Research Article

Aurélie Liard*, Carmen María Martínez Varea, François Orange, Jean-Paul Huot, Benjamin Marquebielle, Auréade Henry*

Environment and Plant Use at La Tourasse (South-West France) at the Late Glacial–Holocene Transition

Abstract: The aim of this study is to present new data on vegetation dynamics and plant collecting practices during the Late Glacial and the Early Holocene in southwestern France. La Tourasse cave is located in the Pyrenean piedmont plain, where the Azilian cultural complex was initially defined. The last excavations of the site took place in the 1980s and 1990s and the recovered materials are currently being studied or revisited from a multidisciplinary perspective. We present here the results of the charcoal analysis performed on La Tourasse's Azilian (ca. 13000–11500 cal. BP) and Mesolithic (ca. 10500–9000 cal. BP) levels, complemented by the study of a small seed assemblage. Our results document the shift from an open landscape towards a forested environment, with the gradual passage from open vegetation dominated by shrubs of the Rose family (*Prunus* spp.) to the mixed oak forest, which speaks in favor of the biochronological coherence of this sequence. However, marked differences in taxonomic richness and state of the wood from one level to another, unrelated to the prevailing environmental conditions, suggest variable behavior of humans toward wood that could be the result of differing mobility strategies, hearth functionalities, or taxonomic preferences.

Keywords: Archaeobotany, firewood, plant economy, Late Glacial, Azilian, Mesolithic, Southwest France

1 Introduction

The Pleistocene–Holocene transition, punctuated by abrupt climatic oscillations, was characterized by global warming leading to significant changes in topography, flora, and fauna, which had a deep impact

* **Corresponding author: Aurélie Liard,** Université Côte d'Azur, Laboratoire Cultures, Environnements, Préhistoire, Antiquité, Moyen-âge, CNRS UMR 7264- CEPAM, Nice, France, e-mail: aurelie.liard@cepam.cnrs.fr
* **Corresponding author: Auréade Henry,** Université Côte d'Azur, Laboratoire Cultures, Environnements, Préhistoire, Antiquité, Moyen-âge, CNRS UMR 7264- CEPAM, Nice, France, e-mail: aureade.henry@cnrs.fr
Carmen María Martínez Varea: Université Montpellier 2, Institut des Sciences de l'évolution de Montpellier, CNRS UMR 5554-ISEM, Montpellier, France; Universitat de València, Departament de Prehistòria, Arqueologia i Història Antiga, GIUV 2015-213 PREMEDOC, València, Spain; Universidad de Salamanca, Departamento de Prehistoria, Historia Antigua y Arqueología, GIR-PREHUSAL, Salamanca, Spain
François Orange: Université Côte d'Azur, Centre Commun de Microscopie Appliquée, (CCMA), Nice, France
Jean-Paul Huot: Independent Researcher, Saint-Mandé, France
Benjamin Marquebielle: Université Toulouse 2-Jean Jaurès, Laboratoire Travaux et Recherches Archéologiques sur les Cultures, les Espaces, et les Sociétés CNRS UMR 5608-TRACES, Toulouse, France

