Peer Community In Archaeology

RESEARCH ARTICLE

Open Access

Open Data

Open Code

Open Peer-Review

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

Anaïs Vignoles¹, William E. Banks^{1,4}, Laurent Klaric², Masa Kageyama³, Marlon E. Cobos⁴, Daniel Romero-Alvarez⁴

¹UMR-5199 PACEA, Université de Bordeaux, Bordeaux (FR)

²UMR-7055 Préhistoire et Technologie, Université Paris X-Nanterre, Nanterre (FR)

³UMR-8212 LSCE, Université Paris-Saclay, Gif-sur-Yvette (FR)

⁴Biodiversity Institute and Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence (KS, USA)

Cite as: Vignoles A., Banks W. E., Klaric L., Kageyama M., Cobos M. E., Romero-Alvarez D. (2020) Investigating relationships between technological variability and ecology in the Middle Gravettian (ca. 32-28 ka cal. BP) in France. OSF, ud3hj, ver. 3 peer reviewed and recommended by PCI Archaeology. doi: 10.31219/osf.io/ud3hj

This article has been peer-reviewed and recommended by
Peer Community in Archaeology

doi: <https://doi.org/10.24072/pci.archaeo.100003>

Posted: created 22/03/2020, last edited 15/06/2020

Recommender: Felix Riede

Reviewers: Andreas Maier and João Marreiros

Correspondence: anaïs.vignoles@u-bordeaux.fr

ABSTRACT

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

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

that the niche associated with the northern Middle Gravettian is broader than that of the Pyrenees Noaillian. We propose that this pattern reflects different technological, subsistence and mobility strategies linked to the development of the Rayssie method in the North, which was likely more advantageous in such environmental contexts than those employed by the Pyrenees populations

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

1. Introduction

The Gravettian is an Upper Paleolithic techno-complex (*sensu* Clarke, 1968) that has been the subject of extensive research since its recognition (e.g. Klaric, 2003; de la Peña-Alonso, 2009, 2011; Noiret, 2013; Pesesse, 2013, 2017). Spanning *ca.* 34,000–26,000 calibrated years before present (y. cal. BP), its main unifying characteristics are Gravette-style backed blades and bladelets (Pesesse, 2013), diagnostic graphic expressions (Féruglio *et al.*, 2011), as well as a high frequency of burials (Henry-Gambier, 2008) compared to the preceding and following archaeological cultures. These common characteristics are observed in sites across Europe, from Portugal to the Don Valley in western Russia (Otte, 2013). However, the term “Gravettian” groups together a wide variety of cultural traditions, especially concerning lithic and osseous technology (de la Peña-Alonso, 2009; Pesesse, 2013; Noiret, 2013; Goutas, 2013a). This diversity is challenging to explain since it is characterized by disparate data, many of which were obtained with non-modern excavation methods decades ago or differing analytical approaches (de la Peña-Alonso, 2011; Pesesse, 2017). Moreover, sites that date to the same chronological interval but that lack typical Gravettian features (i.e. Gravette-style points) serve to challenge the definition of this techno-complex (e.g. Morala, 2011; Klaric *et al.*, 2011, 2018). Various hypotheses have been proposed to explain this diversity, such as differences in site activities (e.g. Laville & Rigaud, 1973; Rigaud, 1988), the nature of our archaeological definitions (e.g. Touzé, 2013; Pesesse, 2017), regionally differentiated populations that did not share the same technological knowledge or traditions (e.g. Klaric *et al.*, 2009), or differential environmental influences (e.g. David, 1985; Djindjian *et al.*, 1999). Efforts to identify and evaluate the mechanisms—defined as “a constellation of factors and components that through the process of their interaction with one another stimulates the trajectory of a system” (d’Errico & Banks, 2013, p. 374)—that influenced these cultural traditions can aid in assessing these various hypotheses.

1.1. The French Middle Gravettian

In France, the Middle Gravettian occurs between *ca.* 32–28.5 ky cal. BP and is defined by two *faciès*¹, termed the “Noaillian” and the “Rayssian” that are characterized principally on the basis of their lithic industries (Touzé, 2013). The Noaillian is a typological *faciès*, defined solely by the presence of Noailles burins²

¹ The term “*faciès*” (in French) is used to describe an archaeological entity according to “the nature of the considered remains and the method employed to study them” (Touzé, 2013, p. 397). This neutral term is especially useful in the case of the Middle Gravettian, since the two *faciès* are not defined equally.

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

(Bardon & Bouyssonies, 1903; Tixier, 1958), whereas the Rayssian is a typo-technological *faciès*, defined by a reduction method aimed at removing, from Raysse burins, bladelets that were used as armatures (Figure 1, Movius & David, 1970; Klaric *et al.*, 2002; Lucas, 2002; Pottier, 2006; Klaric, 2017), as well as a strong conceptual parallel between both bladelet and blade reduction sequences (Klaric, 2003, 2008).

