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

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17  
18 **Abstract**

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

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

44

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

47

## 48 1 Introduction

49           The Gravettian is an Upper Paleolithic techno-complex (*sensu* Clarke, 1968) that has  
50 been the subject of extensive research since its recognition (e.g. Klima, 1976; Roebroeks *et al.*,  
51 1999; Rigaud, 2008, 2009; de las Heras *et al.*, 2013; Otte, 2013; Wojtal *et al.*, 2015). Spanning  
52 *ca.* 34,000–26,000 calibrated years before present (y. cal. BP), its main unifying characteristics  
53 are Gravette-style backed blades and bladelets (Pesesse, 2013), diagnostic graphic expressions  
54 (Féreglio *et al.*, 2011), as well as a high frequency of burials (Henry-Gambier, 2008) compared  
55 to preceding and subsequent archaeological cultures. These common characteristics are  
56 observed in sites across Europe, from Portugal to the Don Valley in western Russia (Otte, 2013).  
57 However, the term “Gravettian” groups together a wide variety of cultural traditions, especially  
58 concerning lithic and osseous technology (de la Peña-Alonso, 2009; Pesesse, 2013; Noiret,  
59 2013; Goutas, 2013a). This diversity is challenging to explain since it is characterized by  
60 disparate data, many of which were obtained with non-modern excavation methods decades  
61 ago or differing analytical approaches (de la Peña-Alonso, 2011; Pesesse, 2017). Moreover,  
62 sites that date to the same chronological interval but that lack typical Gravettian features (i.e.  
63 Gravette-style points) serve to challenge the definition of this techno-complex (e.g. Morala,  
64 2011; Klaric *et al.*, 2011, 2018). In Western Europe, various hypotheses have been proposed to  
65 explain this diversity, such as differences in site activities (e.g. Laville & Rigaud, 1973; Rigaud,  
66 1988), the nature of our archaeological definitions (e.g. Touzé, 2013; Pesesse, 2017), regionally  
67 differentiated populations that did not share the same technological knowledge or traditions  
68 (e.g. Klaric *et al.*, 2009), or differential environmental influences (e.g. David, 1985; Djindjian  
69 *et al.*, 1999). Efforts to identify and evaluate the mechanisms—defined as “a constellation of  
70 factors and components that through the process of their interaction with one another stimulates  
71 the trajectory of a system” (d’Errico & Banks, 2013, p. 374)—that influenced these cultural  
72 traditions can aid in assessing these various hypotheses.

## 73 **1.1. The French Middle Gravettian**

74 In France, the Middle Gravettian occurs between *ca.* 32-28.5 ky cal. BP and is defined by  
75 two *faciès*, termed the “Noaillian” and the “Rayssian” that are characterized principally on the  
76 basis of their lithic industries (Touzé, 2013). The term “*faciès*” (in French) is used to describe  
77 an archaeological entity according to “the nature of the considered remains and the method  
78 employed to study them” (Touzé, 2013, p. 397). This neutral term is especially useful in the  
79 case of the Middle Gravettian, since the two *faciès* are not defined equally. The Noaillian is a  
80 typological *faciès*, defined solely by the presence of Noailles burins (Bardon & Bouyssonies,  
81 1903; Tixier, 1958) and sometimes by the presence of bone or antler points called “Isturitz  
82 points”, although this point type’s precise chrono-cultural status remains uncertain (Goutas,  
83 2013b). On the other hand, the Rayssian is a typo-technological *faciès*, defined by a reduction  
84 method aimed at removing, from Raysse burins, bladelets that were used as implements on  
85 projectiles (Figure 1, Movius & David, 1970; Klaric *et al.*, 2002; Lucas, 2002; Pottier, 2006;  
86 Klaric, 2017). Furthermore, Rayssian bladelet and blade reduction sequences show strong  
87 conceptual parallels and technical similarities (Klaric, 2003; Klaric, 2008).

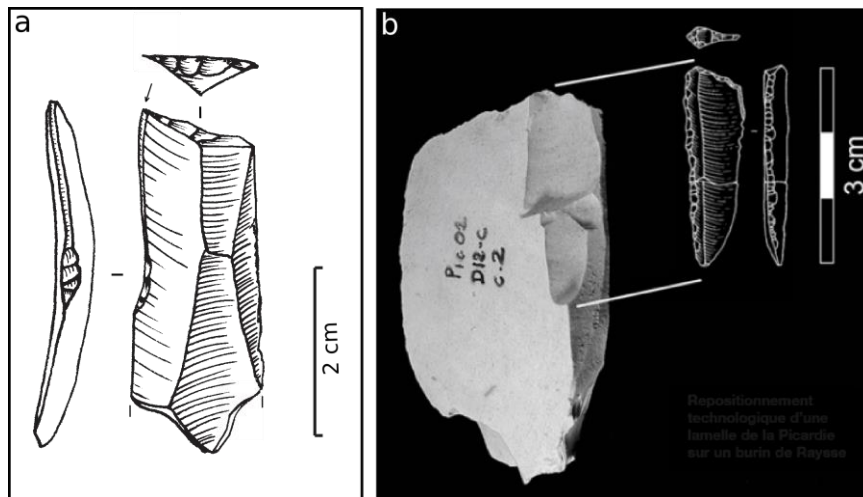
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93  
 94 **Figure 1.** Diagnostic Middle Gravettian artifact types. **a.** Noailles burin from Fourneau du Diable,  
 95 Dordogne, France (drawing: A.Vignoles). **b.** Technological position of a “Picardie” bladelet on a Raysse  
 96 burin-core from La Picardie, Indre-et-Loire, France (from Klaric, 2008)

97         The chronological relationship between the Noaillian and the Rayssian has yet to be  
 98 determined with precision. This is due to the fact that very few contextually reliable <sup>14</sup>C ages  
 99 are associated with these two *faciès*, and for regions north of the Garonne River the low number  
 100 of available ages renders any chronological comparison between the two phases uninformative  
 101 at present (Banks *et al.*, 2019). This situation is complicated by the fact that Noailles burins and  
 102 the Raysse method are frequently found together within the same archaeological layer in the  
 103 region of overlap. Past and on-going studies suggest that, at many sites, this association is not  
 104 culturally meaningful due to imprecise excavation methods and/or disturbed stratigraphic  
 105 contexts (e.g. Klaric, 2003, 2007; Vignoles *et al.*, 2019). However, in a few stratified contexts,  
 106 the development of the Raysse method is always stratigraphically younger than the Noaillian  
 107 (e.g., Abri Pataud and Flageolet I sites; David, 1985; Rigaud, 1982; Klaric, 2003). An exception  
 108 to this statement is found at Les Jambes, a site where Noailles burins are described as being  
 109 stratigraphically *above* the Raysse burins (Célérier, 1967). This configuration, though, remains  
 110 to be verified. First, the two levels identified by Célérier have been described as part of a slope  
 111 deposit which raises doubts as to the integrity of the levels. Moreover, stratigraphic projections  
 112 of artifacts show that the levels defined by Célérier correspond to a single archaeological layer.

113 Finally, an ongoing reexamination (conducted by A.V) of the site's assemblage demonstrates  
114 that most of the "Noailles burins" do not correspond to the classic typological definition. In  
115 fact, only one artifact can be considered a typical Noailles burin, while all the others are highly  
116 atypical. Technological characterization of the blade/bladelet reduction sequences may provide  
117 new data with which to discuss the presence of Gravette points—a class of tool traditionally  
118 associated with the Noaillian rather than the Rayssian—at Les Jambes.

119 Numerous hypotheses have been proposed to explain the co-occurrence of Noaillian  
120 and Rayssian materials in the same archaeological level, such as a gradual replacement of the  
121 Noaillian by the Rayssian (David, 1985; Pottier, 2005), differing site activities (Laville &  
122 Rigaud, 1973; Rigaud, 2008, 2011), the use of different typo-technological traditions within a  
123 broad regional population (Touzé, 2013) or the result of post-depositional mixing or the  
124 inability of old excavation methods to differentiate between discrete occupations (Klaric, 2003,  
125 2007; Vignoles *et al.*, 2019). Unfortunately, taphonomic evaluations of individual sites are not  
126 yet sufficiently numerous to evaluate these hypotheses adequately (Klaric, 2003, 2007; Pottier,  
127 2005; Agsous, 2008; Michel, 2010; Gottardi, 2011).

128 With respect to geography, these two archaeological traditions have only partially  
129 overlapping distributions (Figure 2). The Noaillian is observed in regions south of the Loire  
130 River, as well as a very isolated presence in the Vosges region, with extensions into Cantabrian  
131 Spain and the Italian Peninsula. The Rayssian is restricted to a smaller geographic area situated  
132 between the Garonne River and the southern portion of the Paris Basin, with extensions into  
133 Burgundy and Brittany (Klaric, 2003, 2017; Touzé, 2013). Despite mentions of the presence of  
134 Raysse burins at the sites of La Carane-3, Isturitz and Tuto de Camalhot by David (1985), the  
135 presence of the Raysse method south of the Garonne River has not been unequivocally  
136 demonstrated: none of these artifacts have been described or pictured, nor do recent  
137 technological studies (e.g. Simonet, 2009a) mention them. The demonstration of the Raysse

138 method relies on precise technical criteria and more specifically on the identification of the  
139 bladelet component associated with Raysse burin-cores, and David (1985) did not use such  
140 criteria to describe the Late Noaillian (i.e. Rayssian) in these southern contexts. It is also  
141 important to point out that look-alike artifacts (*faux-amis*) have been described at Brassempouy  
142 (Klaric, 2006). The examples reported by David could therefore be misleading in the same way.

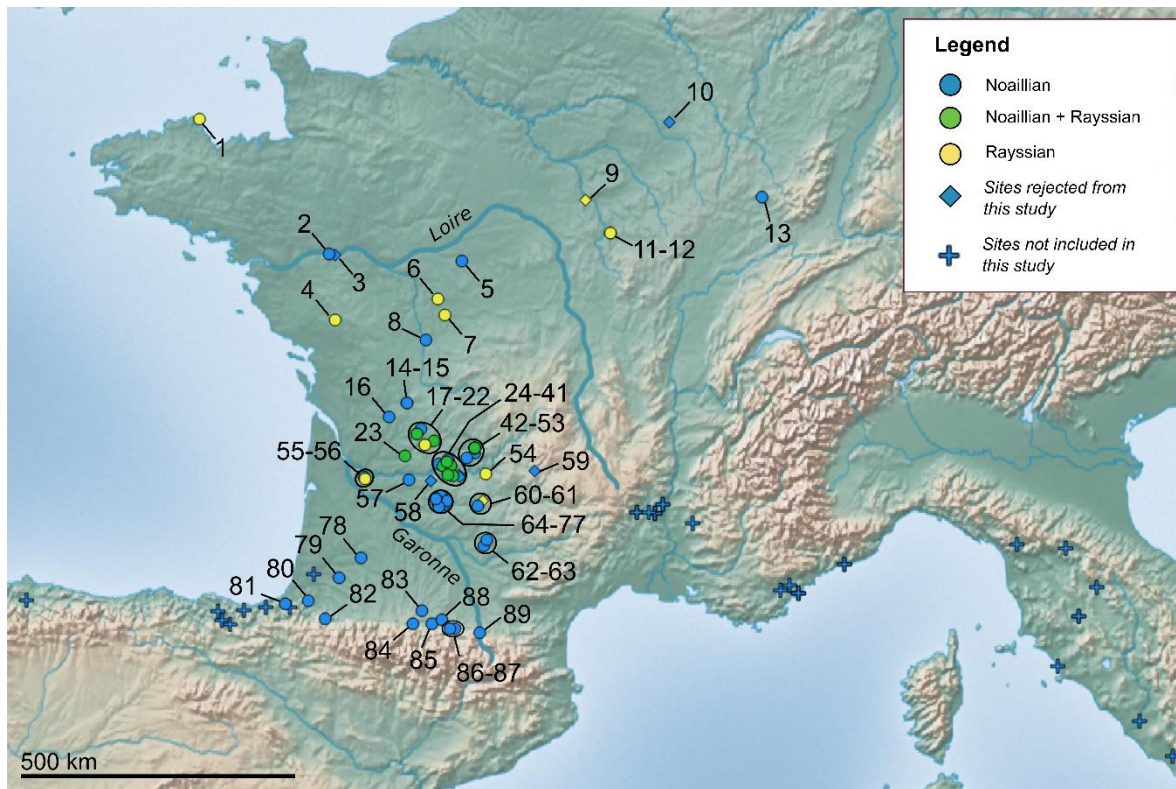
143         The absence of the Raysse method south of the Garonne River suggests that this valley  
144 may have played a role in the separation of the two different technological trajectories. This is  
145 also paired with the fact that the Noaillian in the Pyrenees appears to have lasted as long as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

## 150         **1.2. Research question and approach**

151         Here, we test the hypothesis that the typo-technological differences observed on either side  
152 of the Garonne River valley during the Middle Gravettian reflect the exploitation of different  
153 environmental conditions via different technological (i.e. cultural) adaptations. The application  
154 of Ecological Niche Modeling (ENM) methods to the archaeological record is one means with  
155 which to conduct such a test (Banks, 2017; d’Errico & Banks, 2013). ENM (the terminology  
156 employed in this study, cf. Peterson & Soberón, 2012; Warren, 2012) provides a means for  
157 estimating the ecological niches of past hunter-gatherer populations, employing archaeological  
158 sites as occurrence data and environmental variables derived from high-resolution  
159 paleoclimatic simulations. These data are then used by predictive modeling algorithms to  
160 identify sets of environmental parameters associated with known archaeological sites and create  
161 an estimation of the presence of suitable environmental conditions (i.e. the ecological niche)  
162 across the study area. Niche estimations can be compared with one another in order to



163 characterize and evaluate potential differences between niches (e.g. Warren *et al.*, 2008). The  
164 use of these tools has been demonstrated to be a valuable approach for assessing culture-  
165 environment relationships of past hunter-gatherer populations, both synchronically and  
166 diachronically (e.g. Banks *et al.*, 2008, 2009, 2011, 2013; d’Errico *et al.*, 2017). Research  
167 focused on material culture variability observed in the archaeological record is often polarized  
168 between two sets of explanations, cultural *vs.* functional, mirroring the well-known Bordes-  
169 Binford debate concerning Mousterian lithic industries. An advantage of ENM is that it allows  
170 one to approach evaluations of such variability from a different angle by taking into account  
171 the ecological niches exploited by archaeological hunter-gatherer populations. For example,  
172 comparisons of the ecological niches associated with two archaeological cultures or lithic  
173 industries allow one to evaluate to what extent cultural (i.e. technological) differences have an  
174 ecological basis. In such scenario, one would expect their ecological niches to differ from one  
175 another significantly due to the fact that the different typo-techno complexes represent  
176 adaptations to distinct ecological niches more than purely social factors. If their niches are  
177 highly similar, one could interpret technological variability to be more the result of internal  
178 cultural dynamics that led to the development of two cultural trajectories. As stated earlier,  
179 multiple hypotheses have been proposed to explain the typo-technological variability observed  
180 within the French Middle Gravettian and no consensus has been reached. The objective of this  
181 study is to provide new data on the ecological niches of these hunter-gatherer populations in  
182 order to evaluate to what extent ecological factors may have played a role in the observed  
183 material culture variability.



