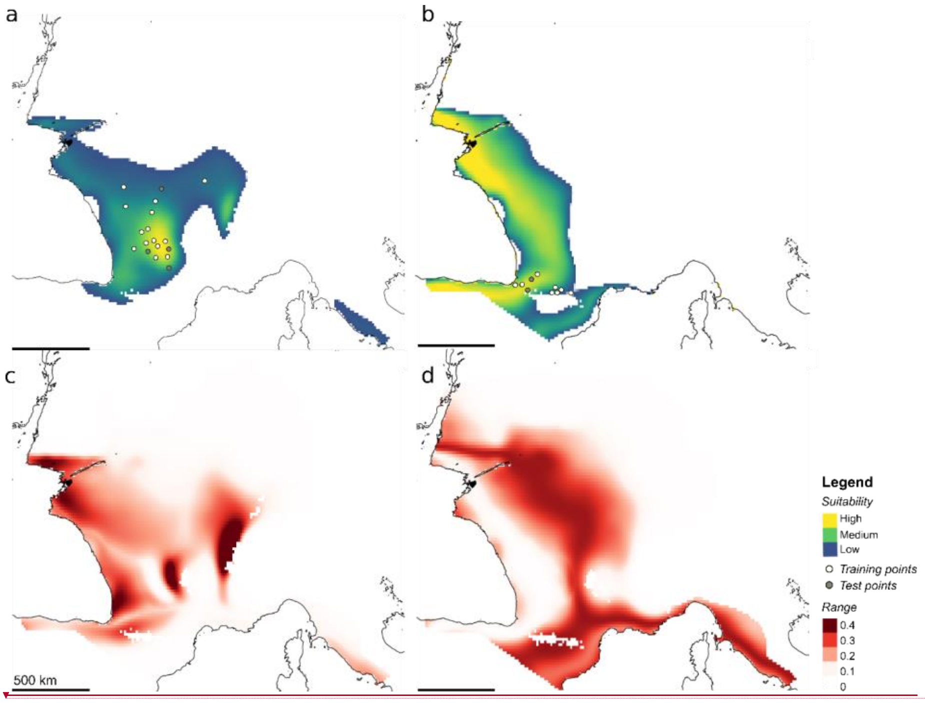

Figure 5: Geographic projections of Maxent-produced median niche estimations. **a.** Northern Middle Gravettian. **b.** Pyrenees Noaillian. **c.** Variability map for the northern Middle Gravettian prediction showing the suitability range of 10 models produced with the same data. **d**. Variability map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

3.2. Niche comparisons

The Pyrenees Noaillian and the northern Middle Gravettian niches are highly similar in geographic space (Figure 6). However, these niches are not identical and 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

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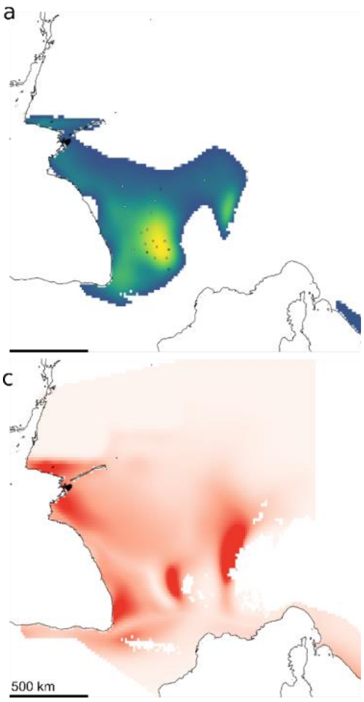

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statistical significance achieved if $p < 0.05$; Figure 6). With respect to environmental dimensions, our analysis shows that the niches overlap significantly (MVE overlap volume = 1.110, which corresponds to 97% of the Pyrenees Noaillian ellipsoid volume and 7% of the Northern Middle Gravettian ellipsoid volume; Figure 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 (Figure 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.