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

The chronological relationship between the Noaillian and the Rayssian has yet to be determined with precision. This is due to the fact that very few contextually reliable ^{14}C ages are associated with these two *faciès*, and for regions north of the Garonne River the low number of available ages renders any chronological comparison between the two phases uninformative at present (Banks *et al.*, 2019). This situation is complicated by the fact that Noailles burins and the Raysse method are frequently found together within the same archaeological layer in the region of overlap. Past and on-going studies suggest that, at many sites, this association is not culturally meaningful due to imprecise excavation methods and / or disturbed stratigraphic contexts (e.g. Klaric, 2003, 2007; Vignoles *et al.*, 2019; A. Vignoles, PhD thesis on-going). However, in a few stratified contexts, the development of the Raysse method is always stratigraphically younger than the Noaillian³ (e.g., Abri Pataud and Flageolet I sites; David, 1985; Rigaud, 1982; Klaric, 2003). Numerous hypotheses have been proposed to explain the co-occurrence of Noaillian and Rayssian materials in the same archaeological level, such as a gradual replacement of the Noaillian by the Rayssian (David, 1985; Pottier,

³ Except for Les Jambes site, where Noailles burins are described as being stratigraphically *above* the Raysse burins (Célrier, 1967). This configuration, though, remains to be validated. First, the two levels identified by Célrier have been described as part of a slope deposit which raises doubts as to the integrity of the levels. Moreover, stratigraphic projections of artifacts show that the levels defined by Célrier correspond in fact to a single archaeological layer. Finally, a recent reexamination of the site's assemblage has shown that most of the “Noailles burins” do not correspond to the classic typological definition (A. Vignoles, on-going study). In fact, only one artifact can be considered a typical Noailles burin, while all the others are highly atypical. Technological characterization of the blade/bladelet reduction sequences (A. Vignoles, on-going study) may provide new data with which to discuss the presence of Gravette projectile points—a class of tool traditionally associated with the Noaillian rather than the Rayssian—at Les Jambes.

relationships of past hunter-gatherer populations, both synchronically and diachronically (e.g. Banks *et al.*, 2008, 2009, 2011, 2013; d'Errico *et al.*, 2017).

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

3. Topographic background: <http://www.natureearthdata.com>

2. Materials and Methods

2.1. Conceptual framework of ecological niche modelling

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

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

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

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

and typologies, with a few exceptions (e.g. Simonet, 2010), thus rendering difficult comparisons to sites studied via the methods traditionally used in France. An additional difficulty is related to this record's chronology. Noailles burins have been recovered from Cantabrian contexts that are contemporaneous with the Late Aurignacian in southwestern France and extending into the Solutrean (de la Peña-Alonso, 2011, p. 681). Noailles burin contexts in Italy are also interpreted as being younger than those in France (Touzé, 2013), but the majority of their associated radiocarbon ages were produced decades ago (non-AMS) and evaluations of their archaeological association are lacking, thus rendering any comparison to the French archaeological record unreliable at present.

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

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

In an effort to retain only sites for which a reliable techno-typological attribution could be made, published studies were carefully evaluated with respect to the pertinence of the data they contained. A source was considered pertinent if it provided precise typological (tool type) counts and detailed descriptions of artifact characteristics based on the most recent definitions, preferably supplemented with artifact drawings or photos. We also included personal observations made during the course of on-going and yet-to-be-published studies (L. Klaric and A. Vignoles). We, thus, did not retain sites for which one or both phases were only suspected to be present⁵ in order to avoid potentially aberrant attributions based on look-alike artifacts (such as for the “Raysse burins” from Brassempouy or Le Gratadis; Klaric, 2003, 2006; and for the “Noailles burins” from Les Jambes; A. Vignoles, on-going study). We also eliminated sites for which the presence of Raysse burin cores is not consensual, such as Chamvres in Yonne (Klaric, 2003 vs. Sarrazin, 2018). In the end, 74 sites were retained for our analysis. North of the Garonne River, there are 9 Rayssian sites, 40 Noaillian sites, as well as 13 additional sites that yield both *faciès*. In the Pyrenees piedmont and plateau, 12 Noaillian sites were retained (Figure 4; Table 1). More sites will certainly be added to this corpus in the future as existing collections are reexamined, as new excavations are undertaken at known sites, and as new sites are excavated.

⁵ e.g., sites where Raysse burins are depicted in published drawings (Klaric, 2003) but that have not been confirmed by us via direct observation and where the presence of the associated bladelet component has not yet been evaluated, such as the site of Roc de Gavaudun in Lot-et-Garonne or Lespoux shelter in Gironde (Monméjean *et al.*, 1964; Krtolitz & Lenoir, 1998) ; also sites where Noailles burins are all atypical, such as at Peutille site in Lot-et-Garonne (Morala, 1984), or sites where only one or two Noailles burins are reported and their presence is not supported by published drawings, such as La Verpillière I cave in Saône-et-Loire (Floss *et al.*, 2013).

Table 1. Sites retained or rejected based on a critical review of the literature, along with their geographic coordinates and references. Geographic coordinates correspond to the commune in which the site is localized. Although these coordinates do not necessarily correspond to the site itself, their resolution is more than adequate considering the 11.5 km-grid resolution of the environmental data.