on the social, economic and territorial organization, of European hunter-gatherer societies (Binney et al., 2017; Brewer, Cheddadi, de Beaulieu, & Reille, 2002; Costamagno et al., 2008, 2016; Isarin & Bohncke, 1999; Jalut et al., 1992; Naughton et al., 2016; Protin et al., 2021; Rasmussen et al., 2014). In the southwest of France, one of the cradles of Prehistoric research, there have been very early attempts of confronting cultural, bioarchaeological, and stratigraphic data to understand human lifeways in the context of climate change (e.g., de Mortillet, 1895; Piette, 1895, 1907). While contributing to the worldwide renown of major sites, the excavations performed until the 1960's irremediably destroyed crucial archaeological evidence due to the excavation methods of the time and unsystematic or selective sampling strategies (Barrière, 1959; Breuil, 1950; Piette, 1895). Sometime until fairly recently, macrobotanical remains constituted a particularly overlooked category of vestiges that were not systematically or properly retrieved from the archaeological sediments (e.g., Badal García, 1992; Bazile-Robert, 1984). In the course of the last 50 years, the emergence of charcoal analysis and the constant improvement in archaeobotanical methodologies and protocols has allowed reconstructing local vegetation histories and plant use at a number of sites (Barbaza, 2011; Heinz & Thiébault, 1998; Henry & Boboeuf, 2016; Krauss-Marguet, 1980; Vernet, 1980). In the 1980's, off-site paleoenvironmental sequences were already providing palynological coverage for the Late Glacial and Early Holocene in the Pyrenees, the Rhone valley, and the southern Massif Central (Andrieu, Hubschman, Jalut, & Hérail, 1988; De Beaulieu, Pons, & Reille, 1985; Jalut et al., 1992; Reille, 1990; Triat-Laval, 1982). On the French side of the Pyrenees, many of these archaeological and natural sequences are a little outdated and lack high resolution records, while the last anthracological studies were published in the 1990's (Barbaza & Heinz, 1992; Heinz, 1991, 1999; Heinz & Barbaza, 1998; Heinz, Ruas, & Vaquer, 1992). Thus, there is currently a lack of data for certain areas and we still lack chronological resolution to understand more precisely the timing of the environmental changes and their impact on the landscape. The conditions of the development of the vegetation during the last interstadial and of the vegetational response to the Younger Dryas stadial seem to have varied between sites not only due to the broad climatic influences to which the area is subjected, Atlantic or Mediterranean, but also due to local conditions (Andrieu, Hubschman, Jalut, & Hérail, 1988; Beaudouin, Jouet, Suc, Berné, & Escarguel, 2007; Heinz, 1999; Jalut & Turu i Michels, 2006).

On the other hand, we still know little about the relationships of the successive hunter-gatherer cultures with the vegetal world. The carpological evidence at the scale of southwest France is still scarce, with very punctual data regarding the Azilian period, and rather poor taxonomic spectra usually dominated by hazel regarding the Mesolithic, the latter being at least partly overrepresented due to insufficient sampling protocols (Bouby & Surmely, 2004; Henry, Bouby, & Valdeyron, 2011; Marinval, 1988; 2007; Valdeyron et al., 2011; Vaquer & Ruas, 2009). This study proposes a reconstruction of the woody landscape and human practices related to plant resources between ca. 13.3 and 8.5 ka cal. BP, based on charcoal and seed remains from La Tourasse, a small cave located in the Pyrenean foothills of south-west France. It is an attempt to obtain new archaeobotanical data from one of these old sites that were actively (and very selectively) excavated since the nineteenth century.

The last excavations at La Tourasse were made by one of the authors, J.P. Huot, during the period 1980–1990 and allowed us to retrieve macrobotanical remains from several Azilian and Mesolithic occupation levels. Recent AMS radiocarbon dates place these occupations at the end of the Allerød and the beginning of the Younger Dryas, the Preboreal-Boreal, and the very early Atlantic (Henry, Liard, Oberlin, Orliac, & Huot, 2022). The archaeobotanical study we present in this work is part of a current collaborative effort aiming at reexamining the site's assemblages from an interdisciplinary perspective including bioarchaeological material never studied before such as charcoal, seed, and microfaunal remains (ongoing study by V. Mistrot, Musée d'Aquitaine). Here we provide an assessment of the biostratigraphic coherence of the floristic assemblages in regard of the complicated site history and potential human-induced biases. Past vegetation patterns and plant use are discussed in light of the available archaeo- and paleobotanical evidence.

2 La Tourasse: Environmental and Archaeological Context

2.1 Location and Present-Day Vegetation

The Tourasse site (43º08′51″N, 0º56′39″E) is located near the village of Saint-Martory, about 70 km south-west of Toulouse (Figure 1). The site opens at an altitude of 290 m in a rocky spur of Maastrichtian limestone (Mesozoic sedimentary formation), overhanging the Garonne River by about 20 m (Rodet, 2000). Currently, it is a small cave made of several galleries that open onto different parts of the spur. The alluvial terraces of the Garonne were formed by surface formations and quaternary alterations, which mark the landscape from the passage of great ice ages such as the Würm or Mindel (Monod, 2013).

