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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).

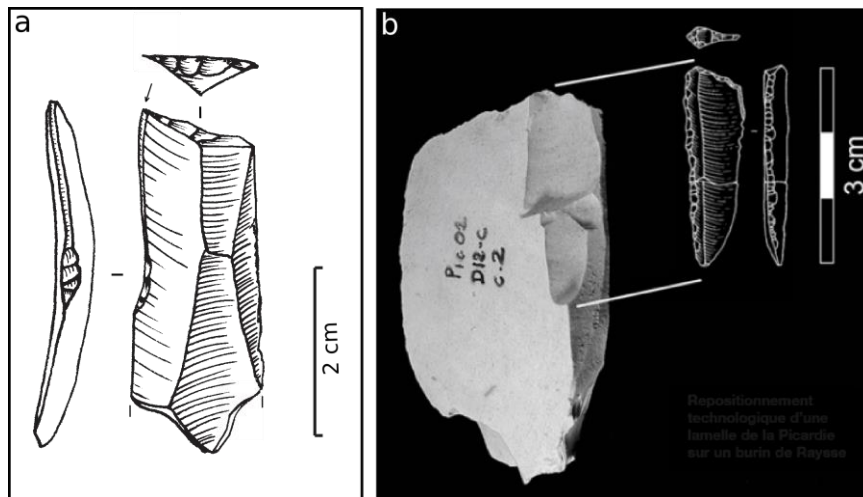
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 94 **Figure 1.** Diagnostic Middle Gravettian artifact types. **a.** Noailles burin from Fourneau du Diable,
 95 Dordogne, France (drawing: A.Vignoles). **b.** Technological position of a “Picardie” bladelet on a Raysse
 96 burin-core from La Picardie, 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 ¹⁴C 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

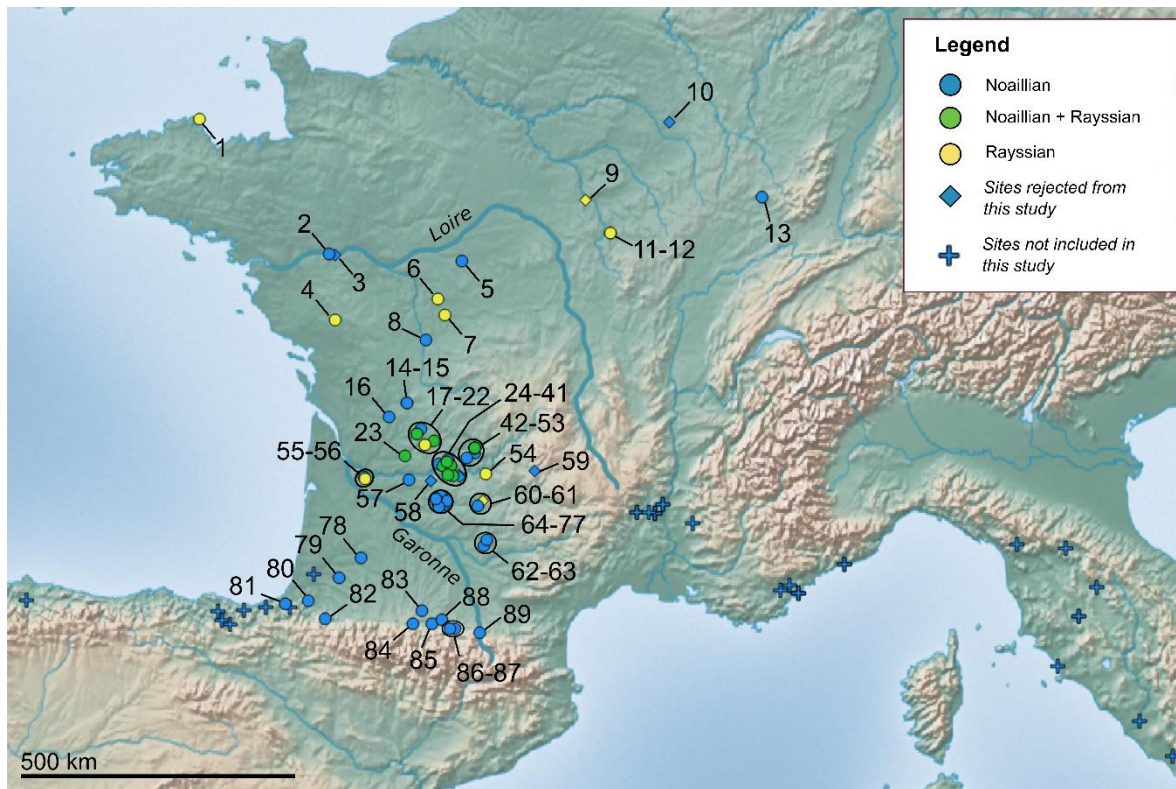
138 method relies on precise technical criteria and more specifically on the identification of the
139 bladelet component associated with Raysse burin-cores, and David (1985) did not use such
140 criteria to describe the Late Noaillian (i.e. Rayssian) in these southern contexts. It is also
141 important 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>