184  
 185 **Figure 2.** Sites where Noailles burins and/or Raysse burins have been found (after Touzé, 2013; Klaric,  
 186 2017; the present study). Sites are labeled according to their number presented in Table 1 (cf. 2.2.1).  
 187 Topographic background: <http://www.naturalearthdata.com>

188

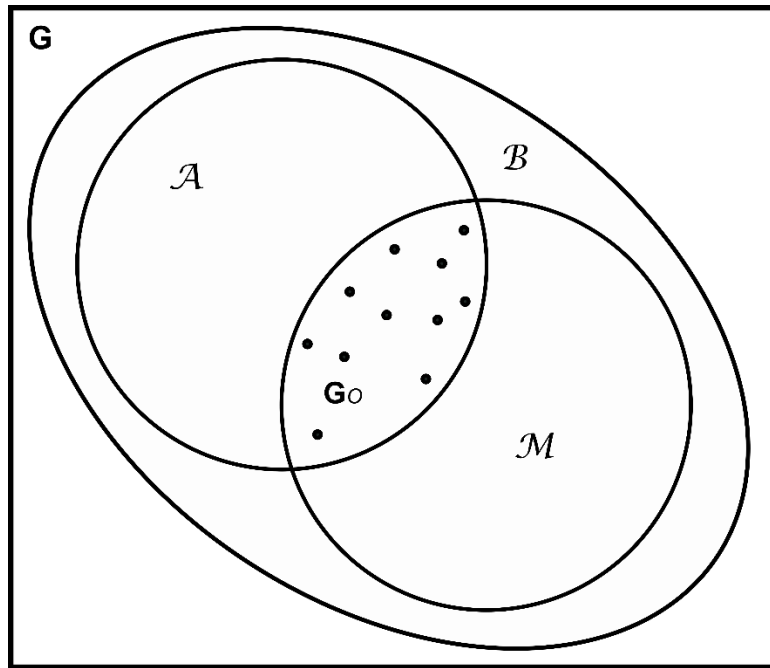
## 189 2. Materials and Methods

### 190 2.1. Conceptual framework of ecological niche modelling

191 The conceptual framework of ENM is based on Hutchinson's (1957) definition of the  
 192 fundamental niche ( $N_F$ ): an  $n$ -dimensional hypervolume whose dimensions are the non-  
 193 interactive environmental variables (i.e. scenopoetic variables) necessary for a species to  
 194 maintain populations indefinitely without immigrational subsidy. Following Peterson and  
 195 Soberón (2005, 2012), we consider the Biotic-Abiotic-Mobility framework (**BAM**, Figure 3) to  
 196 describe factors constraining geographic distribution of species. The projection of  $N_F$  in  
 197 geographic space ( $G$ ), i.e. the geographic localities corresponding to  $N_F$ , identifies areas with  
 198 conditions favorable to the species ( $A$ ). However, the geographic distribution of a species can

199 be constrained by at least two other types of factors: biotic interactions (**B**), i.e. the species'  
200 positive or negative interactions with other species or resources that are present, and the areas  
201 that have been physically accessible to the species over a relevant period of time (**M**). The  
202 intersection of **A** and **B** is the potential distributional area ( $G_P$ ), which is the geographic  
203 expression of the realized niche ( $N_R$ ) defined by Hutchinson (1957). In this study, we focus on  
204  $N_F$ , defined solely on the basis of non-interactive variables, following the Eltonian-noise  
205 hypothesis, which argues that biotic interactions may often be manifested at fine spatial  
206 resolutions and thus may not have a significant or limiting effect on a species' distribution at  
207 broad geographic scales (Soberón, 2007). Finally, the intersection of  $G_P$  with **M** defines the  
208 occupied distributional area ( $G_O$ ). In environmental space, the intersection between  $N_F$  and the  
209 environments associated with **M** define the existing fundamental niche ( $N_F^*$ ), which is the  
210 portion of the fundamental niche that is actually observable in nature (Peterson & Soberón,  
211 2012).

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



218  
 219 **Figure 3.** BAM diagram representing the factors that constrain the geographic distribution of a species  
 220 at broad geographic scales, if the Eltonian-noise hypothesis holds true (after Soberón & Peterson, 2005,  
 221 2012; modified). Circles represent the different factors and black dots represent the observed distribution  
 222 of the species. **G**: geographic space; **A**: non-interactive variables; **B**: biotic interactions; **M**: areas  
 223 accessible to the species; **G<sub>o</sub>**: occupied distributional area.

224

## 225 **2.2. Data**

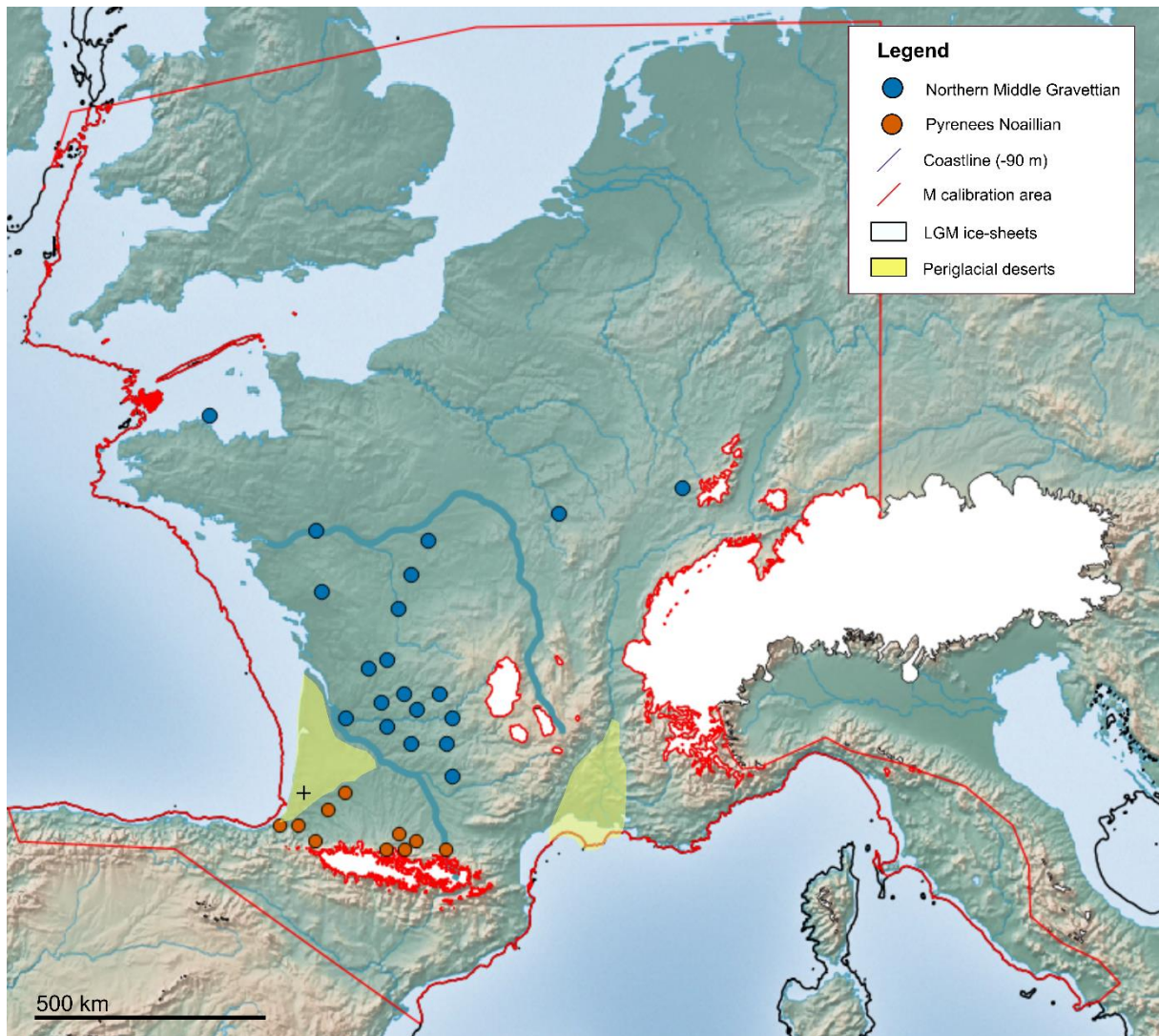
### 226 **2.2.1. Archaeological data**

227 Occurrence data consist of the geographic coordinates of archaeological sites where  
 228 Noaillian and/or Rayssian material culture assemblages have been identified (Figure 4). These  
 229 data were assembled through a critical examination of the literature, although one must keep in  
 230 mind that this approach has certain limitations. First, most sites were excavated and studied in  
 231 the late 19<sup>th</sup> and first half of the 20<sup>th</sup> century, sometimes in an expeditious manner. Due to the  
 232 fact that excavated sediments were rarely sieved and often only large, diagnostic tools were  
 233 kept, many assemblages are biased and do not necessarily contain artifacts that allow the two  
 234 typo-technological *faciès* to be reliably recognized, since their diagnostic artifacts are of small

235 size (e.g., Raysse and Picardie bladelets, some Noailles burins, Noailles burins spalls), and/or  
236 correspond to flint knapping by-products (e.g., Raysse bladelets, blades with oblique lateralized  
237 faceted platforms). As a result, there are numerous sites where one or both of these Middle  
238 Gravettian *faciès* was not initially recognized (e.g., Fourneau du Diable, Laussel or Combe-  
239 Saunière I; Klaric, 2017; Vignoles *et al.*, 2019) and this is likely the case for many others.  
240 Therefore, the corpus of sites associated with these two archaeological *faciès* should be  
241 considered incomplete at present. Furthermore, many assemblages, even those that were rather  
242 well-excavated (piece-plotted artefacts, sieved archaeological sediments, collection of  
243 unretouched artifacts) often have not been subjected to recent contextual examinations or typo-  
244 technological re-evaluations (e.g., Les Jambes, Le Facteur). This is especially a problem for the  
245 bibliographic identification of the Raysse method. Although the Raysse burin type was first  
246 described in the 1950s (Pradel, 1953; Couchard & de Sonneville-Bordes, 1960; Movius &  
247 David, 1970), its function as a core for producing standardized projectile point implements was  
248 only demonstrated in the early 2000s (Klaric *et al.*, 2002; Lucas, 2002). It is therefore necessary  
249 to reconsider, from a technological standpoint, all previously identified Raysse burins and to  
250 identify the presence of the associated bladelet component in order to avoid attributing  
251 archaeological levels to this *faciès* on the basis of look-alike (*faux-amis*) artifacts (Klaric, 2003,  
252 2006).

253 Another problem is the unequal definition of the Noaillian (i.e. sole presence of Noailles  
254 burins in an assemblage) and the Rayssian (Touzé, 2013). The latter's technical system is  
255 relatively well-described across its area of expression (Lucas, 2000, 2002; Klaric, 2003, 2017;  
256 Pottier, 2005, 2006; Guillermin, 2006; Touzé, 2011, 2013; Gottardi, 2011; Sarrazin, 2017,  
257 2018). Variability in the use of the Raysse method has been attributed mainly to blank selection,  
258 the availability of suitable lithic raw materials, levels of technological expertise and  
259 contingencies of the reduction sequence (Klaric *et al.*, 2009; Klaric, 2017, 2018). To the

260 contrary, the technical system associated with Noailles burins has only been the subject of  
261 isolated studies in the Landes (e.g. Klaric, 2003; Simonet, 2009a, 2011a; Lacarrière *et al.*,  
262 2011), the Pyrenees piedmont and plateau (e.g. Foucher, 2004; Simonet, 2009a), and to lesser  
263 extents the Perigord region (Lucas, 2000; Pottier, 2005) and the southern Paris Basin (Kildea  
264 & Lang, 2011), thus rendering evaluations of its homogeneity difficult. Typo-technological  
265 studies conducted on assemblages from Cantabrian Spain (e.g. de la Peña-Alonso, 2011), the  
266 French Mediterranean coast (e.g. Onoratini, 1982; Santaniello, 2016), and the Italian peninsula  
267 (e.g. Onoratini, 1982; Aranguren *et al.*, 2006, 2015; Simonet, 2010; Santaniello, 2016;  
268 Santaniello & Grimaldi, 2019) have employed different methodological approaches for  
269 characterizing reduction sequences (i.e. *chaînes opératoires*) and typologies, with a few  
270 exceptions (e.g. Simonet, 2010), thus making comparisons to sites studied via the methods  
271 traditionally used in France difficult. An additional obstacle is related to this record's  
272 chronology. Noailles burins have been recovered from Cantabrian contexts that are  
273 contemporaneous with the Late Aurignacian in southwestern France, as well as contexts that  
274 extend into the Solutrean (de la Peña-Alonso, 2011, p. 681). Noailles burin contexts in Italy are  
275 also interpreted as being younger than those in France (Touzé, 2013), but the majority of their  
276 associated radiocarbon ages were produced decades ago (non-AMS) and evaluations of their  
277 archaeological association are lacking, thus rendering any comparison to the French  
278 archaeological record unreliable at present.



279  
 280 **Figure 4.** Noaillian and Raysian site locations used for calibration and the study's defined accessible  
 281 area (**M**) hypothesis. Topographic background: <http://www.natureearthdata.com>; Coastlines: Siddall *et*  
 282 *al.*, 2003; Glacier extent: Ehlers & Gibbard, 2004; Periglacial cold deserts: Bertran *et al.*, 2013; Bosq *et*  
 283 *al.*, 2018

284

285 Taking into account these limitations, we constrain our analysis to the comparison of two  
 286 adjacent regions that are thought to represent coherent territories during the Middle Gravettian:  
 287 1) the Pyrenees piedmont and plateau, based on assemblages that are regionally coherent with  
 288 respect of lithic typo-technology (i.e. contexts that contain Noailles burins and in which the  
 289 Raysse method is absent) and raw material circulation for the entirety of the Middle Gravettian  
 290 (Foucher *et al.*, 2008; Foucher, 2013; Simonet, 2009a, 2017; Banks *et al.*, 2019), and 2) the

291 area constrained along its southern margin by the Garonne River Valley and by the most  
292 northerly sites where the “Raysse method” has been observed (Klaric, 2017). The latter territory  
293 is characterized by both the Noaillian and the Rayssian *faciès*, and the lack of precision, at  
294 present, concerning their chronological relationship required that we group them together,  
295 mirroring the approach employed by Banks *et al.* (2019).