Today, two main vegetation types coexist near the cave: a dominant, supramediterranean to collinean one, and one of more pronounced mesomediterranean tonality, restricted to superficial soils with higher insolation. Below and around La Tourasse, the supramediterranean vegetation consists of a pubescent oak (*Quercus pubescens*) woodland, rich in Montpellier maple (*Acer monspessulanum*), country maple (*Acer campestre*), hazel (*Corylus avellana*), blackthorn (*Prunus spinosa*), and hawthorn (*Crataegus monogyna*).

Figure 1: Location of La Tourasse and views of the surroundings.

This vegetation type alternates with the collinean one, characterized by sessile oak (*Quercus petraea*) formations (Gaussen & Rey, 1947, authors' personal observations). These can grow in mixed stands with the pubescent oak, leading to many hybrid forms between the two species; however, sessile oak is better adapted to more decalcified soils such as those found in the high terraces of the Garonne. As the dry climate of the area tends to favor pubescent oak, sessile oak is more prone to be found in the more humid heart of the massifs (Gaussen & Rey, *op. cit.*). Just above La Tourasse, the vegetation appears as a degradation facies of the mesomediterranean evergreen oak (*Quercus ilex*) forest in the form of a scrubland with mock privet (*Phillyrea media*), Mediterranean buckthorn (*Rhamnus alaternus*), and boxwood (*Buxus sempervirens*).

2.2 Chronostratigraphy and Taphonomy

Since the nineteenth century, the Tourasse cave has been the object of many visits by local scholars, archaeologists, and even looters (for a detailed site history and chronostratigraphy, see Supplement 1). The last series of excavations were conducted by M. Orliac between 1965 and 1975. These were later completed by one of the authors (J.P. Huot) in the 1980s and 1990s (Huot, 1985, 1991a,b; Huot, Capdevielle, & Christensen, 1991).

The chronostratigraphy identified by Orliac comprises 32 stratigraphic levels, some of them dated, containing stratified evidence of a succession of Paleolithic to Neolithic occupations (Huot et al., 1991; Orliac & Orliac, 1972). The two sectors where Huot's excavations took place revealed a succession of 11 levels attributed to the Azilian and the Mesolithic, for most of which correspondences have been established with those excavated by Orliac. This long history of digging at the site has direct implications on our study as the deposits have been affected deeply and recurrently over time by a series of natural and anthropogenic factors. Huot's excavations were the last attempt to rescue residual occupation levels, which at the most represent no more than 12m^2, while the extension of some levels was much more limited than that (Figure 2). In other terms, it is possible that there might be representativeness biases linked to the
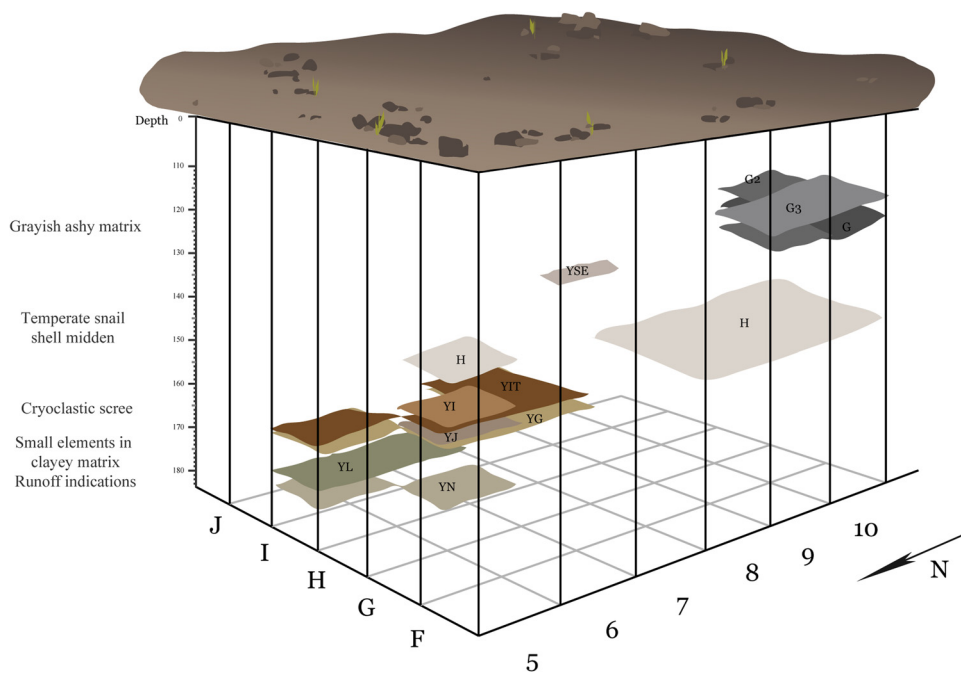