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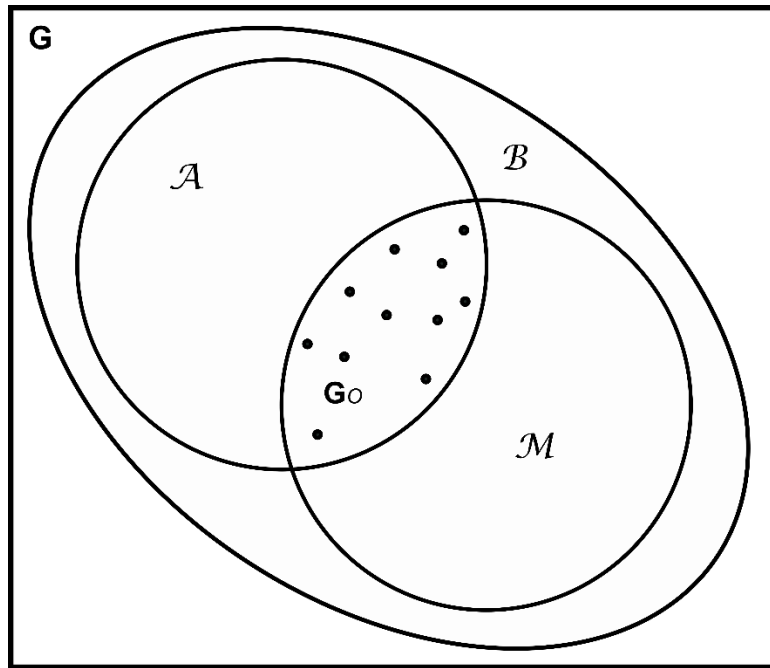
189 2. Materials and Methods

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_o**: occupied distributional area.