Sites	Long. (E)	Lat. (N)	Noailles burins	Raysse method	References
<i>Middle Gravettian North of the Garonne River occurrence dataset</i>					
Abri André Ragout	0.42	45.68	presence	insufficient	Tixier, 1958; David, 1985
Abri Charbonnier	1.04	46.68	absence	presence	Aubry <i>et al.</i> , 2013; Klaric, pers. obs.
Abri de la Bergerie	1.58	44.48	presence	absence	Clottes <i>et al.</i> , 1990
Abri du Chasseur	0.42	45.68	presence	absence	Tixier, 1958; David, 1985
Abri du Couvert	1.02	44.49	presence	absence	Morala, 1984
Abri du Facteur	1.04	44.97	presence	presence	Delporte, 1968; David, 1985; Vignoles, pers. obs.
Abri du Poisson	1.01	44.94	presence	absence	de Sonneville-Bordes, 1960; David, 1985
Abri du Raysse	1.54	45.16	presence	presence	David, 1985; Touzé, 2011
Abri Durand-Ruel	0.65	45.37	presence	suspected	de Sonneville-Bordes, 1960; Daniel & Schmider, 1972; David, 1985
Abri Labattut	1.11	45.00	presence	insufficient	de Sonneville-Bordes, 1960; David, 1985
Abri Laroux	0.73	46.40	presence	suspected	de Sonneville-Bordes, 1960; David, 1985
Abri Lespaux	-0.29	44.82	presence	suspected	David, 1985; Krtoliza & Lenoir, 1998
Abri Pagès	1.04	44.97	presence	absence	de Sonneville-Bordes, 1960; David, 1985
Abri Pataud	1.01	44.94	presence	presence	David, 1985; Bricker (dir.), 1995; Pottier, 2005, 2006; Nespoulet, 2008
Abri Peyrony	0.89	44.56	presence	absence	Le Tensorer, 1981; David, 1985
Bassaler-Nord	1.54	45.16	presence	presence	David, 1985; Touzé, 2011
Combe Saunière	0.87	45.24	presence	presence	Klaric, 2017; Klaric, pers. obs.
Gisement de la Chèvre	0.59	45.32	presence	insufficient	David, 1985; Arambourou & Jude, 1964
Grand-abri de Laussel	1.14	44.94	presence	presence	Roussot, 1985; David, 1985; Klaric, 2017; Klaric, pers. obs.
Grotte "Chez Serre"	1.53	45.10	presence	absence	David, 1985
Grotte Bouyssonie	1.54	45.16	presence	presence	Touzé, 2011; Klaric, 2017; Klaric, pers. obs.
Grotte de Champ	1.53	45.16	presence	insufficient	David, 1985; Daniel, 1969

Table 1. continued

Sites	Long. (E)	Lat. (N)	Noailles burins	Raysse method	References
Grotte de Rouzet	1.69	44.00	presence	absence	Foucher <i>et al.</i> , 2008
Grotte d'Oreille d'Enfer	1.01	44.94	presence	absence	de Sonneville-Bordes, 1960; David, 1985; Pradel, 1959
Grotte du Renne	3.76	47.60	absence	presence	Klaric, 2003
Grotte du Trilobite	3.76	47.60	absence	presence	Klaric, 2003; David, 1985
Grotte Lacoste	1.54	45.16	presence	absence	David, 1985
Grotte Maldidier	1.18	44.83	presence	presence	Klaric, 2017; Caux <i>in</i> Boudadi-Maligne, 2012
Grotte Thévenard	1.54	45.16	presence	insufficient	David, 1985
Guiraudel	0.95	44.54	presence	absence	Morala, 1984
Hautmougey	6.26	48.00	presence	absence	Hans, 1997
La Croix-de- Bagneux	1.33	47.29	presence	absence	Kildea & Lang, 2011, 2013
La Ferrassie	0.95	44.97	presence	absence	de Sonneville-Bordes, 1960; David, 1985
La Font-Robert	1.54	45.16	presence	insufficient	de Sonneville-Bordes, 1960; David, 1985
La Martinière	-0.86	47.36	presence	suspected	Allard, 1986
La Picardie	0.93	46.86	absence	presence	Klaric, 2003; Klaric <i>et al.</i> , 2011; Klaric <i>et al.</i> , 2018
La Rochette	1.09	45.01	presence	suspected	de Sonneville-Bordes, 1960; Schmider, 1969; David, 1985; Klaric, 2003, p.220
La Roque Saint- Christophe	1.08	44.99	presence	presence	de Sonneville-Bordes, 1960; David, 1985; Vignoles, pers. obs.
Las Pélénos	0.93	44.50	presence	absence	Morala, 1984
Le Caillou	0.45	44.78	presence	absence	Boyer <i>et al.</i> , 1984
Le Callan	0.97	44.60	presence	absence	Morala, 2011
Le Flageolet I	1.09	44.84	presence	presence	Rigaud, 1982; David, 1985; Lucas, 2000; Gottardi, 2011
Le Fourneau du Diable	0.59	45.32	presence	presence	David, 1985; Klaric, 2003, 2017; Vignoles <i>et al.</i> , 2019
Le Petit- Puyrousseau	0.72	45.19	presence	insufficient	de Sonneville-Bordes, 1960; Daniel, 1967; David, 1985
Le Roc de Cavart	1.07	44.54	presence	absence	Le Tensorer, 1981; David, 1985
Le Roc de Gavaudun	0.89	44.56	presence	suspected	de Sonneville-Bordes, 1960; Monméjean <i>et al.</i> , 1964; Le Tensorer, 1981; David, 1985
Le Taillis des Coteaux	-0.77	46.62	absence	presence	Klaric, 2017
Les Artigaux	-0.27	44.79	unlikely	presence	Lenoir, 1977; Klaric, 2003; Vignoles, obs. pers

Table 1. continued

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

Table 1. continued

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

2.2.2. Environmental predictors

In order to employ the appropriate environmental data, it is paramount to determine accurately the precise chronology of the target archaeological culture so that it can be correlated to the appropriate climatic event or events (Banks, 2015; Banks *et al.*, 2019). Based on the results presented by Banks *et al.*, (2019), the Middle Gravettian was present during Greenland Stadial 5 (GS.5), during which occurred Heinrich Event 3 (HE3).