296 In an effort to retain only sites for which a reliable techno-typological attribution could be  
297 made, published studies were carefully evaluated with respect to the pertinence of the data they  
298 contained (see Appendix). A source was considered pertinent if it provided precise counts of  
299 tool types based on the most recent typo-technological definitions (e.g. for the “Noailles burin”  
300 type: Bardon & Bouyssonies, 1903; Tixier, 1958; for “Picardie bladelet” type and “Raysse  
301 burin-core”: Klaric *et al.*, 2002; Klaric, 2003; Klaric, 2017), preferably supplemented with  
302 artifact drawings or photos. We also included personal observations made during the course of  
303 on-going and yet-to-be-published studies (L. Klaric and A. Vignoles). We, thus, did not retain  
304 sites for which one or both *faciès* were only suspected to be present in order to avoid potentially  
305 aberrant attributions based on look-alike artifacts. For example, “Raysse burins” reported in  
306 Brassempouy or Le Gratadis have been shown to not be actual Raysse burin-cores aimed at the  
307 production of La Picardie bladelets (Klaric, 2003, 2006). Bearing this in mind, we did not retain  
308 sites where Raysse burins were only mentioned with no demonstration of the presence of the  
309 Raysse method (e.g. Abri André Ragout; David, 1985). Also, sites where Raysse burins are  
310 depicted in published drawings (Klaric, 2003) but that have not been confirmed by us via direct  
311 observation and where the presence of the associated bladelet component has not yet been  
312 evaluated, such as the site of Roc de Gavaudun in Lot-et-Garonne or Lespoux shelter in Gironde  
313 (Monméjean *et al.*, 1964; Krtolitza & Lenoir, 1998), were not included. Finally, we also  
314 eliminated sites for which the presence of Raysse burin cores is not consensual, such as  
315 Chamvres in Yonne (Klaric, 2003 vs. Sarrazin, 2018). In the same vein, we did not retain sites



316 where reported “Noailles burins” have been demonstrated to be look-alike artifacts, such as the  
317 site of Les Jambes (ongoing examination by A.V.). Moreover, sites where Noailles burins are  
318 all atypical, such as Peuille in Lot-et-Garonne (Morala, 1984), or sites where only one or two  
319 Noailles burins are reported and their presence is not supported by published drawings, such as  
320 La Verpillière I cave in Saône-et-Loire (Floss *et al.*, 2013), were eliminated from consideration.  
321 In the end, we retained 74 sites for our analysis. North of the Garonne River, there are 9  
322 Rayssian sites, 40 Noaillian sites, as well as 13 additional sites that yield both *faciès*. In the  
323 Pyrenees piedmont and plateau, 12 Noaillian sites were retained (Figure 4; Table 1).  
324 **Table 1.** Sites retained or rejected based on a critical review of the literature, along with their geographic  
325 coordinates and references. A site was assigned to a specific data set or rejected based on criteria detailed  
326 in the Appendix. Geographic coordinates correspond to the commune (i.e. town administrative territory)  
327 in which the site is localized. Although these coordinates do not necessarily correspond to the site itself,  
328 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	<i>rejected</i>	Allard & Gruet, 1976; Gruet, 1984; Hinguant & 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 & Lang, 2011, 2013
6	La Picardie	0,93	46,86	absence	presence	Northern Middle Gravettian	Klaric, 2003; Klaric <i>et al.</i> , 2011; Klaric <i>et al.</i> , 2018
7	Abri Charbonnier	1,04	46,68	absence	presence	Northern Middle Gravettian	Aubry <i>et al.</i> , 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	<i>rejected</i>	Klaric, 2003, 2013; Sarrazin, 2018
10	Grotte de la Verpillière I	4,73	48,81	insufficient	absence	<i>rejected</i>	Floss <i>et al.</i> , 2013
11	Grotte du Renne	3,76	47,60	absence	presence	Northern Middle Gravettian	Klaric, 2003

**Table 1 - continued**

N°	Site	Lat. (N)	Long. (E)	Noailles burins	Raysse method	Data set	References
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 & Schmider, 1972; David, 1985
19	Gisement de la Chèvre	0,59	45,32	presence	insufficient	Northern Middle Gravettian	David, 1985; Arambourou & 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 <i>et al.</i> , 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	<i>rejected</i>	de Sonneville-Bordes, 1960; David, 1985
25	Abri de Fongal	1,08	44,99	insufficient	insufficient	<i>rejected</i>	de Sonneville-Bordes, 1960, p.97; David, 1985
26	Abri des Merveilles	1,11	45,00	suspected	absence	<i>rejected</i>	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

**Table 1 - continued**

N°	Site	Lat. (N)	Long. (E)	Noailles burins	Raysse method	Data set	References
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 (dir.), 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	Northern Middle Gravettian	Klaric, 2017; Caux <i>in</i> Boudadi-Maligne, 2012
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	<i>rejected</i>	Tixier, 1958; David, 1985
41	Grotte de Péchialet	1,29	44,82	suspected	absence	<i>rejected</i>	David, 1985; Breuil, 1927
42	Grotte du Bos-del-Ser	1,54	45,16	insufficient	insufficient	<i>rejected</i>	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 Thévenard	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.

**Table 1 - continued**

N°	Site	Lat. (N)	Long. (E)	Noailles burins	Raysse method	Data set	References
56	Abri Lespaux	-0,29	44,82	presence	suspected	Northern Middle Gravettian	David, 1985; Krtoliza & Lenoir, 1998
57	Le Caillou	0,45	44,78	presence	absence	Northern Middle Gravettian	Boyer <i>et al.</i> , 1984
58	Roc de Combe-Capelle	0,82	44,77	insufficient	absence	<i>rejected</i>	de Sonneville-Bordes, 1960; David, 1985
59	Grotte du Roc de Vézac	2,52	44,89	insufficient	absence	<i>rejected</i>	Rigaud, 1982, p.262; Aujoulat <i>in</i> Leroi-Gourhan, 1984
60	Abri des Peyrugues	1,67	44,54	absence	insufficient	<i>rejected</i>	Guillermin, 2011
61	Abri de la Bergerie	1,58	44,48	presence	absence	Northern Middle Gravettian	Clottes <i>et al.</i> , 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 <i>et al.</i> , 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	<i>rejected</i>	Le Tensorer, 1974, p.467
72	Peutille	0,97	44,58	suspected	absence	<i>rejected</i>	Morala, 1984
73	Termo-Pialat	0,82	44,77	suspected	absence	<i>rejected</i>	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 <i>et al.</i> , 1964; Le Tensorer, 1981; David, 1985
78	Hin-de-Diou	-0,33	43,86	presence	absence	Pyrenees Noaillian	Briand <i>et al.</i> , 2010
79	Brassempouy	-0,69	43,63	presence	absence	Pyrenees Noaillian	Klaric, 2003; Foucher <i>et al.</i> , 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 <i>et al.</i> , 2008; Simonet, 2009a; Lacarrière <i>et al.</i> , 2011
81	Lézia	-1,58	43,31	presence	absence	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008; Simonet, 2009a
82	Gatzarria	-0,92	43,14	presence	absence	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008; Simonet, 2009a
83	Grotte des Rideaux	0,67	43,23	presence	absence	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008; Simonet, 2009a
84	Gargas	0,52	43,07	presence	absence	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008, 2012
85	Bois de Touaa	0,83	43,07	presence	absence	Pyrenees Noaillian	Foucher <i>et al.</i> , 2008; Clottes, 1985, p. 346
86	Tuto de Camalhot	1,13	43,01	presence	absence	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008; Simonet, 2009a
87	Grotte d'Enlène	1,20	43,02	presence	absence	Pyrenees Noaillian	Foucher <i>et al.</i> , 2008; Simonet, 2009a
88	Tarté	0,99	43,12	presence	absence	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008; Simonet, 2009a
89	La Carane-3	1,61	42,96	presence	insufficient	Pyrenees Noaillian	David, 1985; Foucher <i>et al.</i> , 2008; Simonet, 2009a

329

### 330 2.2.2. Environmental predictors

331 In order to employ the appropriate environmental data, it is paramount to determine  
332 accurately the precise chronology of the target archaeological culture so that it can be correlated  
333 to the appropriate climatic event or events (Banks, 2015; Banks *et al.*, 2019). Based on the  
334 results presented by Banks *et al.*, (2019), the Middle Gravettian begins between the latter part  
335 of Greenland Interstadial 5.2 (GI 5.2) and Greenland Stadial 5.2 (GS 5.2) and ends between the  
336 latter part of GS 5.1 and GI 4. It was thus present during GS 5.2 and 5.1, during which occurred  
337 Heinrich Event 3 (HE3), as well as GI 5.1. Considering the lack of chronological resolution  
338 facing this portion of the Upper Paleolithic, two important assumptions were made for the  
339 choice of the best possible environmental data. First, since most Middle Gravettian occupations  
340 have not been dated or are not associated with reliable dates, we must assume that all sites date

341 to some point between *ca.* 32 and 28.5 ky cal. BP (after Banks *et al.*, 2019). Second, the  
342 chronological resolution of individual radiocarbon measurements does not allow us to  
343 determine whether a specific dated occupation is associated with a specific Interstadial or  
344 Stadial (GI 5.1 or GS 5.1 for example). This limitation makes it impossible to create separate  
345 occurrence data sets such that correspond to specific Stadial or Interstadial events. Therefore,  
346 we choose environmental data such that correspond to stadial conditions since those were  
347 present during the majority of the period concerned by this study (*ca.* 2.5 ky for GS 5.2 and 5.1  
348 combined *vs.* *ca.* 0.5 ky for GI 5.1).

349 We employed as environmental background climatic variables derived from a high-  
350 resolution paleoclimatic simulation obtained with the Atmospheric Global Circulation Model  
351 (AGCM) LMDZ5A (Hourdin *et al.*, 2013). It was run with a zoomed grid permitting a spatial  
352 resolution of *ca.* 50 km over Europe, following Sima *et al.* (2009, 2013). We used the same  
353 coastlines and ice-sheet configuration as Sima *et al.* (2009, 2013), i.e. those corresponding to  
354 the Last Glacial Maximum (LGM; Figure 4). Atmospheric greenhouse gas concentrations were  
355 also left at their LGM values (CO<sub>2</sub> = 185 ppm, CH<sub>4</sub> = 350 ppb, N<sub>2</sub>O = 200 ppb). The orbital  
356 parameters are set to 32 ky cal. BP (Berger *et al.*, 1978), which correspond to the beginning of  
357 GS 5.2. Initial boundary conditions for prescribed sea surface temperatures (SSTs) and sea ice  
358 cover were computed with the coupled atmosphere-ocean general circulation model IPSLCM4  
359 (Marti *et al.*, 2010). This model was obtained by setting forcing and boundary conditions of the  
360 PMIP3 LGM experiment described in Alkama *et al.* (2008) and Kageyama *et al.* (2013) to 32  
361 ky cal. BP, thus producing an enhanced seasonal cycle of incoming insolation and surface  
362 temperatures in the Northern hemisphere.

363 Results were further downscaled to a spatial resolution of 11.5 km via the spline  
364 interpolation available in ArcMap 10.7.1. The simulated variables employed in this analysis are  
365 mean annual precipitation, warmest month temperature and coldest month temperature. We did

366 not use elevation as a covariate in this process. Elevation is usually considered to be a proxy  
367 for temperature, because these two variables are highly correlated. Moreover, elevation is also  
368 taken into account during the paleoclimatic simulation process. These reasons make it a  
369 redundant and non-informative variable for the niche analyses presented here.

370

## 371 **2.3. Ecological niche modeling**

### 372 **2.3.1. Modeling preparation**

373 Prior to estimating niches, we analyzed and filtered the occurrence datasets to reduce  
374 potential spatial biases. First, we trimmed duplicate site occurrences from each grid-cell, so that  
375 a grid-cell contained only a single occurrence point, thus ensuring that the training and testing  
376 occurrence datasets would be spatially unique (i.e., no shared occurrences). Next, we thinned  
377 the occurrence datasets to eliminate clusters of sites, thereby preventing oversampling of  
378 environmental conditions from certain areas (e.g., the northern Aquitaine area) and reducing  
379 potential spatial autocorrelation (Anderson & Gonzalez, 2011; Boria *et al.*, 2014). This  
380 consisted of eliminating occurrences such that the minimum distance between any pair of  
381 occurrence points was twice the grid resolution, i.e. *ca.* 23 km. This step was performed  
382 manually using the “Measure line” tool in QGIS 2.18.28. The final datasets consisted of 10  
383 occurrence points for the Noaillian in the Pyrenees piedmont and plateau, and 20 occurrences  
384 for the Middle Gravettian north of the Garonne River (Noaillian and Rayssian combined).

385 The definition of a calibration area (**M**) relies on biogeographic assumptions (Peterson *et*  
386 *al.*, 2011 p. 135; Barve *et al.*, 2011). To define (**M**) for Middle Gravettian hunter-gatherers in  
387 our region of study (Figure 4), we assume that these populations could not live in regions in  
388 close proximity to ice sheets, and that they could have occupied areas exposed by the period’s  
389 lower sea levels. We therefore masked the environmental variables with coast lines 90 m below

390 present day sea level (Waelbroeck *et al.*, 2002; Siddall *et al.*, 2003), as well as with LGM ice  
391 sheet coverage reconstructions in the Alps, Pyrenees and the Massif Central (Ehlers & Gibbard,  
392 2004). While these reconstructions slightly over-estimate ice coverage for *ca.* 32 ky cal. BP,  
393 they still serve as an adequate proxy since the areas in question would have been characterized  
394 by cold and dry, if not periglacial, conditions during the corresponding stadials and HE.  
395 Furthermore, based on the nature of raw material (flint) circulation in the Pyrenees region  
396 (Foucher *et al.*, 2008; Simonet, 2017), we allowed the predictive modeling architecture to  
397 extrapolate into the regions of Cantabria and Catalonia. Finally, the Rhône River Valley in the  
398 East may have served to limit the movements of hunter-gatherer populations (no raw material  
399 circulation across the valley, cf. Santaniello, 2016). Furthermore, recent geomorphological  
400 studies show that the lower and middle Rhône Valley, as well as the Mediterranean continental  
401 shelf, likely consisted of a desert, with deflation-related landforms (e.g., yardangs, pans, desert  
402 pavements) and sand deposits (dunes, sand ramps) surrounded by loess accumulations during  
403 the coldest events of the Last Glacial period (Bosq *et al.*, 2018). However, the presence of  
404 Noailles burins and Gravette points to the east indicates that they were permeable barriers. Thus,  
405 we included in our (M) coastal regions of Liguria, Tuscany, Lazio and Campania in present-  
406 day Italy where Noailles burins are observed in the archaeological record (Palma di Cesnola,  
407 1991; Touzé, 2013). This step was performed with QGIS 2.18.28.

### 408 **2.3.2. Model calibration and selection**

409 Model calibration and selection were performed using the kuenm R package (Cobos *et*  
410 *al.*, 2019a), which employs Maxent 3.4 (Phillips *et al.*, 2006, 2017). In R 3.6.1 (R Core Team,  
411 2019), we created a total of 448 candidate models for each occurrence dataset using distinct  
412 parameter settings resulting from the combination of 16 regularization multiplier values, 7  
413 response types representing all possible combinations of the three feature classes (linear,  
414 quadratic and product), and four sets of environmental predictors derived from all possible



415 combinations of the three paleoclimatic variables, following Cobos *et al.* (2019b). Threshold  
416 and hinge feature classes were not used in order to reduce model complexity and overfitting.  
417 The kuenm package allows the evaluation of statistical significance via partial ROC measures  
418 (Peterson *et al.*, 2008), omission rates based on a maximum allowed error ( $E = 5\%$ , user defined;  
419 Anderson *et al.*, 2003; Peterson *et al.*, 2008), and model complexity by means of the Akaike  
420 information criterion corrected for small sample sizes (AICc; Warren & Seifert, 2011). For the  
421 retention of the best performing models among those that were statistically significant, we  
422 selected those with omission rates lower than  $E$  and of those we retained only the models with  
423  $\Delta_{\text{AICc}}$  values lower than two (i.e.  $\Delta_{\text{AICc}} = \text{AICc}_i - \text{AICc}_{\text{min}}$ , where  $\text{AICc}_i$  is the AICc of the  $i$ th  
424 model and  $\text{AICc}_{\text{min}}$  is the lowest AICc among all significant models for which omission rates  
425 are below 5%).