224

225 **2.2. Data**

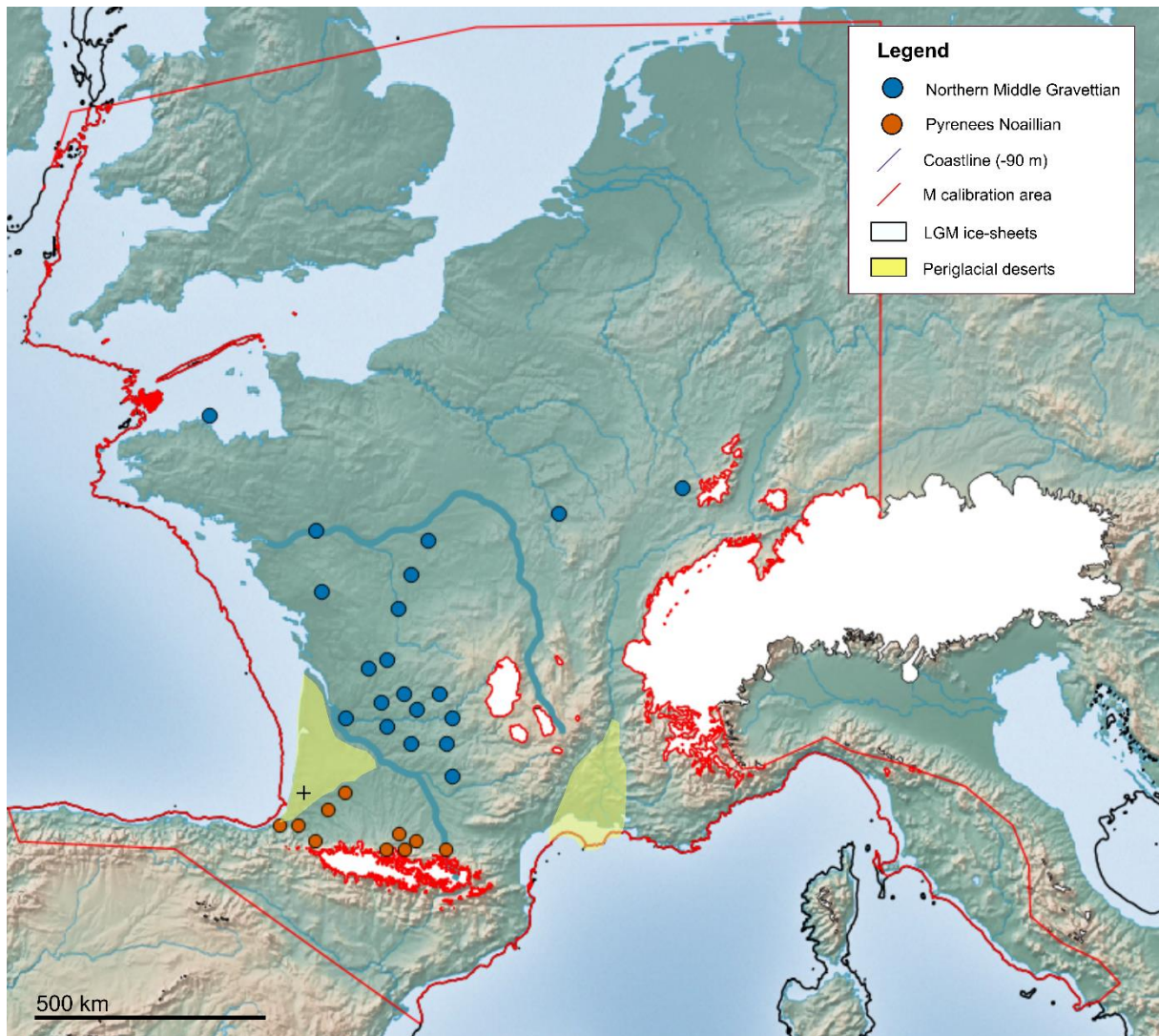
226 **2.2.1. Archaeological data**

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 19th and first half of the 20th 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 Lespaux 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 (CO₂ = 185 ppm, CH₄ = 350 ppb, N₂O = 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 Δ_{AICc} values lower than two (i.e. $\Delta_{\text{AICc}} = \text{AICc}_i - \text{AICc}_{\text{min}}$, where AICc_i is the AICc of the i th
424 model and AICc_{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	Δ_{AICc}	Number of parameters
<i>Northern Middle Gravettian</i>							
0.3	LQP	All	0	0	311.258	0	4
<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
0.5	QP	ctemp, wtemp	0	0	172.306	1.724	2
1	Q	All	0	0	172.306	1.724	2
1	Q	ctemp, wtemp	0	0	172.306	1.724	2
5	Q	ctemp, mprec	0	0	172.311	1.729	1
5	LQ	ctemp, mprec	0	0	172.311	1.729	1
0.9	LQ	ctemp, mprec	0	0	172.366	1.783	2
0.6	QP	ctemp, wtemp	0	0	172.404	1.822	2
0.6	LQP	ctemp, wtemp	0	0	172.404	1.822	2
0.5	LQP	ctemp, mprec	0	0	172.433	1.851	2
1	LQ	ctemp, mprec	0	0	172.433	1.851	2
0.7	QP	ctemp, wtemp	0	0	172.513	1.930	2
0.7	LQP	ctemp, wtemp	0	0	172.513	1.930	2

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.