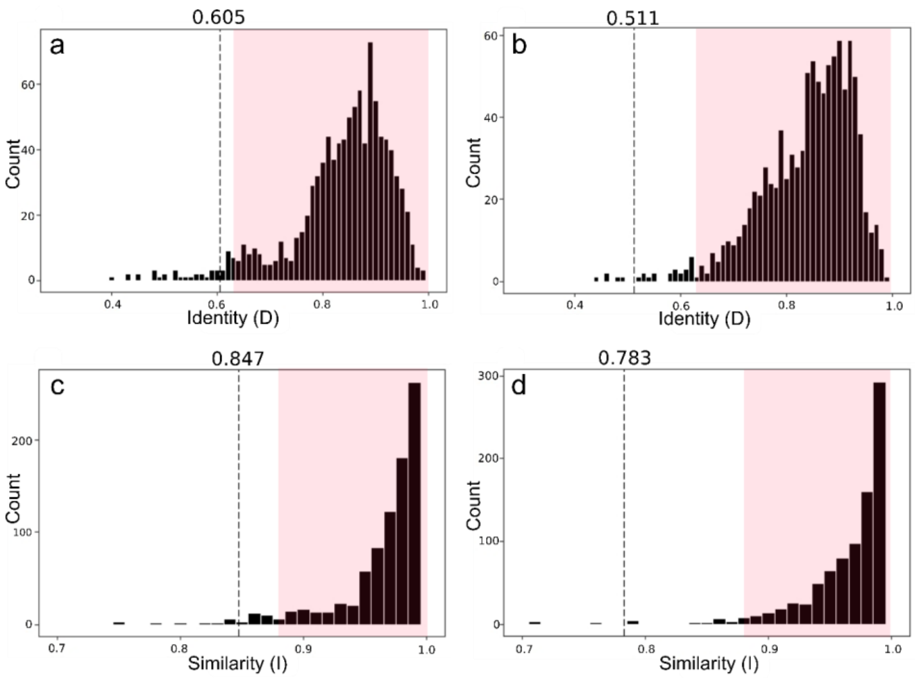

Figure 6: Background similarity and identity tests results for comparisons between the northern Middle Gravettian *vs.* the Pyrenees Noaillian (**a.** and **c.**), and the Pyrenees Noaillian *vs.* the northern Middle Gravettian (**b.** and **d.**). Dashed lines represent measures between the empirical 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

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 may be linked to the exploitation of a significantly expanded niche composed of colder, drier conditions that

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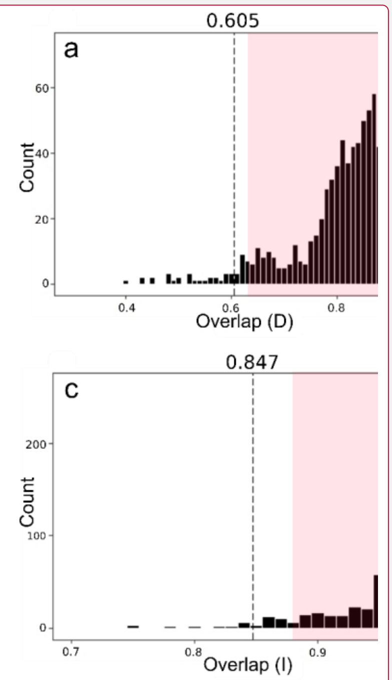

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correspond to more open landscapes and associated large mammal prey species. Available archaeological data support this hypothesis.