Figure 2: Schematic drawing of La Tourasse's stratigraphy, squares excavated by Huot.
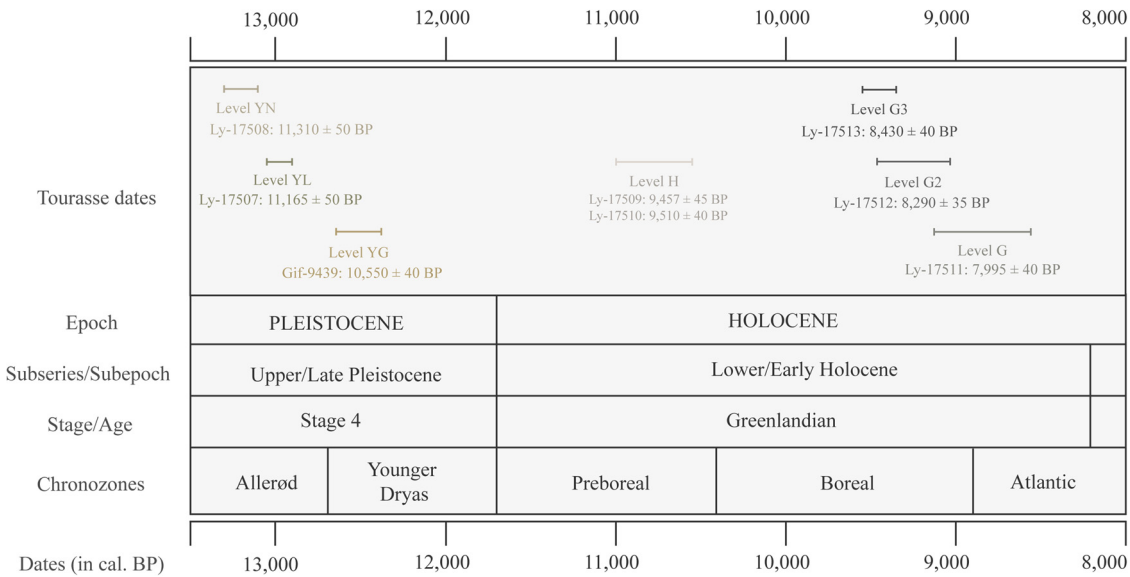
Figure 3: Chronology of Azilian and Mesolithic occupations at La Tourasse.

reduced excavation surface or even perturbations that were not recognized on the field. These are impossible to evaluate *a priori* but must be kept in mind.

At the base of Huot's stratigraphy, we find two levels, YN and YL, whose formation was initially attributed to the Bølling–Allerød interstadial on the basis of biostratigraphical and sedimentological observations. This is confirmed by two radiocarbon dates yielding ages comprised between 13300 and 12900 cal. BP (Figure 3). YN and YL are surmounted by a greenish pebbly-clayey level, YG, whose status – Allerød or Younger Dryas – remained unclear. Indeed, YG forms a transitional layer between YL and a potent cryoclastic scree formed by the levels YJ, YI, and YIT, attributed to the Younger Dryas. One AMS date was made on charcoal for level YG, while two conventional radiocarbon measures made on bone material date the scree in Orliac's excavation sector. These three dates are equivalent and point toward a human frequentation of La Tourasse at the beginning of the Younger Dryas (i.e., between ca. 12700 and 12450 cal. BP) (Henry et al., 2022). These levels have all yielded archaeological material attributed to the Pyrenean Azilian (Fat Cheung, 2015; Fat Cheung et al., 2014). Based on their (not very diagnostic) archaeological contents and chronostratigraphic observations, the upper levels of the sequence were attributed to different stages of the Holocene and the Early Mesolithic. Level H is a thick and hardened layer of temperate snail shell fragments extremely rich in charcoal that was attributed to the Preboreal, which is coherent with the two AMS radiocarbon measurements that gave an age between ca. 11000 and 10600 years cal. BP. Finally, three small residual levels G3, G2, and G form an ensemble characterized by a greyish ashy matrix, dated from the second half of the Boreal (layers G3–G2: ca. 9500–9000 cal. BP), and the very beginning of the Atlantic (layer G: ca. 9100–8600 cal. BP).