We employed as environmental background climatic variables derived from a high-resolution paleoclimatic simulation obtained with the Atmospheric Global Circulation Model (AGCM) LMDZ5A (Hourdin

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

Results were further downscaled to a spatial resolution of 11.5 km via the spline interpolation available in ArcMap 10.7.1. The simulated variables employed in this analysis are mean annual precipitation, warmest month temperature and coldest month temperature. We did not use elevation as a covariate in this process considering its high correlation with temperature.

2.3. Ecological niche modeling

2.3.1. Modeling preparation

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

The definition of the calibration area (**M**) relies on biogeographic assumptions (Peterson *et al.*, 2011 p. 135; Barve *et al.*, 2011). To define (**M**) for Middle Gravettian hunter-gatherers in our region of study (Figure 4), we hypothesize that these populations could not live in regions in close proximity to ice sheets, and that they could have occupied areas exposed by the period's lower sea levels. We therefore masked the environmental variables with coast lines 90 m below present day sea level (Waelbroeck *et al.*, 2002; Siddall *et al.*, 2003), as well as with LGM ice sheet coverage reconstructions in the Alps, Pyrenees and the Massif Central (Ehlers & Gibbard, 2004). While these reconstructions over-estimate ice coverage for *ca.* 32 ky cal. BP, they still serve as an adequate proxy since the areas in question would have been characterized by cold and dry, if not periglacial, conditions during the corresponding stadial and HE. Furthermore, the nature of raw material

(flint) circulation in the Pyrenees region (Foucher *et al.*, 2008; Simonet, 2017) led us to permit the predictive modeling architectures to extrapolate into the regions of Cantabria and Catalonia. Finally, the Rhône River Valley in the East may have served to limit the movements of hunter-gatherer populations (no raw material circulation between either sides of the Valley, cf. Santaniello, 2016). Indeed, recent geomorphological studies show that the lower and middle Rhône Valley as well as the Mediterranean continental shelf likely consisted of a desert, with deflation-related landforms (e.g., yardangs, pans, desert pavements) and sands deposits (dunes, sand ramps) surrounded by loess accumulations during the coldest events of the Last Glacial period (Bosq *et al.*, 2018). However, the presence of Noailles burins and Gravette points to the east indicates that they were permeable barriers. Thus, we included in our **(M)** coastal regions of Liguria, Tuscany, Lazio and Campania in present-day Italy where Noailles burins are observed in the archaeological record (Palma di Cesnola, 1991; Touzé, 2013). This step was performed in QGIS 2.18.28.

2.3.2. Model calibration and selection

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

2.3.3. Creation of final models and model comparisons

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

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

Parameters			Evaluation results				
Regularization multiplier	Features	Environmental variables	Partial ROC	Omission rates below 5%	AICc	Δ_{AICc}	Number of parameters
<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	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

Table 2. *continued*

Regularization multiplier	Features	Environmental variables	Partial ROC	Omission rates below 5%	AICc	ΔAICc	Number of parameters
0.9	Q	ctemp, wtemp	0	0	172.262	1.679	2
0.9	Q	All	0	0	172.262	1.679	2
0.4	LQP	ctemp, mprec	0	0	172.303	1.721	2
0.8	LQ	ctemp, mprec	0	0	172.303	1.721	2
0.5	QP	ctemp, wtemp	0	0	172.306	1.724	2
1	Q	All	0	0	172.306	1.724	2
1	Q	ctemp, wtemp	0	0	172.306	1.724	2
5	Q	ctemp, mprec	0	0	172.311	1.729	1
5	LQ	ctemp, mprec	0	0	172.311	1.729	1
0.9	LQ	ctemp, mprec	0	0	172.366	1.783	2
0.6	QP	ctemp, wtemp	0	0	172.404	1.822	2
0.6	LQP	ctemp, wtemp	0	0	172.404	1.822	2
0.5	LQP	ctemp, mprec	0	0	172.433	1.851	2
1	LQ	ctemp, mprec	0	0	172.433	1.851	2
0.7	QP	ctemp, wtemp	0	0	172.513	1.930	2
0.7	LQP	ctemp, wtemp	0	0	172.513	1.930	2

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

Model comparisons were performed in both geographic and environmental spaces. To compare the geographic projections of the niches, we used the background similarity and identity tests (Warren *et al.*, 2008, 2017) which quantifies the similarity / identity between two predictions by measuring their geographic overlap and then comparing the result to a null distribution. The two metrics recommended for such comparisons are Schoener (1968)'s statistic *D* for niche overlap and the similarity statistic *I*. They range from 0 (no similarity / identity) to 1 (total similarity / identity) and are obtained via the comparison of the two empirical niche predictions. The measurement is then compared to those obtained from 1000 sets of null niche predictions produced using occurrences randomly sampled from the environmental background of the calibration area. The difference between the two predictions is deemed to be significant if the empirical value fall below the 95% limits of the null distribution, respectively. To compare niches in environmental space, we used NicheA (Qiao *et al.*, 2016). We employed a three-dimensional environmental background using the three retained paleoclimatic variables to develop minimum volume ellipsoid (MVE) niche estimations, with a precision of 0.01, for the Pyrenees Noaillian and the northern Middle Gravettian (Figure 4). The volume of each ellipsoid was measured, and their level of environmental overlap was calculated using the Jaccard index (Qiao *et al.*, 2016; Qiao *et al.*, 2017).