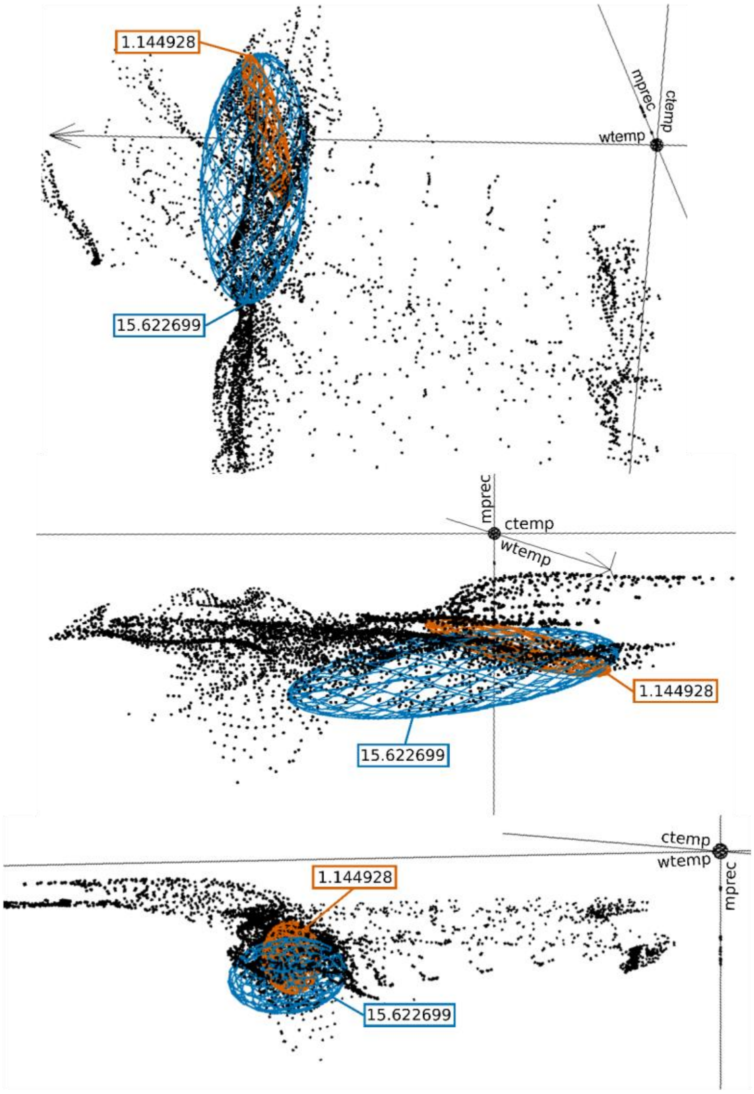

Figure 7: NicheA Minimum Volume Ellipsoids (MVE) for the northern Middle Gravettian (yellow) and the Pyrenees Noaillian (blue) in environmental space during GS 5 (black points). The environmental dimensions are temperature of the coldest month (ctemp), temperature of the warmest month (wtemp) and mean annual precipitation (mprec). The MVE volumes are displayed in the corresponding colored boxes.

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The Raysse method is a highly standardized reduction method 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 that were likely part of a composite and maintainable hunting weaponry toolkit, an adaptation 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 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 flint knapping debris and artifacts that appear to have been produced by apprentices or individuals who still 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 styles are more diverse: Gravette points, microgravettes, bi-truncated backed bladelets, and simple backed implements made from blades or bladelets (Klaric, 2003; Simonet, 2009a, 2011b, 2017). While these armature types need to be 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 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 armatures were integrated into weapon systems (e.g., axial points *vs.* lateral mounting) 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 the choice of medium to large prey species and in turn, the subsistence strategies and mobility patterns used to exploit them.

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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 may be linked to the exploitation of a significantly expanded niche composed of colder, drier conditions and thus more open landscapes and associated large mammal prey species. Available archaeological data from the archaeological record support this hypothesis.¶

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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 (*ibid.*, 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.

To the north, on the other hand, 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 to 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 on or near raw material sources, such as the site of La Picardie[7]. With respect to curation, Raysse burins (i.e. bladelet cores) from the Grotte du Renne often have double bladelet production platforms, 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: bladelets can be more twisted, they 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 represent a technological specialization directed at producing armatures for hunting reindeer. 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

[7] 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).