3 Materials and Methods

3.1 Charcoal Remains

Another challenge affecting the outcome of this study was that charcoal was recovered in the field following different methods of which we do not always have a record. We know that manual collection took place rather systematically and that it was sometimes complemented by dry screening, and more recently, by flotation of sediment samples done by us at 2 and 0.5 mm screen openings at the CEPAM laboratory in Nice.

Hence, our results may be affected by representativeness biases induced by manual collection as this type of sampling may lead to an overrepresentation of the most frequent taxa and/or a relative taxonomic paucity (Chabal, Fabre, Terral, & Théry-Parisot, 1999; Vidal-Matutano, 2016, but see Henry & Puech, 2022). As charcoal was not very abundant, except in layer H, we were not able to choose according to sampling contexts and methods; thus, we integrated all the available materials. In this regard, it should be added that some charcoals were collected in hearth areas (for detailed information and tables featuring the number of charcoals from scattered vs concentrated areas and methods of retrieval, see Supplement 3). Conversely to the charcoals scattered within the sediments of the site, these may correspond to more punctual deposits only partially reflecting the ligneous diversity of the wood gathering area and may thus deliver truncated palaeoecological information (Chabal, 1992, 1994, 1997).

For the study, charcoal fragments were randomly selected, fractured manually following the three anatomical sections of the wood and observed with a brightfield/darkfield reflection microscope at different magnifications (50×, 100×, 200×, 500×, and 1,000×). Microscopic observations were then compared with wood anatomy atlases (Schweingruber, 1978, 1990; Vernet, Ogereau, Figueiral, Machado Yanes, & Uzquiano, 2001) and the charred wood reference collection of the CEPAM laboratory (https://www.cepam.cnrs.fr/datas/anthracotheque/).

When present, other anatomical features such as wood degradation features (or fungal alteration; FA) and radial cracks (RC) were also recorded, providing different kinds of taphonomical data (Badal & Carrión 2004; Caruso Fermé, Théry-Parisot, Carré, & Fernández, 2018; Henry & Théry-Parisot, 2014; Moskal-del Hoyo, Wachowiak & Blanchette, 2010; Théry-Parisot, 2001a; Théry-Parisot, Chabal, & Chrzavzez, 2010; Théry-Parisot & Henry, 2012). The objective was to gather information regarding the state (green, seasoned, decayed) of the fuel used at La Tourasse to evaluate the possibility to discuss firewood management practices.

Scanning Electron Microscopy (SEM) was performed at the CCMA (Nice, France) with a Tescan Vega3 XMU SEM (Tescan France, Fuveau, France). Samples were coated with a 3 nm layer of Platinum (Pt) prior to observations, which were made at magnifications from 250× up to 30k×.

As most samples yielded an insufficient quantity of remains, all fragments over 1 mm were observed, except for the charcoal-rich H layer, for which taxonomic accumulation curves (Kabukcu & Chabal, 2021) were used to determine an optimal number of studied fragments.

The unnormal distribution of our charcoal data justified the use of non-parametric statistical analyses. These were made with the software Excel stat while always using a confidence interval of 0.05. Multivariate analyses, chi-square analyses, and Pearson's residual calculations were used to analyze the floristic data and its variability. Correspondence analysis (CA) based on a chi-square calculation was aimed at identifying correspondences between the taxa and the archaeological levels, while the chi-square calculation allowed to test the independence between the rows and the columns (H_0 hypothesis). The chi-square calculation by cell and Pearson's residuals were used to further characterize the observed variability and its statistical significance by testing the differences between the observed and the theoretical values (i.e., the over- or underrepresentation of the values under the null hypothesis). We ran these three tests (CA, chi-square, and Pearson's residuals) on the same simplified contingency table, where the archaeological levels were entered as columns and the taxa as rows (for step-by-step procedures and detailed tables, comments, and results, see Supplement 4). We used the main coordinates generated by the CA for the three first factorial axes of the columns (archaeological levels) to run an Agglomerative hierarchical clustering (AHC) analysis based on the Euclidean distance and Ward's method in order to identify similarities between the floristic contents of the different archaeological levels. One of the underlying ideas of these multiple tests was to be able to work on larger charcoal quantities by associating certain levels together, allowing for more robust environmental reconstructions in a context of relatively low chronological resolution. In addition to the available chronostratigraphical information, these results were used to create a synthetic charcoal diagram to discuss the taxonomic profiles.