426

### 427 **2.3.3. Creation of final models and model comparisons**

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

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

Parameters			Evaluation results				
Regularization multiplier	Features	Environmental variables	Partial ROC	Omission rates below 5%	AICc	$\Delta_{AICc}$	Number of parameters
<i>Northern Middle Gravettian</i>							
<b>0.3</b>	<b>LQP</b>	<b>All</b>	<b>0</b>	<b>0</b>	<b>311.258</b>	<b>0</b>	<b>4</b>
<i>Pyrenees Noaillian</i>							
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

**Table 2.** *continued*

Regularization multiplier	Features	Environmental variables	Partial ROC	Omission rates below 5%	AICc	ΔAICc	Number of parameters
0.4	LQP	ctemp, mprec	0	0	172.303	1.721	2
0.8	LQ	ctemp, mprec	0	0	172.303	1.721	2
<b>0.5</b>	<b>QP</b>	<b>ctemp, wtemp</b>	<b>0</b>	<b>0</b>	<b>172.306</b>	<b>1.724</b>	<b>2</b>
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

444

445

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.

450

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

459

460 predictions is deemed to be significant if the empirical value falls below the 5% limits of the  
461 null distribution. To compare niches in environmental space, we used NicheA (Qiao *et al.*,  
462 2016). We employed a three-dimensional environmental background using the three  
463 paleoclimatic variables to develop minimum volume ellipsoid (MVE) niche estimations, with  
464 a precision of 0.01, for the Pyrenees Noaillian and the northern Middle Gravettian (Figure 4).  
465 We measured the volume of each ellipsoid and calculated the level of environmental overlap  
466 between them using the Jaccard index (Qiao *et al.*, 2016; Qiao *et al.*, 2017).

467

## 468 **3. Results**

### 469 **3.1. Niche predictions**

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

482 The Pyrenees Noaillian niche prediction (Figure 5b) is geographically extensive and is  
483 significantly larger than the distribution of archaeological occurrence data. The estimated niche

484 displays continuous high suitability scores from the coast of Cantabrian Spain up to southern  
485 Britain. The lowest predicted occurrence point is that of the site of La Carane-3, and all other  
486 sites from the central Pyrenees are located in areas with low to medium suitability scores.

487 Variability maps indicate that the northern Middle Gravettian model is probably more  
488 reliable than that of the Pyrenees Noaillian (Figure 5c and 5d). The northern Middle Gravettian  
489 variability map displays few and relatively small areas with a range higher than 0.3. The highest  
490 suitability ranges occur in Brittany and southern Britain, the Landes platform area, the Massif  
491 Central as well as the northern Alps. The Pyrenees Noaillian variability map, however, shows  
492 variability ranges higher than 0.3 in areas along the Mediterranean coasts, the Eastern side of  
493 the Pyrenees, the Massif Central, as well as along the Atlantic coast and in the Landes  
494 periglacial desert area. The suitability estimates in these areas should therefore be considered  
495 less reliable since they can vary substantially between models.

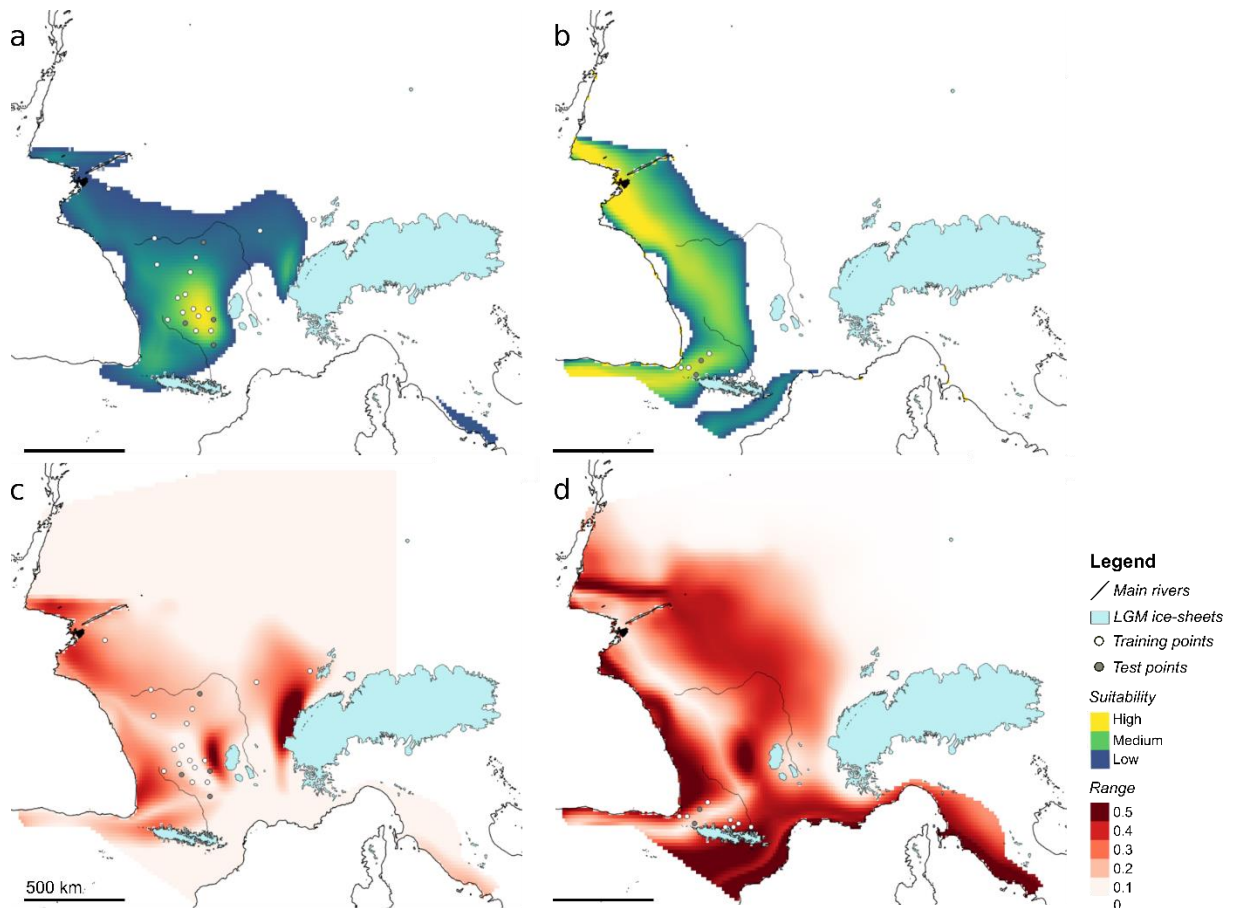
496

### 497 **3.2. Niche comparisons**

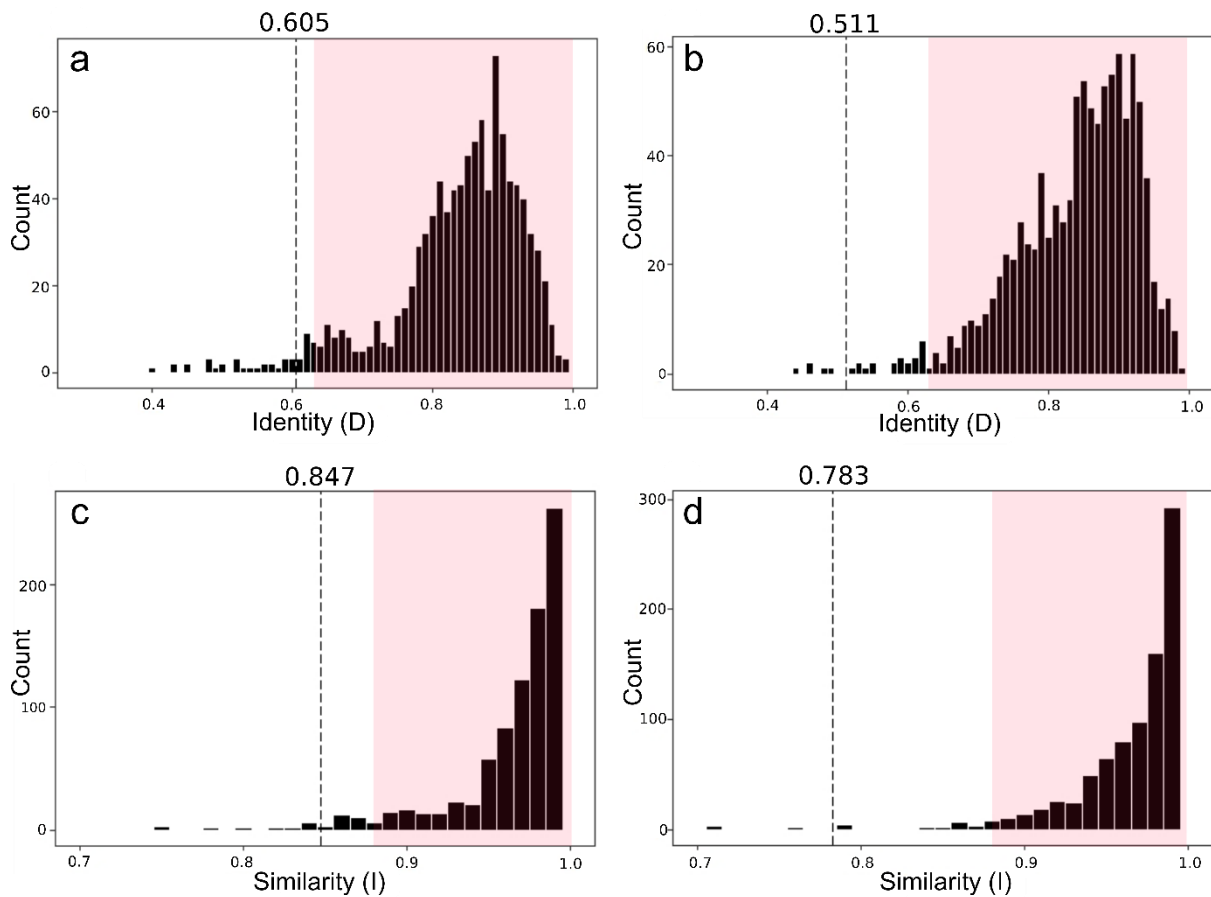
498 The Pyrenees Noaillian and the northern Middle Gravettian niches are highly similar in  
499 geographic space (Figure 6). However, their differences are significant and they are  
500 significantly less similar than would be expected by chance (D metric: North vs. Pyrenees:  $p =$   
501  $0.03$ ; Pyrenees vs. North:  $p = 0.006$ ; I metric: North vs. Pyrenees:  $p = 0.029$ ; Pyrenees vs. North:  
502  $p = 0.007$ ; for a statistical significance achieved if  $p < 0.05$ ; Figure 6). With respect to  
503 environmental dimensions, our analysis shows that the niches overlap significantly (MVE  
504 overlap volume = 1.110, which corresponds to 97% of the Pyrenees Noaillian ellipsoid volume  
505 and 7% of the Northern Middle Gravettian ellipsoid volume; Figure 7). Comparisons  
506 demonstrate that the Pyrenees Noaillian niche is smaller and less broad than that of the northern  
507 Middle Gravettian, and is primarily contained within the latter (Figure 7). It is worth noting,  
508 however, that a small portion of the Pyrenees Noaillian ellipsoid falls outside of the northern

509 Middle Gravettian ellipsoid, thus occupying a subset of environmental conditions not present  
510 in the latter's niche estimation.

511



512 **Figure 5.** Geographic projections of Maxent-produced median niche estimations. **a.** Northern Middle  
513 Gravettian. **b.** Pyrenees Noaillian. **c.** Variability map for the northern Middle Gravettian prediction  
514 showing the suitability range of 10 models produced with the same data. **d.** Variability map for the  
515 Pyrenees Noaillian prediction showing the suitability range of all 45 significant models.  
516

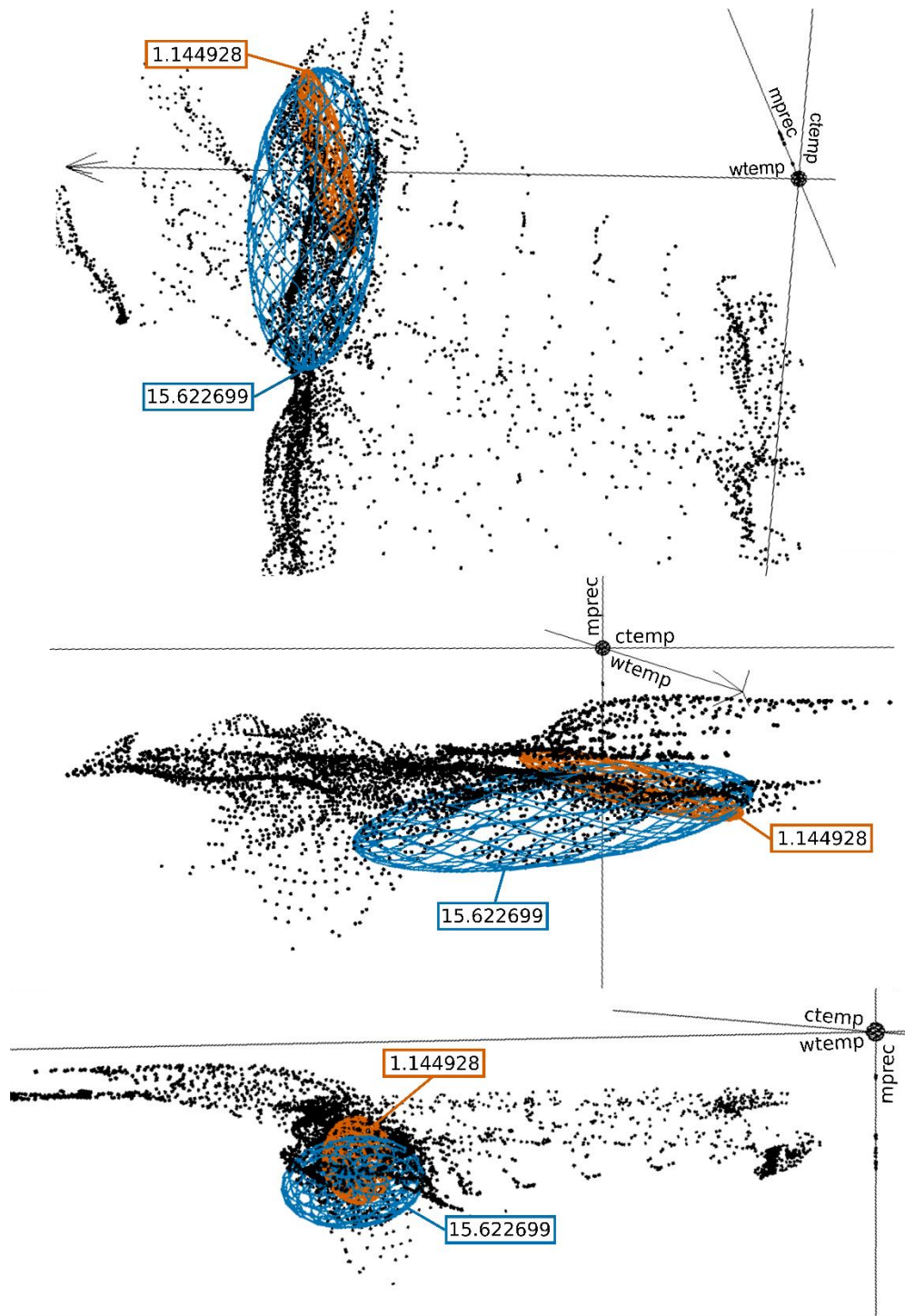


517  
 518 **Figure 6.** Background similarity and identity tests results for comparisons between the northern Middle  
 519 Gravettian vs. the Pyrenees Noaillian (**a.** and **c.**), and the Pyrenees Noaillian vs. the northern Middle  
 520 Gravettian (**b.** and **d.**). Dashed lines represent measures between the empirical models and the  
 521 histograms depict measures from 1000 background-derived comparisons. The colored areas represent  
 522 the non-significance range above the 5<sup>th</sup> percentile of the distribution

523

## 524 **4. Discussion**

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



530  
 531 **Figure 7.** NicheA Minimum Volume Ellipsoids (MVE) for the northern Middle Gravettian (blue) and  
 532 the Pyrenees Noaillian (red) in environmental space during GS.5 (black points) according to different  
 533 orientations of the axes. The environmental dimensions are temperature of the coldest month (ctemp),  
 534 temperature of the warmest month (wtemp) and mean annual precipitation (mprec). The MVE volumes  
 535 are displayed in the corresponding colored boxes.