3. Results

3.1. Niche predictions

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

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

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

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

3.2. Niche comparisons

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

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

4. Discussion

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

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

The Raysse method is a highly standardized reduction method that can be applied to a wide variety of blanks, from blades to thick flakes produced during various stages of the blade reduction sequences or other less standardized reduction sequences (e.g., production of flakes or blade-like flakes). The bladelets produced with the Raysse method did not require further intensive modification due to their standardized morphology. Furthermore, if a problem was encountered during the final stages of their production, only minimal investment was needed to produce a new or replacement bladelet (Klaric *et al.*, 2002, 2009; Klaric, 2003, 2008, 2017). This highly standardized bladelet production system served to create end-products that could be easily transformed into armatures that were likely part of a composite and maintainable hunting weaponry toolkit, an adaptation commonly observed in highly mobile hunter-gatherers that operate in landscapes where access to resources needed to maintain weaponry is unpredictable (Binford 1977; Bleed, 1986). The importance placed on producing highly standardized components for a maintainable and curated hunting toolkit is further supported by the emphasis that appears to have been placed on transmitting and maintaining this technique (Klaric, 2017, 2018). This has been inferred from the numerous technical details that one must take into account when using the Raysse method to replicate La Picardie bladelet blanks, and this is further supported by the frequent presence of flint knapping debris and artifacts that appear to have been produced by apprentices or individuals who still did not completely master the intricacies of the method (Klaric, 2017, 2018).

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

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

narrow ecological niche. The high prey species diversity could therefore be the result of a more generalized hunting strategy within a reduced territory.

To the north, on the other hand, the wider range of environmental conditions (i.e., broader ecological niche) exploited by the northern Middle Gravettian populations would suggest a higher degree of mobility than is observed in the Pyrenees since the main prey species identified in northern archaeological assemblages is reindeer (Lacarrière, 2015). Higher mobility is supported by technological data. For example, the Grotte du Renne site is located some distance from high quality lithic raw material sources (35 to 120 km according to Klaric *et al.*, 2009), and its Middle Gravettian assemblage shows a high degree of curation, in contrast to other sites that are situated on or near raw material sources, such as the site of La Picardie⁶. With respect to curation, Raysse burins (i.e. bladelet cores) from the Grotte du Renne often have double bladelet production platforms, are smaller than those recovered from La Picardie, and the blanks selected to make La Picardie bladelets are generally smaller and are not always typical: bladelets can be more twisted, they do not always have a *pan-revers* and/or a pointed distal end (Klaric, 2006, 2017; Klaric *et al.*, 2009). In this scenario, the Raysse method could represent a technological specialization directed at producing armatures for hunting reindeer. Nevertheless, one must be careful to not generalize this pattern, since it relies on only a handful of studies, and numerous sites have assemblages that contain both by-products of the Raysse method and Gravette points, two conceptually different *chaînes opératoires* (i.e. reduction sequences), and thus different kinds of composite hunting weapons. Whether these two types of armatures—la Picardie bladelets and Gravettes/microgravettes—were associated with the same hunting tool-kit or whether their association in the same archaeological level is the result of post-depositional processes or palimpsest deposits⁷, is a subject that requires further study. At present, only the site of Callan represents specialized occupations or activities north of the Garonne River (Morala, 2011). It has a lithic assemblage dominated by Noailles burins and no armatures have been recovered. This general absence of specialized sites suggests that groups in these higher latitude regions had a higher level of residential mobility than those in the Pyrenees. Such a pattern of highly mobile groups using highly standardized and curated toolkits to exploit large territories via a residential system of mobility is in sharp contradiction to the pattern observed during the same period in the Pyrenees. This pattern, though, may be accentuated by the lack of chronological resolution for this time-period, which is the result of reduced stratigraphic resolution due to imprecise excavation methods, to post-depositional mixing of levels, palimpsest deposits and the standard errors associated with radiocarbon ages for this period. Such factors make determinations of discrete activity episodes difficult, if not impossible, and the potential homogenization of archaeological levels renders making inferences of how human activities were organized across the landscape difficult.

⁶ Although a small percentage of artifacts at La Picardie are made from raw materials coming from sources located in the Charente region, some 200 km away (Delvigne *et al.*, 2020).

⁷ We must bear in mind that occurrences of Picardie bladelets and Gravettes together are observed exclusively within cave or rockshelter deposits, where archaeological levels represent palimpsests of multiple occupations and were often subjected to complex post-depositional processes that can homogenize initially distinct occupations. The co-occurrence of the two armature types is also observed at two open-air sites: the site of Solvieux in Dordogne (Sackett, 1999), where the stratigraphic setting is extremely complex and Sackett's analysis has raised doubts concerning the full homogeneity of its archaeological assemblages, and the site of Les Jambes in Dordogne (Célérier, 1967), where slope depositional processes were predominant in the site's formation (Klaric, 2003, p. 222), thus raising doubts as to whether the distinct archaeological levels defined by Célérier are valid (A. Vignoles, on-going study).