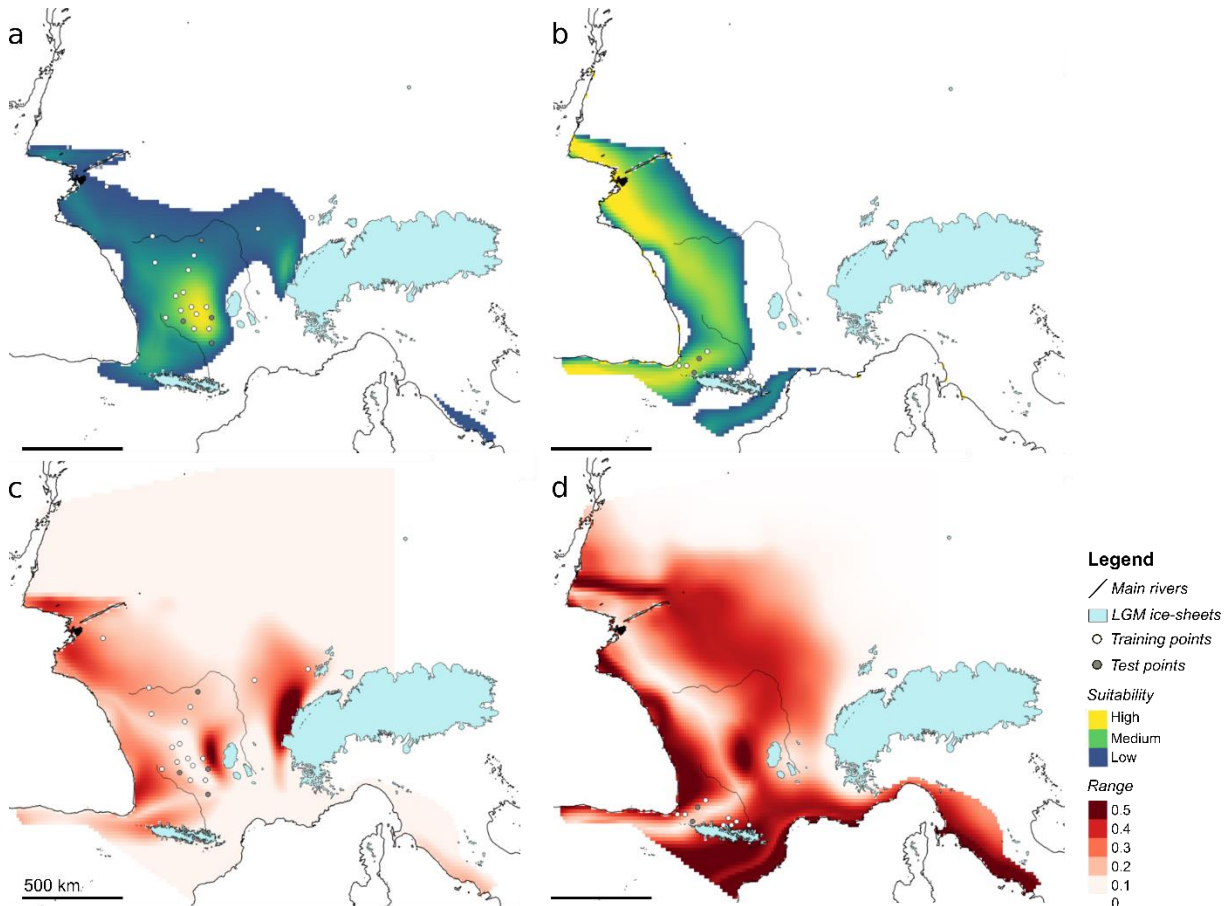
496

497 **3.2. Niche comparisons**

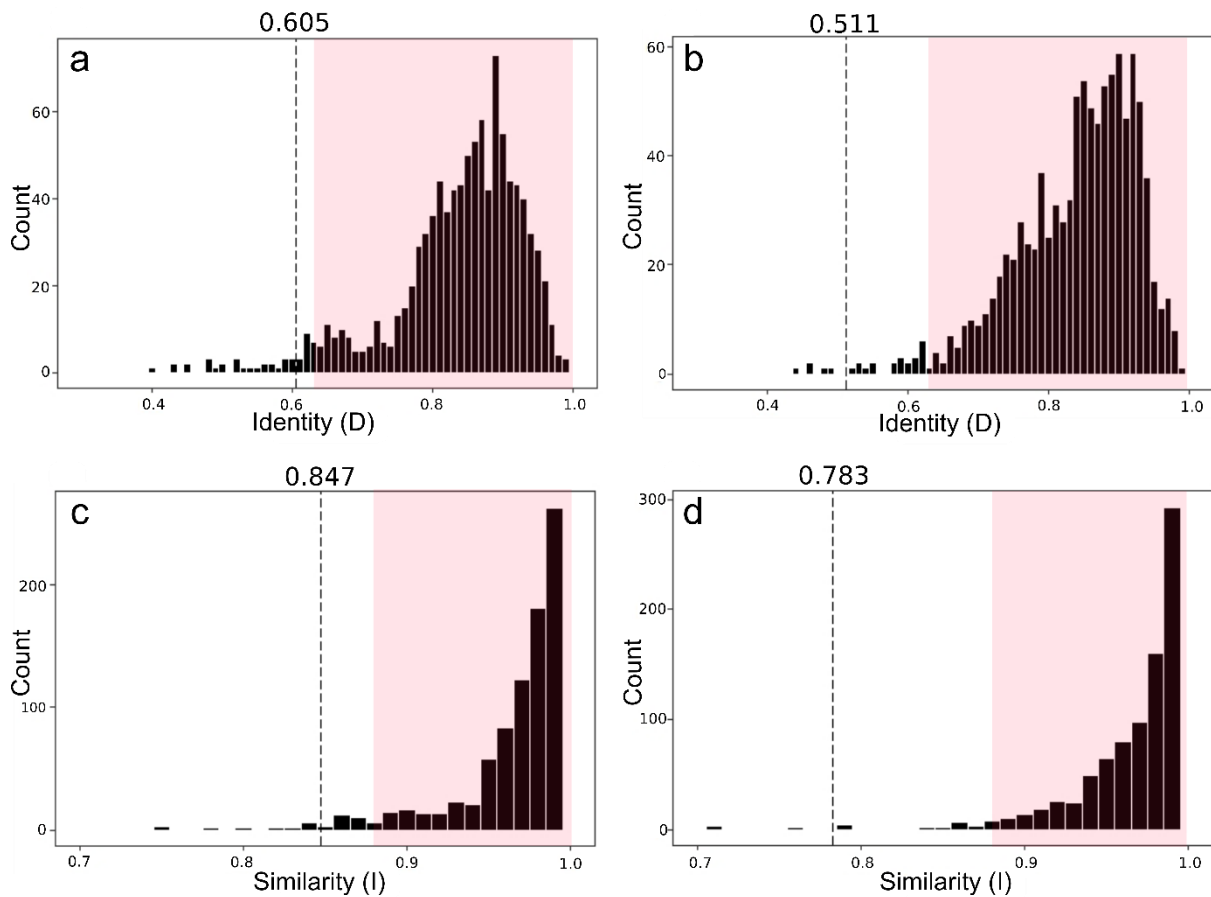
498 The Pyrenees Noaillian and the northern Middle Gravettian niches are highly similar in
499 geographic space (Figure 6). However, their differences are significant and they are
500 significantly less similar than would be expected by chance (D metric: North vs. Pyrenees: $p =$
501 0.03 ; Pyrenees 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