536           The Raysse method is a highly standardized reduction process that can be applied to a  
537 wide variety of blanks, from blades to thick flakes produced during various stages of the blade  
538 reduction sequences or other less standardized reduction sequences (e.g., production of flakes  
539 or blade-like flakes). The bladelets produced with the Raysse method did not require further  
540 intensive modification due to their standardized morphology. Furthermore, if a problem was  
541 encountered during the final stages of their production, only minimal investment was needed to  
542 produce a new or replacement bladelet (Klaric *et al.*, 2002, 2009; Klaric, 2003, 2008, 2017).  
543 This highly standardized bladelet production system served to create end-products that could  
544 be easily transformed into *armatures* (a French term commonly used in technological and  
545 functional studies to designate either the lithic point hafted on the tip/head of a projectile or the  
546 lithic implements hafted laterally on a projectile's foreshaft) that were likely part of a composite  
547 and readily maintainable hunting weaponry toolkit. Such a technological adaptation is  
548 commonly observed in highly mobile hunter-gatherers that operate in landscapes where access  
549 to resources needed to maintain weaponry is unpredictable (Binford 1977; Bleed, 1986). The  
550 importance placed on producing highly standardized components for a maintainable and  
551 curated hunting toolkit is further supported by the emphasis that appears to have been placed  
552 on transmitting and maintaining this technique (Klaric, 2017, 2018). This has been inferred  
553 from the numerous technical details that one must take into account when using the Raysse  
554 method to replicate La Picardie bladelet blanks, and this is further supported by the frequent  
555 presence of unretouched flint knapping debris and retouched objects that appear to have been  
556 produced by apprentices or individuals who did not completely master the intricacies of the  
557 method (Klaric, 2017, 2018).

558           The opposite appears to have been the case in the Pyrenees, where *armature* forms are  
559 more diverse: Gravette points, microgravettes points, bi-truncated backed bladelets, and simple  
560 backed implements made from blades or bladelets (Klaric, 2003; Simonet, 2009a, 2011b, 2017).

561 While these *armature* types were made from straight blade or bladelet blanks, the latter do not  
562 need to be highly standardized and can be obtained from a variety of reduction methods.  
563 Intensive retouch is all that is necessary to transform an initial blank into one of these *armature*  
564 types (e.g., Gravettes points broken during fabrication indicate that the blank's width can be  
565 reduced up to 50%; Klaric, 2003, p. 257; Simonet, 2009a, fig. 21). The higher typological  
566 diversity of *armatures* in the Pyrenees may reflect a higher degree of variability in how these  
567 points were integrated into weapon systems (e.g., axial points *vs.* laterally mounted elements)  
568 used by these populations. These different technological strategies for producing hunting  
569 equipment between the northern Middle Gravettian and the Pyrenees Noaillian archaeological  
570 records are likely related to differences in targeted medium to large prey species and, in turn,  
571 the subsistence strategies and mobility patterns employed to exploit them.

572 Faunal data indicate that populations in the Pyrenees hunted a variety of animals, such  
573 as reindeer, bovids, horse, chamois, bison, deer and fox, whereas northern groups relied  
574 principally on reindeer (Lacarrière, 2015). This fact does not necessarily indicate that the  
575 availability of prey species was different between these two regions (Lacarrière, 2015, p. 347),  
576 but it is worth noting that the smaller Pyrenees niche is associated with a more diverse spectrum  
577 of prey species. Thus, it would appear that the Pyrenees piedmont plateau and plains, with its  
578 more reduced range of environmental conditions, contained a wide variety of prey species that,  
579 as indicated by seasonality data (Lacarrière, 2015), were present throughout the year. These  
580 data are consistent with inferred Gravettian occupation of the region, which is dominated by  
581 small, specialized sites (e.g., Tercis, Gatzarria) situated some distance from larger aggregation  
582 sites (e.g., Isturitz, Brassempouy), as well as an exploitation of predominantly local lithic raw  
583 materials (Simonet, 2017). Pyrenees populations, thus, were likely logistically mobile with a  
584 well-organized exploitation of resources within a relatively restricted region and narrow  
585 ecological niche. The high prey species diversity could therefore be the result of a more

586 generalized hunting strategy within a reduced territory. In this framework, *armature* diversity  
587 could be interpreted as an adaptation to the exploitation of a more diverse prey species spectrum  
588 within a smaller and more rugged territory, allowing hunters to easily adapt to different  
589 situations by changing their hunting weaponry (e.g. prey type, topography etc.).

590 To the north, in contrast, the wider range of environmental conditions (i.e., broader  
591 ecological niche) exploited by the northern Middle Gravettian populations would suggest a  
592 higher degree of mobility than is observed in the Pyrenees since the main prey species identified  
593 in northern archaeological assemblages is reindeer (Lacarrière, 2015). Higher mobility is  
594 supported by technological data. For example, the Grotte du Renne site is located some distance  
595 from high quality lithic raw material sources (35 to 120 km according to Klaric *et al.*, 2009),  
596 and its Middle Gravettian assemblage shows a high degree of curation, in contrast to other sites  
597 that are situated at or near raw material sources, such as the site of La Picardie (although a small  
598 percentage of artifacts at La Picardie are made from raw materials coming from sources located  
599 in the Charente region, some 200 km away; Delvigne *et al.*, 2020). With respect to curation,  
600 Raysse burins (i.e. bladelet cores) from the Grotte du Renne often have double bladelet  
601 production platforms, are smaller than those recovered from La Picardie, and the blanks  
602 selected to make La Picardie bladelets are generally smaller and are not always typical: many  
603 bladelets are more twisted and do not always have a *pan-revers* and/or a pointed distal end  
604 (Klaric, 2006, 2017; Klaric *et al.*, 2009). In this scenario, the Raysse method could reflect a  
605 technological specialization directed at producing *armatures* for hunting reindeer. It does not  
606 mean that reindeer was the only available species in the environment; in fact, other species are  
607 always present to a lesser extent in faunal assemblages (Lacarrière, 2015). This could therefore  
608 be the result of a cultural choice of northern populations focusing on reindeer (Klaric *et al.*, in  
609 press)—a choice that would require higher mobility. Nevertheless, one must be careful to not  
610 generalize this pattern, since it relies on only a handful of studies, and numerous sites have

611 assemblages that contain both by-products of the Raysse method and Gravette points, two  
612 conceptually different *chaînes opératoires* (i.e. reduction sequences), and thus different kinds  
613 of composite hunting weapons. However, we must bear in mind that occurrences of Picardie  
614 bladelets and Gravette points together are observed almost exclusively within cave or rock  
615 shelter deposits, where archaeological levels represent palimpsests of multiple occupations that  
616 often were subjected to complex post-depositional processes that can homogenize initially  
617 distinct occupations. The co-occurrence of the two *armature* types is also observed at two open-  
618 air sites: the site of Solvieux in Dordogne (Sackett, 1999), where the stratigraphic setting is  
619 extremely complex, and Sackett's analysis has raised doubts concerning the integrity of its  
620 archaeological assemblages; and the site of Les Jambes in Dordogne (Célérier, 1967), where  
621 slope depositional processes influenced the site's formation (Klaric, 2003, p. 222), thus raising  
622 doubts as to whether the distinct archaeological levels defined by Célérier are valid. Whether  
623 these two types of *armatures*—la Picardie bladelets and Gravette/microgravette points—were  
624 associated with the same hunting tool-kit or whether their association in the same  
625 archaeological level is the result of post-depositional processes or palimpsest deposits, is a  
626 subject that requires further study.

627         At present, the site of Callan represents the only known location of specialized  
628 occupations or activities north of the Garonne River (Morala, 2011). Its lithic assemblage is  
629 dominated by Noailles burins and no *armatures* have been recovered. This general absence of  
630 specialized sites suggests that groups in these higher latitude regions had a higher level of  
631 residential mobility than those in the Pyrenees. Such a pattern of highly mobile groups using  
632 highly standardized and curated toolkits to exploit large territories via a residential system of  
633 mobility is in sharp contradiction with the pattern observed during the same period in the  
634 Pyrenees. This pattern, though, may be influenced by the lack of chronological resolution for  
635 this time-period, which is the result of reduced stratigraphic resolution due to imprecise

636 excavation methods, to post-depositional mixing of levels, palimpsest deposits and the standard  
637 errors associated with radiocarbon ages for this period. Such factors make determinations of  
638 discrete activity episodes difficult, if not impossible, and the potential homogenization of  
639 archaeological levels renders making inferences of how human activities were organized across  
640 the landscape difficult.

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

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

## 685 5. Conclusions

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

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

720

## 721 **Supplementary material**

722 Codes used in R to perform the steps described in sections 2.3.2 and 2.3.3 and models  
723 calibration results are available online at  
724 [https://osf.io/35pb4/?view\\_only=4f84e08e6ba84754b2090e349bc2ebf4](https://osf.io/35pb4/?view_only=4f84e08e6ba84754b2090e349bc2ebf4). Attached to the article  
725 is an additional appendix containing a table of criteria used to identify reliable identifications  
726 of the Rayssian and the Noaillian in the literature.

727

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737

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743

## 744 **References**

745         Agsous, S. (2008). *Stratigraphie et sédimentologie de l’abri Pataud (Les Eyzies-de-*  
746 *Tayac, Dordogne, France). Contribution à l’étude des paléoenvironnements des cultures du*  
747 *Paléolithique supérieur ancien du Périgord*. [doctoral thesis]. Paris: Muséum National  
748 d’Histoire Naturelle.

749         Alaux, J.-F. (1967). Burins du type “Le Raysse” de l’abri des Battuts (Tarn). *Bulletin*  
750 *de la Société préhistorique française. Comptes rendus des séances mensuelles*, 64(8), 242–  
751 247. <https://doi.org/10.3406/bspf.1967.8976>

752         Alaux, J.-F. (1971). Burins de Noailles inachevés et burins « de technique Noailles »  
753 de l’Abri des Battuts, commune de Penne (Tarn). *Bulletin de la Société préhistorique*  
754 *française*, 68(8), 239–242. <https://doi.org/10.3406/bspf.1971.4332>

755 Alkama, R., Kageyama, M., Ramstein, G., Marti, O., Ribstein, P., & Swingedouw, D.  
756 (2008). Impact of a realistic river routing in coupled ocean–atmosphere simulations of the  
757 Last Glacial Maximum climate. *Climate Dynamics*, 30(7–8), 855–869.

758 <https://doi.org/10.1007/s00382-007-0330-1>

759 Allard, M. (1986). Le gisement préhistorique de La Martinière à La Pommeraye (M.-  
760 et-L.). Mise en évidence de périgordien supérieur à burins de Noailles. *Bulletin de la Société*  
761 *préhistorique française*, 83, 78–82. <https://doi.org/10.3406/bspf.1986.8738>

762 Allard, M., & Gruet, M. (1976). Les civilisations du Paléolithique supérieur dans les  
763 Pays de la Loire. In H. de Lumley (dir.) *La Préhistoire française. Tome I : civilisations*  
764 *paléolithiques et mésolithiques* (Vol. 2, pp. 1305–1310). Paris : Editions du CNRS.

765 Anderson, R. P., Lew, D., & Peterson, A. T. (2003). Evaluating predictive models of  
766 species' distributions: criteria for selecting optimal models. *Ecological Modelling*, 162(3),  
767 211–232. [https://doi.org/10.1016/S0304-3800\(02\)00349-6](https://doi.org/10.1016/S0304-3800(02)00349-6)

768 Anderson, R. P., & Gonzalez, I. J. (2011). Species-specific tuning increases robustness  
769 to sampling bias in models of species distributions: an implementation with Maxent.  
770 *Ecological Modelling*, 222, 279–2811. <https://doi.org/10.1016/j.ecolmodel.2011.04.011>

771 Angevin, R., Kildéa, F., Djemmali, N., Alilaire, P., Delvigne, V., Depont, J., Lafarge,  
772 A., Mevel, L., Schemmama, V., Surmely, F., & Verjux, C. (2018). Le Paléolithique supérieur  
773 dans le sud du Bassin parisien à la lumière des découvertes récentes : faits attendus, faits  
774 nouveaux. In O. Troubat (Ed.) *Préhistoire de la France centrale: actes du colloque,*  
775 *Montluçon, 19 novembre 2016* (pp. 49–71). Montluçon: Cercle archéologique de Montluçon  
776 et de la région.

777 Arambourou, R., & Jude, P. E. (1964). *Le Gisement de La Chèvre à Bourdeilles*,  
778 *Dordogne*. Bordeaux: R. & M. Magne.

779 Aranguren, B. M., Longo, L., Pallecchi, P., & Revedin, A. (2006). Eléments de la  
780 chaîne opératoire-fonctionnelle des burins de Noailles de Bilancino (Florence, Italie). In  
781 Lebrun-Ricalens F. (Ed.) *Burins préhistoriques : formes, fonctionnements, fonctions* (n°2, pp.  
782 143–162). Luxembourg: Archéologiques.