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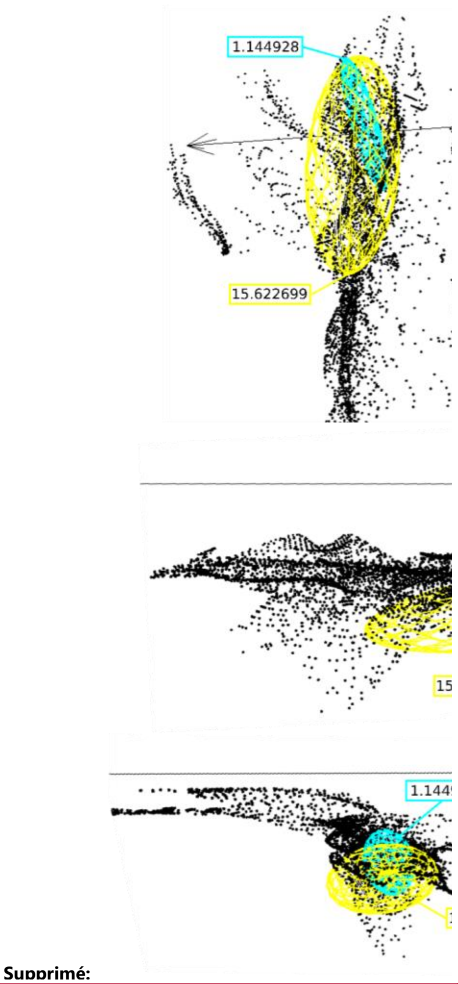

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method and Gravette points, two conceptually different *chaînes opératoires* (i.e. reduction sequences), and thus different kinds of composite hunting weapons. Whether these two types of armatures–la Picardie bladelets and Gravettes/microgravettes–were 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[8], is a subject that requires further study. At present, only the site of Callan represents specialized occupations or activities north of the Garonne River (Morala, 2011). It has a lithic assemblage 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 to the pattern observed during the same period in the Pyrenees. This pattern, though, may be accentuated 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 served as an ecological barrier that played a role in the territories exploited by Middle Gravettian hunter-gatherer populations. This barrier would have prevented the unconstrained diffusion of the Raysse method to the Pyrenees area. This idea is however challenged by the fact that this region is identified as suitable (Figure 5), although this suitability is very low. This contradiction, though, can be explained by the fact that the Landes' cold desert is more the result of a particular geographic and geomorphological context rather than specific climatic conditions (Bertran, pers. com.). In this case, the climatic variables used for this study

[8] We must bear in mind that occurrences of Picardie bladelets and Gravettes together are observed exclusively within cave or rockshelter deposits, where archaeological levels represent palimpsests of multiple occupations and were often subjected 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 full homogeneity of its archaeological assemblages, and the site of Les Jambes in Dordogne (Célérier, 1967), where slope depositional processes were predominant in the site's formation (Klaric, 2003, p. 222), thus raising doubts as to whether the distinct archaeological levels defined by Célérier are valid (A. Vignoles, on-going study).

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would not be sufficient to capture the particular conditions of a cold desert. Another scenario that can explain this low suitability area is that the barrier between these two regions might have been cultural. This hypothesis would explain the fact that the Pyrenees Noaillian's existing niche is more geographically extended that the distribution of sites used to reconstruct it, whereas the northern Middle Gravettian niche is more fitted to its occurrence data. In this case, the presence of another population in these northern suitable habitats would have prevented the Pyrenees populations from occupying their entire niche.

Another interesting 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. However, this hypothesis 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, this region is characterized by high variability depending on model parametrization, thereby indicating that the suitability estimates are less reliable in this area (Figure 5d). More niche predictions, comparisons, and tests that take into account Italian sites, as well as detailed examinations of their lithic industries that compare them to assemblages to the west would be necessary to further evaluate this hypothesis. To the west, the Cantabrian region is characterized by a high suitability 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 hypothesis 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 hypothesis should be tested further with both detailed studies of the archaeological assemblages and with new niche predictions that take into account these sites. It would also be 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.