With respect to the geographic expressions of the estimated niches and the technological differentiation observed between the two regions, what factors potentially influenced these patterns? We propose that the cold desert of the Landes region (Bertran *et al.*, 2013) and the Garonne River Valley corridor served as an ecological barrier that played a role in the territories exploited by Middle Gravettian hunter-gatherer populations. This barrier would have prevented the unconstrained diffusion of the Raysse method to the Pyrenees area. This idea is however challenged by the fact that this region is identified as suitable (Figure 5), although this suitability is very low. This contradiction, though, can be explained by the fact that the Landes' cold desert is more the result of a particular geographic and geomorphological context rather than specific climatic conditions (Bertran, pers. com.). In this case, the climatic variables used for this study would not be sufficient to capture the particular conditions of a cold desert. Another scenario that can explain this low suitability area is that the barrier between these two regions might have been cultural. This hypothesis would explain the fact that the Pyrenees Noaillian's existing niche is more geographically extended than the distribution of sites used to reconstruct it, whereas the northern Middle Gravettian niche is more fitted to its occurrence data. In this case, the presence of another population in these northern suitable habitats would have prevented the Pyrenees populations from occupying their entire niche.

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

Finally, the limits of our data and employed methodology need to be kept in mind. Firstly, the Pyrenees Noaillian dataset is very small and comprised of only 10 occurrence points. Although evaluations indicate that the Pyrenees Noaillian Maxent niche estimation is robust, it is possible that comparisons with the northern Middle Gravettian niche, derived from 20 occurrences, could be biased with respect to environmental

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

5. Conclusions

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

Comparisons of the reconstructed niches for these two *faciès*, in both geographic and environmental dimensions, indicate that their respective niches were significantly different, despite their large overlap in environmental space, due to the fact that the northern Middle Gravettian niche was significantly broader than that of the Pyrenees Noaillian. This pattern strongly suggests that the appearance of the Raysse method is related to this significant expansion of the niche, meaning that this new method of producing bladelet armature components is linked to the exploitation of a broader range of ecological conditions. As opposed to what is observed in areas south of the Garonne River, the Raysse method appears to have been associated with mobility and settlement strategies contained within a larger exploited territory or territories. Furthermore, this observed pattern suggests that La Picardie bladelets (products of the Raysse method) represented a technological specialization directly associated with a hunting strategy focused on reindeer. Picardie bladelets may have been more appropriate within this context than backed blades and bladelet armatures (such as Gravettes), although this hypothesis would need further testing in the archaeological record. Furthermore, the Raysse method would have been advantageous in such contexts because it would have been more easily maintainable and more adapted to hunting activities organized within territories where access to raw material resources was less predictable or available. Conversely, the Pyrenees Noaillian's armature diversity may reflect less specialized hunting practices within a smaller territory. In this context, the need for a highly maintainable hunting toolkit was probably not as paramount, since access to raw material resources would have been more predictable or available.

These niche results further support the hypothesis that the Landes cold desert and Garonne River Valley corridor served to limit, at some point in time, technological traditions homogenization between the Pyrenees and regions to the north. The nature of this barrier (i.e. environmental and/or cultural) should be further evaluated by incorporating other potentially pertinent variables (distribution of cold deserts, etc.) in future ecological niche modeling analyses that target archaeological populations. Furthermore, continued investigations centered on identifying Middle Gravettian sites and the typo-technological attributes of their archaeological assemblages are necessary. In turn, these niche modeling results will provide important details

to continued research that addresses chronology, settlement and subsistence strategies, lithic raw material exploitation, lithic and bone technologies, and site function of the Middle Gravettian archaeological record.

Supplementary material

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

Acknowledgements

We thank A. Townsend Peterson for hosting a collaborative trip to the University of Kansas' Biodiversity Institute. The climate simulations were run on the Mercure supercomputer maintained by the Commissariat à l'Energie Atomique's Très Grand Centre de Calculs. We thank A. Townsend Peterson, Mathieu Bosq and Pascal Bertran for their input during the writing of the article. Finally, we thank Andreas Maier and João Marreiros for their critical reviews that served to improve the paper. Version 3 of this preprint has been peer-reviewed and recommended by Peer Community In Archaeology (<https://doi.org/10.24072/pci.archaeo.100003>)

Conflict of interest disclosure

The authors of this preprint declare that they have no financial conflict of interest with the content of this article. W. E. Banks is recommender for PCI Archaeology.

References

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

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

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

Alkama, R., Kageyama, M., Ramstein, G., Marti, O., Ribstein, P., & Swingedouw, D. (2008). Impact of a realistic river routing in coupled ocean–atmosphere simulations of the Last Glacial Maximum climate. *Climate Dynamics*, 30(7–8), 855–869. <https://doi.org/10.1007/s00382-007-0330-1>

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

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

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

Anderson, R. P., & Gonzalez, I. J. (2011). Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. *Ecological Modelling*, 222, 279–281. <https://doi.org/10.1016/j.ecolmodel.2011.04.011>

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

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

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

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

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

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

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

Banks, W. E., d'Errico, F., Peterson, A. T., Vanhaeren, M., Kageyama, M., Sepulchre, P., Ramstein, G., Jost, A., & Lunt, D. (2008). Human ecological niches and ranges during the LGM in Europe derived from an application of eco-cultural niche modeling. *Journal of Archaeological Science*, 35(2), 481–491.

<https://doi.org/10.1016/j.jas.2007.05.011>

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

Banks, W. E., Aubry, T., d'Errico, F., Zilhão, J., Lira-Noriega, A., & Townsend Peterson, A. (2011). Eco-cultural niches of the Badegoulian: Unraveling links between cultural adaptation and ecology during the Last Glacial Maximum in France. *Journal of Anthropological Archaeology*, 30(3), 359–374.