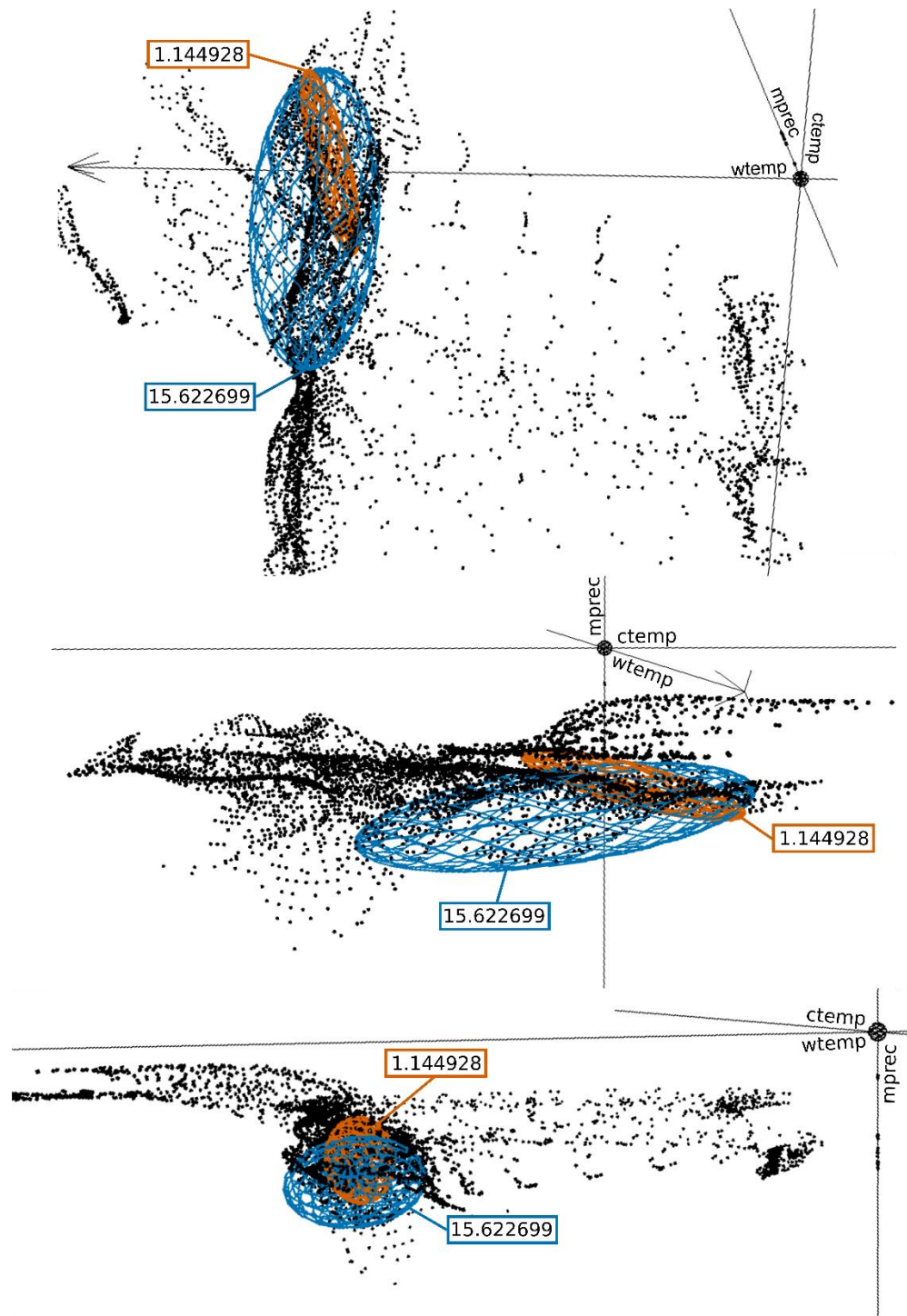


517
 518 **Figure 6.** Background similarity and identity tests results for comparisons between the northern Middle
 519 Gravettian vs. the Pyrenees Noaillian (**a.** and **c.**), and the Pyrenees Noaillian vs. the northern Middle
 520 Gravettian (**b.** and **d.**). Dashed lines represent measures between 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 5th 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 ¹⁴C 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. 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

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