783 Aranguren, B., Cavulli, F., D’Orazio, M., Grimaldi, S., Longo, L., Revedin, A., &  
784 Santaniello, F. (2015). Territorial exploitation in the Tyrrhenian Gravettian Italy: The case-  
785 study of Bilancino (Tuscany). *Quaternary International*, 359–360, 442–451.  
786 <https://doi.org/10.1016/j.quaint.2014.07.009>

787 Aubry, T., Almeida, M., Candela, P., Chauvière, F.-X., Dimuccio, L., Fontana, L.,  
788 Liard, M., Marquet, J.-C., João Neves, M., Peyrouse, J.-B., & Walter, B. (2013). Le  
789 Paléolithique supérieur ancien dans le sud-ouest du Bassin parisien : du Châtelperronien au  
790 Gravettien dans les vallées de la Creuse et de la Claise. In Bodu P., Chehmana L., Klaric L.,  
791 Mevel L., Soriano S., Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l’Europe du*  
792 *Nord-Ouest* (Mémoire 56, pp. 299–318). Paris: Société préhistorique française.

793 Banks, W. E. (2015). Constructing chronologies for the late Middle Paleolithic and  
794 Upper Paleolithic: limitations and means to overcome them. *World Archaeology*, 47(4), 585–  
795 600. <https://doi.org/10.1080/00438243.2015.1052544>

796 Banks, W. E. (2017). The application of Ecological Niche Modeling methods to  
797 archaeological data in order to examine Culture-Environment relationships and cultural  
798 trajectories. *Quaternaire*, 28(2), 271–276. <https://doi.org/10.4000/quaternaire.7966>

799 Banks, W. E., d’Errico, F., Peterson, A. T., Vanhaeren, M., Kageyama, M., Sepulchre,  
800 P., Ramstein, G., Jost, A., & Lunt, D. (2008). Human ecological niches and ranges during the  
801 LGM in Europe derived from an application of eco-cultural niche modeling. *Journal of*  
802 *Archaeological Science*, 35(2), 481–491. <https://doi.org/10.1016/j.jas.2007.05.011>

803 Banks, W. E., Zilhão, J., d’Errico, F., Kageyama, M., Sima, A., & Ronchitelli, A.  
804 (2009). Investigating links between ecology and bifacial tool types in Western Europe during  
805 the Last Glacial Maximum. *Journal of Archaeological Science*, 36(12), 2853–2867.  
806 <https://doi.org/10.1016/j.jas.2009.09.014>

807 Banks, W. E., Aubry, T., d’Errico, F., Zilhão, J., Lira-Noriega, A., & Townsend  
808 Peterson, A. (2011). Eco-cultural niches of the Badegoulian: Unraveling links between  
809 cultural adaptation and ecology during the Last Glacial Maximum in France. *Journal of*  
810 *Anthropological Archaeology*, 30(3), 359–374. <https://doi.org/10.1016/j.jaa.2011.05.003>

811 Banks, W. E., d’Errico, F., & Zilhão, J. (2013). Human–climate interaction during the  
812 Early Upper Paleolithic: testing the hypothesis of an adaptive shift between the Proto-  
813 Aurignacian and the Early Aurignacian. *Journal of Human Evolution*, 64(1), 39–55.  
814 <https://doi.org/10.1016/j.jhevol.2012.10.001>

815 Banks, W. E., Bertran, P., Ducasse, S., Klaric, L., Lanos, P., Renard, C., & Mesa, M.  
816 (2019). An application of hierarchical Bayesian modeling to better constrain the chronologies  
817 of Upper Paleolithic archaeological cultures in France between *ca.* 32,000–21,000 calibrated  
818 years before present. *Quaternary Science Reviews*, 220, 188–214.  
819 <https://doi.org/10.1016/j.quascirev.2019.07.025>

820 Bardon, L., Bouyssonie, J., & Bouyssonie, A. (1903). Un nouveau type de burin.  
821 *Revue de l’Ecole d’Anthropologie*, 13, 165–168.

822 Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson,  
823 A. T., Soberón, J., & Villalobos, F. (2011). The Crucial Role of the Accessible Area in  
824 Ecological Niche Modeling and Species Distribution Modeling. *Ecological Modelling*,  
825 222(11), 1810–19. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>.

826 Berger, A. (1978). Long-term variations of daily insolation and quaternary climatic  
827 changes. *Journal of Atmospheric Sciences*, 35, 2362–2367. [https://doi.org/10.1175/1520-  
828 0469\(1978\)035<2362:LTVODI>2.0.CO;2](https://doi.org/10.1175/1520-0469(1978)035<2362:LTVODI>2.0.CO;2)

829 Bertran, P., Sitzia, L., Banks, W. E., Bateman, M. D., Demars, P.-Y., Hernandez, M.,  
830 Lenoir, M., Mercier, N., & Prodeo, F. (2013). The Landes de Gascogne (southwest France):  
831 periglacial desert and cultural frontier during the Palaeolithic. *Journal of Archaeological  
832 Science*, 40(5), 2274–2285. <https://doi.org/10.1016/j.jas.2013.01.012>

833 Binford, L. R. (1977). Forty-seven trips. A case study in the character of  
834 archaeological formation processes. In R.V.S. Wright (Ed.) *Stone tools as cultural markers:  
835 change, evolution and complexity* (pp. 24–36). Canberra: Australian Institute of Aboriginal  
836 Studies.

837 Bleed, P. (1986). The Optimal Design of Hunting Weapons: Maintainability or  
838 Reliability. *American Antiquity*, 51(4), 737–747. <https://doi.org/10.2307/280862>

839 Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial  
840 filtering to reduce sampling bias can improve the performance of ecological niche models.  
841 *Ecological Modelling*, 275, 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>

842 Bosq, M., Bertran, P., Degeai, J.-P., Kreutzer, S., Queffelec, A., Moine, O., & Morin,  
843 E. (2018). Last Glacial aeolian landforms and deposits in the Rhône Valley (SE France):

844 Spatial distribution and grain-size characterization. *Geomorphology*, 318, 250–269.  
845 <https://doi.org/10.1016/j.geomorph.2018.06.010>

846 Boyer, M., Geneste, J.-M., & Rigaud, J. P. (1984). Le Périgordien supérieur du site de  
847 plein air du Caillou, Rouffignac-de-Sigoulès (Dordogne). *Bulletin de la Société préhistorique*  
848 *française*, 81(81), 302–310. <https://doi.org/10.3406/bspf.1984.8593>

849 Breuil, H. (1927). Oeuvres d’art paléolithique inédites du Périgord et art oriental  
850 d’Espagne. *Revue anthropologique*, 4–6, 101–108.

851 Briand, T., Remicourt, M., Tallet, P., Fernandes, P., Rué, M., Simonet, A., Pasquini,  
852 A., Fedoroff, N., Picavet, R., & Bernad, C. (2010). *Les occupations gravettiennes de Hin-de-*  
853 *Diou, à Pujo-le-Plan. Opération d’archéologie préventive du 05 octobre au 18 décembre*  
854 *2009*. Villard-de-Lans: Paléotime – Service régional de l’archéologie Aquitaine.

855 Bricker, H. M. (1995). *Le Paléolithique supérieur de l’abri Pataud, Dordogne : les*  
856 *fouilles de H. L. Movius Jr. : Suivi d’un inventaire analytique des sites aurignaciens et*  
857 *périgorgiens de Dordogne*. Paris: Ed. de la Maison des sciences de l’Homme.

858 Bruxelles, L., & Jarry, M. (2011). Climatic conditions, settlement patterns and cultures  
859 in the Paleolithic: The example of the Garonne Valley (southwest France). *Journal of Human*  
860 *Evolution*, 61(5), 538–548. <https://doi.org/10.1016/j.jhevol.2011.05.009>

861 Bruxelles, L., & Jarry, M. (2012). Climats et cultures paléolithiques : quand la vallée  
862 devient frontière.... *Archeopages, Hors-série 3*, 72–85.  
863 <https://doi.org/10.4000/archeopages.469>

864 Caux, S. (2012). *Etude de l’industrie lithique*. In Boudadi-Maligne, M. (dir.) *Grotte de*  
865 *Malvidier (La Roque-Gageac, Dordogne), Rapport d’opération de fouille programmée* (pp.

866 111–118). Bordeaux: Service régional de l’archéologie, Direction régionale des affaires  
867 culturelles Aquitaine.

868 Célérier, G. (1967). Le gisement périgordien supérieur des “Jambes”. Commune de  
869 Périgueux (Dordogne). *Bulletin de la Société préhistorique française*, 64(1), 53–68.

870 Clarke, D. L. (1968). *Analytical Archaeology*. London: Methuen & Co Ltd.

871 Clottes, Jean. (1985). Circonscription des Pyrénées. *Gallia Préhistoire*, 28(2), 331–  
872 371

873 Clottes, J., Lorblanchet, M., Fau, M.-F., & Peyre, G. (1990). L’abri périgordien de la  
874 Bergerie, à Saint-Géry (Lot). *Bulletin de la Société préhistorique française*, 87(10), 342–357.  
875 <https://doi.org/10.3406/bspf.1990.9920>

876 Cobos, M. E., Peterson, A. T., Barve, N., & Osorio-Olvera, L. (2019a). Kuenm: An R  
877 Package for Detailed Development of Ecological Niche Models Using Maxent. *PeerJ*, 7,  
878 e6281. <https://doi.org/10.7717/peerj.6281>

879 Cobos, M. E., Peterson, A. T., Osorio-Olvera, L. and Jiménez-García, D. (2019b). An  
880 Exhaustive Analysis of Heuristic Methods for Variable Selection in Ecological Niche  
881 Modeling and Species Distribution Modeling. *Ecological Informatics*, 53, 100983.  
882 <https://doi.org/10.1016/j.ecoinf.2019.100983>.

883 Cobos, M. E., Osorio-Olvera, L., & Peterson, A. T. (2019c). Assessment and  
884 representation of variability in ecological niche model predictions. *BioRxiv*, 603100.  
885 <https://doi.org/10.1101/603100>

886 Couchard, J., & de Sonneville-Bordes, D. (1960). La grotte de Bassaler-Nord, près de  
887 Brive et la question du Périgordien II en Corrèze. *L’Anthropologie*, 64(5–6), 415–437.

888 d'Errico, F., & Banks, W. E. (2013). Identifying Mechanisms behind Middle  
889 Paleolithic and Middle Stone Age Cultural Trajectories. *Current Anthropology*, 54(8), 371–  
890 387. <https://doi.org/10.1086/673388>

891 d'Errico, F., Banks, W. E., Warren, D. L., Sgubin, G., Niekerk, K. van, Henshilwood,  
892 C., Daniau, A.-L., & Goñi, M. F. S. (2017). Identifying early modern human ecological niche  
893 expansions and associated cultural dynamics in the South African Middle Stone Age.  
894 *Proceedings of the National Academy of Sciences*, 114(30), 7869–7876.  
895 <https://doi.org/10.1073/pnas.1620752114>

896 Daniel, R. (1967). Le Périgordien supérieur de Petit-Puyrousseau, commune de  
897 Périgueux (Dordogne). *Bulletin de la Société préhistorique française*, 64(8), 236–241.  
898 <https://doi.org/10.3406/bspf.1967.8975>

899 Daniel, R. (1969). Les burins de Noailles du Fourneau-du-Diable ; Commune de  
900 Bourdeilles (Dordogne). *Bulletin de la Société préhistorique française*, 66(1), 16–18.  
901 <https://doi.org/10.3406/bspf.1969.10325>

902 Daniel, R., & Schmider, B. (1972). L'abri Durand-Ruel, près Brantôme (Dordogne) et  
903 ses problèmes stratigraphiques. *Gallia préhistoire*, 15(2), 323–337.  
904 <https://doi.org/10.3406/galip.1972.1419>

905 David, N. (1985). *The Noaillian (level 4) assemblages and the Noaillian Culture in*  
906 *Western Europe*. Cambridge: Peabody Museum of Archaeology and Ethnology.

907 de la Peña Alonso, P. (2009). Revisión crítica de los conjuntos líticos gravetienses y su  
908 contexto arqueológico en la Península Ibérica. *Complutum*, 20(1), 29–53.



909 de la Peña Alonso, P. (2011). *Sobre la unidad tecnologica del Gravetiense en la*  
910 *peninsula Ibérica : implicaciones para el conocimiento del Paleolitico superior inicial.*  
911 [doctoral thesis]. Madrid: Universidad complutense de Madrid.

912 de las Heras, C., Lasheras, J. A., Arrizabalaga, Á., & de la Rasilla, M. (Eds.) (2013).  
913 *Pensando el Gravetiense: Nuevos datos para la region cantabrica en su contexto peninsular y*  
914 *pyrenaico.* Museo Nacional y Centro de Investigacion de Altamira (monografias 23).

915 de Sonnevile-Bordes, D. (1960). *Recherches sur le Paléolithique supérieur en*  
916 *Périgord* [doctoral thesis]. Paris: Université de Paris.

917 Delage, F. (1936). L’abri des Merveilles à Castel-Merle (Sergeac, Dordogne). *Compte-*  
918 *rendu de la XIIIe session*, 578–608.

919 Delporte, H. (1968). L’abri du Facteur à Tursac (Dordogne). *Gallia Préhistoire*, 11(1),  
920 1–112. <https://doi.org/10.3406/galip.1968.1307>

921 Delvigne, V., Fernandes, P., Tuffery, C., Raynal, J.-P., & Klaric, L. (2020).  
922 Taphonomic methods and a database to establish the origin of sedimentary silicified rocks  
923 from the Middle-recent Gravettian open-air site of La Picardie (Indre-et-Loire, France).  
924 *Journal of Archaeological Science: Reports*, 32, 102369.  
925 <https://doi.org/10.1016/j.jasrep.2020.102369>

926 Demars, P.-Y. (1977). Les industries du Périgordien supérieur des grottes de Pré-  
927 Aubert et des Morts près Brive (Corrèze). *Bulletin de la Société préhistorique française.*  
928 *Comptes rendus des séances mensuelles*, 74(4), 103–111.  
929 <https://doi.org/10.3406/bspf.1977.8490>

930 Djindjian, F., Koslowski, J., & Otte, M. (1999). *Le Paléolithique supérieur en Europe*.  
931 Malakoff: Armand Colin.

932 Ehlers, J., & Gibbard, P. (2004). *Quaternary Glaciations - Extent and Chronology*,  
933 *Part I: Europe* (Vol. 2a). Amsterdam: Elsevier.

934 Féruglio, V., Aujoulat, N., & Jaubert, J. (2011). L'art pariétal gravettien, ce qu'il  
935 révèle de la société en complément de la culture matérielle. In Goutas N., Klaric L., Pesesse  
936 D., Guillermin P. (dir.) *À la recherche des identités gravettiennes. Actualités,*  
937 *questionnements, perspectives* (Mémoire 52, pp. 243–255). Paris: Société préhistorique  
938 française.

939 Floss, H., Dutkiewicz, E., Frick, J., & Hoyer, C. (2013). Le Paléolithique supérieur  
940 ancien en Bourgogne du sud. In Bodu P., Chehmana L., Klaric L., Mevel L., Soriano S.,  
941 Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l'Europe du Nord-Ouest* (Mémoire  
942 56, pp. 331–350). Paris: Société préhistorique française.

943 Fontaine, A. (2006). *Le site des Vachons (commune de Voulgézac, Charente): étude*  
944 *typologique des couches 3 et 3 bis (précédée d'un avant-propos rectificatif)* [master thesis].  
945 Paris: Muséum National d'Histoire Naturelle.

946 Foucher, P. (2004). *Les industries lithiques du complexe Gravettien-Solutréen dans les*  
947 *Pyrénées : techno-typologie et circulation des matières siliceuses de part et d'autre de l'axe*  
948 *Pyrénées-Cantabres*. [doctoral thesis]. Toulouse: Université Toulouse Le Mirail - Toulouse II.