<https://doi.org/10.1016/j.jaa.2011.05.003>

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

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

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

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., Soberón, J., & Villalobos, F. (2011). The Crucial Role of the Accessible Area in Ecological Niche Modeling and Species Distribution Modeling. *Ecological Modelling*, 222(11), 1810–19.

<https://doi.org/10.1016/j.ecolmodel.2011.02.011>.

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

Bertran, P., Sitzia, L., Banks, W. E., Bateman, M. D., Demars, P.-Y., Hernandez, M., Lenoir, M., Mercier, N., & Prodeo, F. (2013). The Landes de Gascogne (southwest France): periglacial desert and cultural frontier during the Palaeolithic. *Journal of Archaeological Science*, 40(5), 2274–2285.

<https://doi.org/10.1016/j.jas.2013.01.012>

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

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

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

Bosq, M., Bertran, P., Degeai, J.-P., Kreutzer, S., Queffelec, A., Moine, O., & Morin, E. (2018). Last Glacial aeolian landforms and deposits in the Rhône Valley (SE France): Spatial distribution and grain-size characterization. *Geomorphology*, 318, 250–269. <https://doi.org/10.1016/j.geomorph.2018.06.010>

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

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

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

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

Caux, S. (2012). *Etude de l'industrie lithique*. In Boudadi-Maligne, M. (dir.) *Grotte de Maudidier (La Roque-Gageac, Dordogne), Rapport d'opération de fouille programmée* (pp. 111–118). Bordeaux: Service régional de l'archéologie, Direction régionale des affaires culturelles Aquitaine.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Delvigne, V., Fernandes, P., Tuffery, C., Raynal, J.-P., & Klaric, L. (2020). Taphonomic methods and a database to establish the origin of sedimentary silicified rocks from the Middle-recent Gravettian open-air

site of La Picardie (Indre-et-Loire, France). *Journal of Archaeological Science: Reports*, 32, 102369.
<https://doi.org/10.1016/j.jasrep.2020.102369>

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

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

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

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

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

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

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

Foucher, P. (2013). Synthèse chrono-culturelle sur le Gravettien des Pyrénées : constat et réflexions sur la stabilité régionale des traditions techniques. In de la Heras C., Lasheras J.A., Arrizalaga A., de la Rasilla M. (dir.). *Pensando el Gravetiense : nuevos datos para la region cantabrica en su contexto peninsular y pirenaico* (monografias 23, pp. 142–159). Santander, Madrid: Museo Nacional y Centro de Investigacion de Altamira.

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

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

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

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

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

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

Guillermin, P. (2006). Les Fieux : une occupation gravettienne du Causse quercinois. *Paléo*, 18, 69–94.

Guillermin, P. (2008). Les « Périgordiens » en Quercy : l'exemple du gisement des Fieux. *Paléo*, 20, 357–372.

Guillermin, P. (2011). La fin du Gravettien dans le sud-ouest de la France : à la recherche de l'identité protomagdalénienne. In Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la recherche des identités gravettiennes. Actualités, questionnements, perspectives* (Mémoire 52, pp. 129–146). Paris: Société préhistorique française.

Hans, J.-M. (1997). Périgordien à burins de Noailles : le site de Hautmougey (canton de Bains-les-Bains, Vosges). *Bulletin de la Société Préhistorique Luxembourgeoise*, 19, 55–66.

Henry-Gambier, D. (2008). Comportement des populations d'Europe au Gravettien : pratiques funéraires et interprétations. *Paléo*, 20, 399–438.

Hinguant, S., & Monnier, J.-L. (2013). Le Paléolithique supérieur ancien dans le Massif armoricain : un état de la question. In Bodu P., Chehmana L., Klaric L., Mevel L., Soriano S., Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l'Europe du Nord-Ouest* (Mémoire 56, pp. 229–238). Paris: Société préhistorique française.

Hourdin, F., Foujols, M.-A., Codron, F., Guemas, V., Dufresne, J.-L., Bony, S., Denvil, S., Guez, L., Lott, F., Ghattas, J., Braconnot, P., Marti, O., Meurdesoif, Y., & Bopp, L. (2013). Impact of the LMDZ atmospheric grid configuration on the climate and sensitivity of the IPSL-CM5A coupled model. *Climate Dynamics*, 40(9–10), 2167–2192. <https://doi.org/10.1007/s00382-012-1411-3>

Hutchinson, G. E. (1957). Population studies: Animal ecology and demography. *Bulletin of Mathematical Biology*, 53(1–2), 193–213.

Kageyama, M., Braconnot, P., Bopp, L., Caubel, A., Foujols, M.-A., Guilyardi, E., Khodri, M., Lloyd, J., Lombard, F., Mariotti, V., Marti, O., Roy, T., & Woillez, M.-N. (2013). Mid-Holocene and Last Glacial Maximum climate simulations with the IPSL model—part I: comparing IPSL_CM5A to IPSL_CM4. *Climate Dynamics*, 40(9–10), 2447–2468. <https://doi.org/10.1007/s00382-012-1488-8>

Kildea, F., & Lang, L. (2011). Le Gravettien de la vallée du Cher : le site de la Croix-de-Bagneux à Mareuil-sur-Cher (Loir-et-Cher, France). In Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la recherche des identités gravettiennes. Actualités, questionnements, perspectives* (Mémoire 52, pp. 273–290). Paris: Société préhistorique française.