Finally, the limits of our data and employed methodology needs to be kept in mind. Firstly, the Pyrenees Noaillian dataset is very small and comprised of only 10 occurrence points.

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Although evaluations indicate that the Pyrenees Noaillian Maxent niche estimation is robust, it is possible that comparisons with the northern Middle Gravettian niche, derived from 20 occurrences, could be biased with respect to environmental sampling. This may also be the case for the NicheA models, because the NicheA algorithm is an envelope model that has limited extrapolation capacities. Another potential limitation is that we used only three climatic predictors to define the environmental background. It is possible that other factors, such as the presence of cold deserts (Bertran *et al.*, 2013; Bosq *et al.*, 2018) and periglacial conditions, which were not considered in this study, could have influenced these hunter-gatherer populations, their settlement systems and cultural adaptations, and in turn the ecological niche that they exploited. Including these predictors would be a means to evaluate the results and hypotheses presented here.

5. Conclusions

This study evaluated whether two different Middle Gravettian cultural *faciès*, the Noaillian and the Rayssian, were associated with different ecological niches in the region of present-day France. To this aim, we compared, both in geographic and environmental spaces, the estimated ecological niche associated with the Pyrenees Noaillian to the niche reconstructed for the Middle Gravettian north of the Garonne River (including both Noaillian and Rayssian *faciès*).

Comparisons of the reconstructed niches for these two *faciès*, in both geographic and environmental dimensions, indicate that their respective niches were significantly different, despite their large overlap in environmental space, due to the fact that the northern Middle Gravettian niche was significantly broader than that of the Pyrenees Noaillian. This pattern strongly suggests that the appearance of the Raysse method is related to this significant expansion of the niche, meaning that this new method of producing bladelet armature components is linked to the exploitation of a broader range of ecological conditions. As opposed to what is observed in areas south of the Garonne River, the Raysse method appears to have been associated with 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 more appropriate within this context than backed blades and bladelet armatures (such as Gravettes), although this hypothesis would need further testing in the archaeological record. Furthermore, the Raysse

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method would have been advantageous in such contexts because it would have been more easily maintainable and more adapted to hunting activities organized within territories where access to raw material resources was less predictable or available. Conversely, the Pyrenees Noaillian’s armature diversity may reflect less specialized hunting practices within a smaller territory. In this context, 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, at some point in time, technological traditions homogenization between the Pyrenees and regions to the north. The nature of this barrier (i.e. environmental and/or cultural) should be further evaluated by incorporating other potentially pertinent variables (distribution of cold deserts, etc.) in future ecological niche modeling analyses that target archaeological populations. Furthermore, continued investigations centered on identifying Middle Gravettian sites and the typo-technological attributes of their archeological assemblages are necessary. In turn, these niche modeling results will provide important details to continued research that addresses chronology, settlement and subsistence strategies, lithic raw material exploitation, lithic and bone technologies, and site function of the Middle Gravettian archaeological record.

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Acknowledgements

We thank A. Townsend Peterson for hosting a collaborative trip to the University of Kansas’ Biodiversity Institute. The climate simulations were run on the Mercure supercomputer maintained by the Commissariat à l’Energie Atomique’s Très Grand Centre de Calculs. Finally, we thank A. Townsend Peterson, Mathieu Bosq and Pascal Bertran for their input during the writing of the article.

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Funding

This research was financed by the LabEx project IMPACT (W. Banks, dir.), and the Nouvelle-Aquitaine region project “GravettoNiches” (W. Banks, dir.). The collaborative trip to the University of Kansas’ Biodiversity Institute was co-funded by the University of Bordeaux’s “Sciences et Environnements” Doctoral School.

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Data availability statement

Codes used in R to perform the steps described in sections 2.3.2 and 2.3.3 and models calibration results are available at https://osf.io/35pb4/?view_only=4f84e08e6ba84754b2090e349bc2ebf4.

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