949 Foucher, P. (2013). Synthèse chrono-culturelle sur le Gravettien des Pyrénées : constat  
950 et réflexions sur la stabilité régionale des traditions techniques. In de la Heras C., Lasheras  
951 J.A., Arrizalaga A., de la Rasilla M. (dir.). *Pensando el Gravetiense : nuevos datos para la*

952 *region cantabrica en su contexto peninsular y pirenaico* (monografias 23, pp. 142–159).  
953 Santander, Madrid: Museo Nacional y Centro de Investigacion de Altamira.

954 Foucher, P., San Juan-Foucher, C., Sacchi, D., & Arrizabalaga, Á. (2008). Le  
955 Gravettien des Pyrénées. *Paléo*, 20, 331–356.

956 Foucher, P., Juan-Foucher, C. S., Vercoutère, C., & Ferrier, C. (2012). La grotte de  
957 Gargas (Hautes-Pyrénées, France): l’apport du contexte archéologique à l’interprétation de  
958 l’art pariétal. In Clottes J. (Ed.) *L’art pléistocène dans le monde / Pleistocen art of the world /*  
959 *Arte pleistoceno en el mundo* (pp. 209–225). Foix: Société préhistorique ariégeoise.

960 Gottardi, G. G. (2011). *La question des faciès au Gravettien : fonctions, traditions ou*  
961 *chronologie ?* [master thesis]. Bordeaux: Université de Bordeaux I.

962 Goutas, N. (2013a). De Brassempouy à Kostienki : l’exploitation technique des  
963 ressources animales dans l’Europe gravettienne. In M. Otte (dir.) *Les Gravettiens* (pp. 105–  
964 160). Paris: Errance.

965 Goutas, N. (2013b). Nouvelles données sur l’industrie osseuse des grottes du Renne et  
966 du Trilobite à Arcy-sur-Cure (Yonne, France). In Bodu P., Chehmana L., Klaric L., Mevel L.,  
967 Soriano S., Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l’Europe du Nord-*  
968 *Ouest* (Mémoire 56, pp. 89–116). Paris: Société préhistorique française.

969 Gruet, M. (1984). L’apport de deux sites angevins à la chronologie des terrasses  
970 fluviales : Roc-en-Pail en Chalonnnes sur Loire et Port-Launay sur la Sarthe. *Bulletin de*  
971 *l’Association française pour l’étude du quaternaire*, 21(1), 13–18.  
972 <https://doi.org/10.3406/quate.1984.1473>

- 973           Guillermin, P. (2006). Les Fieux : une occupation gravettienne du Causse quercinois.  
974 *Paléo*, 18, 69–94.
- 975           Guillermin, P. (2008). Les « Périgordiens » en Quercy : l'exemple du gisement des  
976 Fieux. *Paléo*, 20, 357–372.
- 977           Guillermin, P. (2011). La fin du Gravettien dans le sud-ouest de la France : à la  
978 recherche de l'identité protomagdalénienne. In Goutas N., Klaric L., Pesesse D., Guillermin  
979 P. (dir.) *À la recherche des identités gravettiennes. Actualités, questionnements, perspectives*  
980 (Mémoire 52, pp. 129–146). Paris: Société préhistorique française.
- 981           Hans, J.-M. (1997). Périgordien à burins de Noailles : le site de Hautmougey (canton  
982 de Bains-les-Bains, Vosges). *Bulletin de la Société Préhistorique Luxembourgeoise*, 19, 55–  
983 66.
- 984           Henry-Gambier, D. (2008). Comportement des populations d'Europe au Gravettien :  
985 pratiques funéraires et interprétations. *Paléo*, 20, 399–438.
- 986           Hinguant, S., & Monnier, J.-L. (2013). Le Paléolithique supérieur ancien dans le  
987 Massif armoricain : un état de la question. In Bodu P., Chehmana L., Klaric L., Mevel L.,  
988 Soriano S., Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l'Europe du Nord-*  
989 *Ouest* (Mémoire 56, pp. 229–238). Paris: Société préhistorique française.
- 990           Hourdin, F., Foujols, M.-A., Codron, F., Guemas, V., Dufresne, J.-L., Bony, S.,  
991 Denvil, S., Guez, L., Lott, F., Ghattas, J., Braconnot, P., Marti, O., Meurdesoif, Y., & Bopp,  
992 L. (2013). Impact of the LMDZ atmospheric grid configuration on the climate and sensitivity  
993 of the IPSL-CM5A coupled model. *Climate Dynamics*, 40(9–10), 2167–2192.  
994 <https://doi.org/10.1007/s00382-012-1411-3>

- 995 Hutchinson, G. E. (1957). Population studies: Animal ecology and demography.  
996 *Bulletin of Mathematical Biology*, 53(1–2), 193–213.
- 997 Kageyama, M., Braconnot, P., Bopp, L., Caubel, A., Foujols, M.-A., Guilyardi, E.,  
998 Khodri, M., Lloyd, J., Lombard, F., Mariotti, V., Marti, O., Roy, T., & Woillez, M.-N. (2013).  
999 Mid-Holocene and Last Glacial Maximum climate simulations with the IPSL model—part I:  
1000 comparing IPSL\_CM5A to IPSL\_CM4. *Climate Dynamics*, 40(9–10), 2447–2468.  
1001 <https://doi.org/10.1007/s00382-012-1488-8>
- 1002 Kildea, F., & Lang, L. (2011). Le Gravettien de la vallée du Cher : le site de la Croix-  
1003 de-Bagneux à Mareuil-sur-Cher (Loir-et-Cher, France). In Goutas N., Klaric L., Pesesse D.,  
1004 Guillermin P. (dir.) *À la recherche des identités gravettiennes. Actualités, questionnements,*  
1005 *perspectives* (Mémoire 52, pp. 273–290). Paris: Société préhistorique française.
- 1006 Kildea, F., Griselin, S., Lang, L., & Souffi, B. (2013). Le Paléolithique supérieur  
1007 ancien aux marges méridionales du Bassin parisien : le site de la Croix-de-Bagneux à  
1008 Mareuil-sur-Cher (Loir-et-Cher). In Bodu P., Chehmana L., Klaric L., Mevel L., Soriano S.,  
1009 Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l'Europe du Nord-Ouest* (Mémoire  
1010 56, pp. 317–330). Paris: Société préhistorique française.
- 1011 Klaric, L. (2003). *Technical unity of Raysse burins industries in their diachronical*  
1012 *context. Thoughts about cultural variability during Gravettian, based on the case of La*  
1013 *Picardie, Arcy-sur-Cure, Brasempouy and Le Cirque de la Patrie.* [doctoral thesis]. Paris:  
1014 Université Panthéon-Sorbonne - Paris I.
- 1015 Klaric, L. (2006). Des armatures aux burins : des critères de distinction techniques et  
1016 culturels à partir des productions lamellaires de quelques sites du Gravettien moyen et récent

1017 (France). In Lebrun-Ricalens F. (Ed.) *Burins préhistoriques : formes, fonctionnements,*  
1018 *fonctions* (n°2, pp. 199–223). Luxembourg: Archéologiques.

1019 Klaric, L. (2007). Regional groups in the European middle Gravettian : a  
1020 reconsideration of the Rayssian technology. *Antiquity*.  
1021 <https://doi.org/10.1017/S0003598X00094928>

1022 Klaric, L. (2008). Anciennes et nouvelles hypothèses d'interprétation du gravettien  
1023 moyen en France : la question de la place des industries à burins du Raysse au sein de la  
1024 mosaïque gravettienne. *Paléo*, 20, 257–276.

1025 Klaric, L. (2017). « La réussite d'une production repose sur l'attention prêtée aux  
1026 détails »: l'exemple des débitages lamellaires par méthode du Raysse (Gravettien moyen,  
1027 France). *Journal of Lithic Studies*, 4(2). <https://doi.org/10.2218/jls.v4i2.2547>

1028 Klaric, L. (2018). Levels of flintknapping expertise and apprenticeship during the  
1029 Mid-Upper Palaeolithic: several illustrative examples from the Early and Late Aurignacian  
1030 and Middle Gravettian. In Klaric (dir.) *The Prehistoric apprentice. Investigating*  
1031 *apprenticeship and expertise in prehistoric technologies* (pp. 49–116). Brno, CZ: Dolní  
1032 Věstonice Studies.

1033 Klaric, L., Aubry, T., & Walter, B. (2002). Un nouveau type d'armature en contexte  
1034 gravettien et son mode de production sur les burins du Raysse (la Picardie, commune de  
1035 Preuilley-sur-Claise, Indre-et-Loire). *Bulletin de la Société préhistorique française*, 99(4),  
1036 751–764. <https://doi.org/10.3406/bspf.2002.12754>

1037 Klaric, L., Guillermin, P., & Aubry, T. (2009). Des armatures variées et des modes de  
1038 productions variables. Réflexions à partir de quelques exemples issus du Gravettien d'Europe

1039 occidentale (France, Portugal, Allemagne). *Gallia préhistoire*, 51(1), 113–154.

1040 <https://doi.org/10.3406/galip.2009.2476>

1041 Klaric, L., Liard, M., Bertran, P., Dumarçay, G., de Araujo Igreja, M., Aubry, T., &  
1042 Walter, B. (2011). La Picardie (Preuilly-sur-Claise, Indre-et-Loire) : neuf ans de fouille sur un  
1043 gisement rayssien finalement pas si mal conservé ! In Goutas N., Klaric L., Pesesse D.,  
1044 Guillermin P. (dir.) *À la recherche des identités gravettiennes. Actualités, questionnements,*  
1045 *perspectives* (Mémoire 52, pp. 291–310). Paris: Société préhistorique française.

1046 Klaric, L., Bertran, P., Dumarçay, G., & Liard, M. (2018). A long and winding road:  
1047 Towards a palethnographic interpretation of the middle-Gravettian site of la Picardie (Indre-et-  
1048 Loire, France). *Quaternary International*, 498, 51–68.

1049 <https://doi.org/10.1016/j.quaint.2018.09.035>

1050 Klaric L., Goutas N., Lacarrière J. & Banks W. (in press). Rayssien ? Vous avez dit  
1051 Rayssien ? In O. Touzé, N. Goutas, P. Noiret, H. Salomon (dir.) *NW Europe during the*  
1052 *Gravettian: Contributions of recent research to the understanding of the societies and their*  
1053 *environments*, Proceedings of Liège symposium, 13-14 April 2018.

1054 Klima, B. (Dir.) (1983). *Aurignacien, Périgordien, Gravettien—Actes des colloques*  
1055 *XV et XVI du IXe congrès de l'UISPP, Nice, 1976* (ERAUL, Vol. 1).

1056 Krtolitza, Y., & Lenoir, M. (1998). Un gisement du Gravettien à burins de Noailles en  
1057 Gironde, l'abri Lespoux à Saint-Quentin-de-Baron. *Revue Archéologique de Bordeaux*, 89,  
1058 47–68.

1059 Lacarrière, J. (2015). *Les ressources cynégétiques au Gravettien en France :*  
1060 *acquisition et modalités d'exploitation des animaux durant la phase d'instabilité climatique*

1061 *précédant le dernier maximum glaciaire* [doctoral thesis]. Toulouse: Université Toulouse le  
1062 Mirail - Toulouse II.

1063 Lacarrière, J., Goutas, N., Normand, C., & Simonet, A. (2011). Vers une redéfinition  
1064 des occupations gravettiennes de la grotte d'Isturitz (Pyrénées-Atlantiques, France) : révision  
1065 critique des collections "anciennes" par l'approche intégrée des données lithiques, fauniques  
1066 et de l'industrie osseuse. In Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la*  
1067 *recherche des identités gravettiennes. Actualités, questionnements, perspectives* (Mémoire 52,  
1068 pp. 67–84). Paris: Société préhistorique française.

1069 Laville, H., & Rigaud, J.-P. (1973). The Perigordian V industries in Périgord :  
1070 typological variations, stratigraphy and relative chronology. *World Archaeology*, 4(3), 330–  
1071 338.

1072 Le Mignot, Y. (2000). La question de la production d'armatures sur le site gravettien  
1073 de Plasenn-al-Lomm (Ile de Bréhat, Côtes d'Armor). *Revue archéologique de l'ouest*, 17(1),  
1074 7–24. <https://doi.org/10.3406/rao.2000.1099>

1075 Le Tensorer, J.-M. (1974). Le Périgordien supérieur à burins de Noailles de l'Abri  
1076 Peyrony à Gavaudun (Lot-et-Garonne). *Bulletin de la Société préhistorique française*, 71(2),  
1077 459–468. <https://doi.org/10.3406/bspf.1974.8279>

1078 Le Tensorer, Jean-Marie. (1981). *Le Paléolithique de l'Agenais*. Editions du CNRS.

1079 Lenoir, M. (1977). Un gisement de plein air du Périgordien supérieur en Gironde : les  
1080 Artigaux à Camiac-et-Saint-Denis. *Bulletin de la Société Préhistorique Française*, 74(2),  
1081 518–530. <https://doi.org/10.3406/bspf.1977.8465>



1082           Leroi-Gourhan, A. (1984). *L'art des cavernes: atlas des grottes ornées paléolithiques*  
1083 *françaises*. Paris: Imprimerie nationale.

1084           Lucas, G. (2000). *Les industries lithiques du Flageolet I (Dordogne) : Approche*  
1085 *économique, technologique, fonctionnelle et analyse spatiale* [doctoral thesis]. Bordeaux:  
1086 Université de Bordeaux I.

1087           Lucas, G. (2002). À propos des burins du Raysse du Flageolet I (Dordogne, France).  
1088 *Paléo*, 14, 63–76.

1089           Marti, O., Braconnot, P., Dufresne, J.-L., Bellier, J., Benshila, R., Bony, S.,  
1090 Brockmann, P., Cadule, P., Caubel, A., Codron, F., De Noblet, N., Denvil, S., Fairhead, L.,  
1091 Fichet, T., Foujols, M.-A., Friedlingstein, P., Goosse, H., Grandpeix, J.-Y., Guilyardi, E., ...  
1092 Talandier, C. (2010). Key features of the IPSL ocean atmosphere model and its sensitivity to  
1093 atmospheric resolution. *Climate Dynamics*, 34, 1–26. [https://doi.org/10.1007/s00382-009-](https://doi.org/10.1007/s00382-009-0640-6)  
1094 [0640-6](https://doi.org/10.1007/s00382-009-0640-6)

1095           Michel, A. (2010). *L'Aurignacien récent (post-ancien) dans le Sud-Ouest de la*  
1096 *France : variabilité des productions lithiques. Révision taphonomique et techno-économique*  
1097 *des sites de Caminade-Est, abri Pataud, Roc-de-Combe, Le Flageolet I, La Ferrassie et*  
1098 *Combemenué*. [doctoral thesis]. Bordeaux: Université de Bordeaux I.

1099           Monméjean, E., Bordes, F., & de Sonneville-Bordes, D. (1964). Le Périgordien  
1100 supérieur à burins de Noailles du Roc de Gavaudun (Lot-et-Garonne). *L'anthropologie*, 68(3–  
1101 4), 253–316.