Kildea, F., Griselin, S., Lang, L., & Souffi, B. (2013). Le Paléolithique supérieur ancien aux marges méridionales du Bassin parisien : le site de la Croix-de-Bagneux à Mareuil-sur-Cher (Loir-et-Cher). In Bodu P., Chehmana L., Klaric L., Mevel L., Soriano S., Teyssandier N. (dir.) *Le Paléolithique supérieur ancien de l'Europe du Nord-Ouest* (Mémoire 56, pp. 317–330). Paris: Société préhistorique française.

Klaric, L. (2003). *Technical unity of Raysse burins industries in their diachronical context. Thoughts about cultural variability during Gravettian, based on the case of La Picardie, Arcy-sur-Cure, Brassempouy and Le Cirque de la Patrie*. [doctoral thesis]. Paris: Université Panthéon-Sorbonne - Paris I.

Klaric, L. (2006). Des armatures aux burins : des critères de distinction techniques et culturels à partir des productions lamellaires de quelques sites du Gravettien moyen et récent (France). In Lebrun-Ricalens F. (Ed.) *Burins préhistoriques : formes, fonctionnements, fonctions* (n°2, pp. 199–223). Luxembourg: Archéologiques.

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

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

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

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

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

Klaric, L., Guillermin, P., & Aubry, T. (2009). Des armatures variées et des modes de productions variables. Réflexions à partir de quelques exemples issus du Gravettien d'Europe occidentale (France, Portugal, Allemagne). *Gallia préhistoire*, 51(1), 113–154. <https://doi.org/10.3406/galip.2009.2476>

Klaric, L., Liard, M., Bertran, P., Dumarçay, G., de Araujo Igreja, M., Aubry, T., & Walter, B. (2011). La Picardie (Preuilly-sur-Claise, Indre-et-Loire) : neuf ans de fouille sur un gisement rayssien finalement pas si mal conservé ! In Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la recherche des identités*

gravettiennes. *Actualités, questionnements, perspectives* (Mémoire 52, pp. 291–310). Paris: Société préhistorique française.

Klaric, L., Bertran, P., Dumarçay, G., & Liard, M. (2018). A long and winding road: Towards a palethnographic interpretation of the middle-Gravettian site of la Picardie (Indre-et-Loire, France). *Quaternary International*, 498, 51–68. <https://doi.org/10.1016/j.quaint.2018.09.035>

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

Lacarrière, J. (2015). *Les ressources cynégétiques au Gravettien en France : acquisition et modalités d'exploitation des animaux durant la phase d'instabilité climatique précédant le dernier maximum glaciaire* [doctoral thesis]. Toulouse: Université Toulouse le Mirail - Toulouse II.

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

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

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

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

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

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

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

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

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

Marti, O., Braconnot, P., Dufresne, J.-L., Bellier, J., Benshila, R., Bony, S., Brockmann, P., Cadule, P., Caubel, A., Codron, F., De Noblet, N., Denvil, S., Fairhead, L., Fichet, T., Foujols, M.-A., Friedlingstein, P.,

Goosse, H., Grandpeix, J.-Y., Guilyardi, E., ... Talandier, C. (2010). Key features of the IPSL ocean atmosphere model and its sensitivity to atmospheric resolution. *Climate Dynamics*, 34, 1–26.

<https://doi.org/10.1007/s00382-009-0640-6>

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Rigaud, J.-P. (2011). Révision de quelques archéoséquences de référence du Gravettien du nord de l'Aquitaine. In Goutas N., Klaric L., Pesesse D., Guillermin P. (dir.) *À la recherche des identités gravettiennes. Actualités, questionnements, perspectives* (Mémoire 52, pp. 175–183). Paris: Société préhistorique française.

Roussot, A. (1985). Inventaire typologique des industries de Laussel (tableaux inédits de Jean Bouyssonie). *Bulletin de la Société préhistorique française*, 82(1), 15–19. <https://doi.org/10.3406/pal.1990.1412>

Sackett, J. (1999). *The Archaeology of Solvieux. An Upper Paleolithic Open Air Site in France*. Los Angeles (CA): Institute of Archaeology.

Santaniello, F. (2016). *Il Gravettiano dell'Italia tirrenica nel contesto mediterraneo: definizione delle strategie di insediamento e mobilità attraverso lo studio delle materie prime e delle industrie litiche* [doctoral thesis]. Trento, IT: Università degli studi di Trento, Université Nice Sophia Antipolis.

Santaniello, F., & Grimaldi, S. (2019). Le Gravettien entre l'Italie et la France : nouvelles données sur l'industrie lithique de l'Abri Mochi (Balzi Rossi, Italie). *Bulletin de la Société Préhistorique Française*, 116(2), 255–282.

Sarrazin, C. (2017). *Les burins-nucléus du Raysse de la collection des Morts (Grotte des Morts, Brive-la-Gaillarde). Interprétation du schéma opératoire et analyse des séquences*. [master thesis]. Rennes: Université Rennes 2.

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

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

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

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

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

Sima, A., Kageyama, M., Rousseau, D.-D., Ramstein, G., Balkanski, Y., Antoine, P., & Hatté, C. (2013). Modeling dust emission response to North Atlantic millennial-scale climate variations from the perspective of

East European MIS 3 loess deposits. *Climate of the Past*, 9(4), 1385–1402. <https://doi.org/10.5194/cp-9-1385-2013>

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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