1102           Moralà, A. (1984). *Périgordien et Aurignacien en Haut-Agenais : étude d'ensembles*  
1103 *lithiques*. Paris: Ecole des Hautes Etudes en Sciences Sociales.

1104 Morala, A. (2011). La spécialisation des activités : concept de l'archéologue et réalité  
1105 archéologique ; les données du site gravettien moyen du Callan (Lot-et-Garonne). In Goutas  
1106 N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la recherche des identités gravettiennes.*  
1107 *Actualités, questionnements, perspectives* (Mémoire 52, pp. 343–358). Paris: Société  
1108 préhistorique française.

1109 Movius, H. Jr., & David, N. (1970). Burins avec modification tertiaire du biseau,  
1110 burins-pointe et burins du Raysse à l'Abri Pataud, Les Eyzies (Dordogne). *Bulletin de la*  
1111 *Société préhistorique française*, 67(2), 445–455. <https://doi.org/10.3406/bspf.1970.4209>

1112 Nespoulet, R. (2008). Le Gravettien de l'abri Pataud. Bilan et perspectives. *Paléo*, 20,  
1113 373–380.

1114 Noiret, P. (2013). De quoi Gravettien est-il le nom ? In M. Otte (dir.) *Les Gravettiens*  
1115 (pp. 28–64). Paris: Errance

1116 Onoratini, G. (1982). *Préhistoire, sédiments, climats du Würm III à l'Holocène dans le*  
1117 *Sud-Est de la France* [doctoral thesis]. Aix-en-Provence: Université de droit, d'économie et  
1118 des sciences d'Aix-Marseille.

1119 Onoratini, G., Cauche, D., Celiberti, V., & Simon, P. (2010). Le Noaillien dans le  
1120 complexe Gravettien du sud-est de la France. *Bulletin du Musée d'Anthropologie*  
1121 *préhistorique de Monaco*, 50, 39–53.

1122 Otte, M. (Ed.) (2013). *Les Gravettiens*. Paris: Errance.

1123 Palma di Cesnola, A. (1993). *Il Paleolitico Superiore in Italia*. Firenze: Garlati e  
1124 Razzai.

1125           Pesesse, D. (2013). Le Gravettien existe-t-il ? Le prisme du système technique  
1126 lithiques. In M. Otte (dir.) *Les Gravettiens* (pp. 66–104). Paris: Errance.

1127           Pesesse, D. (2017). Is it still appropriate to talk about the Gravettian? Data from lithic  
1128 industries in Western Europe. *Quartär*, 64, 107–128.

1129           Peterson, A. T., Papeş, M., & Soberón, J. (2008). Rethinking receiver operating  
1130 characteristic analysis applications in ecological niche modeling. *Ecological Modelling*,  
1131 213(1), 63–72. <https://doi.org/10.1016/j.ecolmodel.2007.11.008>

1132           Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martinez-Meyer, E.,  
1133 Nakamura, M., & Araújo, M. B. (2011). *Ecological niches and geographic distributions*.  
1134 Princeton, NJ: Princeton University Press.

1135           Peterson, A. T., & Soberón, J. (2012). Species distribution modeling and ecological  
1136 niche modeling: getting the concepts right. *Natureza & Conservação*, 10(2), 102–107.  
1137 <https://doi.org/10.4322/natcon.2012.0>

1138           Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling  
1139 of species geographic distributions. *Ecological Modelling*, 190(3–4), 231–259.  
1140 <https://doi.org/10.1016/j.ecolmodel.2005.03.026>

1141           Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017).  
1142 Opening the black box: an open-source release of Maxent. *Ecography*, 40(7), 887–893.  
1143 <https://doi.org/10.1111/ecog.03049>

1144           Pottier, C. (2005). *Le Gravettien moyen de l'abri Pataud (Dordogne, France): le*  
1145 *niveau 4 et l'éboulis 3/4. Etude technologique et typologique de l'industrie lithique*. [doctoral  
1146 thesis]. Paris: Muséum d'Histoire Naturelle de Paris.

1147 Pottier, C. (2006). Productions lamellaires et burins du Raysse du Gravettien Moyen  
1148 de l'Abri Pataud (Dordogne, France). In Lebrun-Ricalens F. (Ed.) *Burins préhistoriques :  
1149 formes, fonctionnements, fonctions* (n°2, pp. 121–140). Luxembourg: Archéologiques.

1150 Pradel, L. (1953). Précisions sur les Burins d'Angles et les Burins Plans. *Congrès  
1151 Préhistorique de France*, 545–552.

1152 Pradel, L. (1959). Le niveau de Noailles d'Oreille-d'Enfer, Les Eyzies-de-Tayac  
1153 (Dordogne). *Bulletin de la Société préhistorique de France*, 56(3), 228–235.

1154 Qiao, H., Peterson, A. T., Campbell, L. P., Soberón, J., Ji, L., & Escobar, L. E. (2016).  
1155 NicheA: creating virtual species and ecological niches in multivariate environmental  
1156 scenarios. *Ecography*, 39(8), 805–813. <https://doi.org/10.1111/ecog.01961>

1157 Qiao, H., Escobar, L. E., & Peterson, A. T. (2017). Accessible areas in ecological  
1158 niche comparisons of invasive species: Recognized but still overlooked. *Scientific Reports*,  
1159 7(1). <https://doi.org/10.1038/s41598-017-01313-2>

1160 R Core Team (2019). *R: A Language and Environment for Statistical Computing*  
1161 (version 3.6.1). R. Vienna, Austria: R Foundation for Statistical Computing.

1162 Rigaud, J.-P. (1982). *Le Paléolithique en Périgord : les données du Sud-Ouest  
1163 sarladais et leurs implications* [doctoral thesis]. Bordeaux: Université de Bordeaux I.

1164 Rigaud, J.-P. (1988). The Gravettian Peopling of Southwestern France. In Dibble H. L.  
1165 & Montet-White A. *Upper Pleistocene prehistory of Western Eurasia* (Vol. 54, pp. 387–397).  
1166 Philadelphia: University Museum Monograph.

1167 Rigaud, J.-P. (2008). Les industries lithiques du Gravettien du nord de l'Aquitaine  
1168 dans leur cadre chronologique. *Paléo*, 20, 381–398. <https://doi.org/2101-0420>

- 1169 Rigaud, J.-P. (2011). Révision de quelques archéoséquences de référence du  
1170 Gravettien du nord de l'Aquitaine. In Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À*  
1171 *la recherche des identités gravettiennes. Actualités, questionnements, perspectives* (Mémoire  
1172 52, pp. 175–183). Paris: Société préhistorique française.
- 1173 Roebroeks, W., Mussi, M., Svodoba, J., Fennema, K. & Hahn, J. (Eds.). (1999).  
1174 *Hunters of the golden age: The Mid Upper Palaeolithic of Eurasia 30,000 - 20,000 BP*.  
1175 University of Leiden.
- 1176 Roussot, A. (1985). Inventaire typologique des industries de Laussel (tableaux inédits  
1177 de Jean Bouyssonie). *Bulletin de la Société préhistorique française*, 82(1), 15–19.  
1178 <https://doi.org/10.3406/pal.1990.1412>
- 1179 Sackett, J. (1999). *The Archaeology of Solvieux. An Upper Paleolithic Open Air Site in*  
1180 *France*. Los Angeles (CA): Institute of Archaeology.
- 1181 Santaniello, F. (2016). *Il Gravettiano dell'Italia tirrenica nel contesto mediterraneo:*  
1182 *definizione delle strategie di insediamento e mobilità attraverso lo studio delle materie prime*  
1183 *e delle industrie litiche* [doctoral thesis]. Trento, IT: Università degli studi di Trento,  
1184 Université Nice Sophia Antipolis.
- 1185 Santaniello, F., & Grimaldi, S. (2019). Le Gravettien entre l'Italie et la France :  
1186 nouvelles données sur l'industrie lithique de l'Abri Mochi (Balzi Rossi, Italie). *Bulletin de la*  
1187 *Société Préhistorique Française*, 116(2), 255–282.
- 1188 Sarrazin, C. (2017). *Les burins-nucléus du Raysse de la collection des Morts (Grotte*  
1189 *des Morts, Brive-la-Gaillarde). Interprétation du schéma opératoire et analyse des séquences*.  
1190 [master thesis]. Rennes: Université Rennes 2.

1191 Sarrazin, C. (2018). *Plasenn-al-Lomm et la stabilité du système technique rayssien*  
1192 [master thesis]. Rennes: Université Rennes 2.

1193 Schmider, B. (1969). Contribution à l'étude du Périgordien supérieur de La Rochette  
1194 (Dordogne). *Gallia préhistoire*, 12(1), 259–271. <https://doi.org/10.3406/galip.1969.1342>

1195 Schoener, T. W. (1968). The Anolis Lizards of Bimini: Resource Partitioning in a  
1196 Complex Fauna. *Ecology*, 49(4), 704–726. <https://doi.org/10.2307/1935534>

1197 Siddall, M., Rohling, E. J., Almogi-Labin, A., Hemleben, Ch., Meischner, D.,  
1198 Schmelzer, I., & Smeed, D. A. (2003). Sea-level fluctuations during the last glacial cycle.  
1199 *Nature*, 423, 853–858. <https://doi.org/10.1038/nature01690>

1200 Sima, Adriana, Rousseau, D.-D., Kageyama, M., Ramstein, G., Schulz, M., Balkanski,  
1201 Y., Antoine, P., Dulac, F., & Hatté, C. (2009). Imprint of North-Atlantic abrupt climate  
1202 changes on western European loess deposits as viewed in a dust emission model. *Quaternary*  
1203 *Science Reviews*, 28, 2851–2866. <https://doi.org/10.1016/j.quascirev.2009.07.016>

1204 Sima, A., Kageyama, M., Rousseau, D.-D., Ramstein, G., Balkanski, Y., Antoine, P.,  
1205 & Hatté, C. (2013). Modeling dust emission response to North Atlantic millennial-scale  
1206 climate variations from the perspective of East European MIS 3 loess deposits. *Climate of the*  
1207 *Past*, 9(4), 1385–1402. <https://doi.org/10.5194/cp-9-1385-2013>

1208 Simonet, A. (2009a). *Les gravettiens des Pyrénées. Des armes aux sociétés*. [doctoral  
1209 thesis]. Toulouse: Université Toulouse Le Mirail - Toulouse II.

1210 Simonet, A. (2009b). A Gravettian knapping workshop at Tercis (Landes). A probable  
1211 case of apprenticeship in the fabrication of lithic weapon tips. *P@lethnologie*, 1, 183–210.

1212 Simonet, A. (2010). Les armatures lithiques du Gravettien à burins de Noailles du  
1213 niveau G de la grotte des Enfants (Balzi Rossi, Ligurie, Italie): premiers éléments d'enquête.  
1214 *Bulletin du Musée d'Anthropologie préhistorique de Monaco*, 50, 55–68.

1215 Simonet, A. (2011a). La Pointe des Vachons : nouvelles approches d'un fossile  
1216 directeur controversé du Gravettien à partir des exemplaires du niveau IV de la grotte  
1217 d'Isturitz (Pyrénées-Atlantiques, France) et des niveaux 4 des abris 1 et 2 des Vachons  
1218 (Charente, France). *Paléo*, 22, 271–298.

1219 Simonet, A. (2011b). Le Gravettien du chantier I de Brassempouy (Landes, France). In  
1220 Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la recherche des identités*  
1221 *gravettiennes. Actualités, questionnements, perspectives* (Mémoire 52, pp. 57–66). Paris:  
1222 Société préhistorique française.

1223 Simonet, A. (2013). Des apprentis gravettiens ont-ils confectionné des armatures  
1224 lithiques à Tercis (Landes, France) ? *Paléo*, 23, 1–29.

1225 Simonet, A. (2017). Gravettians at Brassempouy (Landes, France), 30,000 BP: a semi-  
1226 sedentary territorial organization? *World Archaeology*, 49(5), 648–665.  
1227 <https://doi.org/10.1080/00438243.2017.1359109>

1228 Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of  
1229 species. *Ecology Letters*, 10(12), 1115–1123. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2007.01107.x)  
1230 [0248.2007.01107.x](https://doi.org/10.1111/j.1461-0248.2007.01107.x)

1231 Soberón, J., & Peterson, A. T. (2005). Interpretation of Models of Fundamental  
1232 Ecological Niches and Species' Distributional Areas. *Biodiversity Informatics*, 2(0).  
1233 <https://doi.org/10.17161/bi.v2i0.4>

1234 Tixier, J. (1958). Les burins de Noailles de l'Abri André Ragout, Bois-du-Roc,  
1235 Vilhonneur (Charente). *Bulletin de la Société préhistorique française*, 55(10), 628–644.  
1236 <https://doi.org/10.3406/bspf.1958.3707>

1237 Touzé, O. (2011). Caractérisation de la “méthode du Raysse” à Bassaler-nord et au  
1238 Raysse (Corrèze, France). *Archéo-situla*, 31, 3–27.

1239 Touzé, O. (2013). De la signification du Noaillien et du Rayssien. In de la Heras C.,  
1240 Lasheras J.A., Arrizalaga A., de la Rasilla M. (dir.). *Pensando el Gravetiense : nuevos datos*  
1241 *para la region cantabrica en su contexto peninsular y pirenaico* (monografias 23, pp. 383–  
1242 400). Santander, Madrid: Museo Nacional y Centro de Investigacion de Altamira.

1243 Vignoles, A., Klaric, L., Banks, W. E., & Baumann, M. (2019). Le Gravettien du  
1244 Fourneau du Diable (Bourdeilles, Dordogne) : révision chronoculturelle des ensembles  
1245 lithiques de la “Terrasse inférieure”. *Bulletin de la Société Préhistorique Française*, 116(3),  
1246 455–478.

1247 Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.-C., McManus, J. F., Lambeck,  
1248 K., Balbon, E., & Labracherie, M. (2002). Sea-level and deep water temperature changes  
1249 derived from benthic foraminifera isotopic records. *Quaternary Science Reviews*, 21, 295–  
1250 305. [https://doi.org/10.1016/S0277-3791\(01\)00101-9](https://doi.org/10.1016/S0277-3791(01)00101-9)

1251 Warren, D. L. (2012). In defense of ‘niche modeling.’ *Trends in Ecology & Evolution*,  
1252 27(9), 497–500. <https://doi.org/10.1016/j.tree.2012.03.010>

1253 Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental Niche Equivalency  
1254 versus Conservatism: Quantitative Approaches to Niche Evolution. *Evolution*, 62(11), 2868–  
1255 2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>



1256 Warren, D. L., & Seifert, S. N. (2011). Ecological niche modeling in Maxent: the  
1257 importance of model complexity and the performance of model selection criteria. *Ecological*  
1258 *Applications*, 21(2), 335–342. <https://doi.org/10.1890/10-1171.1>

1259 [Warren, D. L., Matzke, N., Cardillo M. & Dinnage, R. \(2017\). ENMTools: Analysis of](#)  
1260 [niche evolution using niche and distribution models. R. package version 0.2.](#)

1261 Wojtal, P., Haynes, G., & Wilczynski, J. (Eds.). (2015). *World of Gravettian Hunters*  
1262 (Quaternary International, Vols. 359–360).

1263