3.2 Seed Remains

The carpological analysis includes the remains recovered by dry screening during the excavations as well as those documented after the flotation of sediment samples at the CEPAM. Sorting of the seeds preserved in the flotation samples and the botanical identification were carried out under a low power microscope Leica MZ8 with magnifications between 10× and 80×. The taxonomical identification of the remains was performed with reference to a specialized bibliography (Bojňanský & Fargašová, 2007; Cappers, Bekker, & Jans, 2006) and with the aid of the collection of modern seeds, fruits, and leaves of the ISEM (CNRS UMR 5554). The carpological remains were photographed with an Infinity 3 of Lumenera camera using Infinity Analyze 6.5.5 and Helicon Focus 7.7.2 software.

The pericarp fragments of *Corylus avellana* were weighed and classified into two groups according to their size ($\geq 16 \, \text{mm}^2$ and $< 16 \, \text{mm}^2$) in order to calculate the minimum number of hazelnuts (or minimum number of individuals, MNI) following different published methods aimed at overcoming the potential representativeness biases of the hazelnut remains (Berihuete-Azorín & Antolín, 2012; Bouby & Surmely, 2004; Mithen, Finlay, Carruthers, Carter, & Ashmore, 2001).

4 Results: Charcoal and Seed Remains from La Tourasse

4.1 Microanatomical Characteristics and Taphonomy of the Charcoal Assemblage

956 charcoal fragments were analyzed, the majority of which come from manual sampling (Table 1).

23 Taxa (minimum number of taxa; MNT: 19) were determined. The preservation state of the assemblage is highly satisfactory, as only one fragment could not be identified, whereas 58 (around 6%) could not be identified at least at the genus level and were labeled as "Angiosperms" (Table 2).

First, it is important to notice that the assemblage is dominated by broad-leaved taxa, while needle woods represent less than 7% of the corpus. The most abundant taxa are Rosaceae, both Prunoideae and Maloideae (especially in the Late Glacial and Preboreal levels) along with deciduous oak (*Quercus* subg. *Quercus*), almost exclusively identified in the Boreal/Atlantic levels. The Rosaceae family comprises a series of shrubs and trees of the Rose family that make up almost 40% of the total effective, within which the genus *Prunus* is particularly well-represented (Figure 4; for a detailed microanatomical description and SEM microphotographs of the taxa, see Supplement 2).

Table 1: Manual sampling vs dry sieving vs flotation of charcoals per layer

Layer	Manual	Dry sieving	Flotation (12L)	Total
YN	27	1		28
YL	36			36
YG	45	17	25	87
YJ	1			1
YIT	31		39	70
YI	1	9		10
YSE			67	67
H	213	135	22	370
G3	67	15		82
G2	71	3	36	110
G	53		42	95
Total	**545**	**180**	**231**	**956**

Table 2: Results of the charcoal analysis (expressed in fragment counts by level)

Period		Final Pleistocene						Holocene					Total	
Taxon	Vernacular name layer	YN	YL	YG	YJ	YIT	YI	YSE	H	G3	G2	G	*n*	%
Abies alba	Fir							1	5				6	0.63
Acer	Maple			1		2			2				5	0.52
Alnus type *glutinosa*	Common alder type					1		2					3	0.31
Betula pendula/pubescens	Birch	5		28		13	3	6	13				68	7.12
Cornus	Dogwood							1	7				8	0.84
Corylus avellana	Hazel							4	12	11	21	24	72	7.54
Juniperus type *communis*	Juniper		1					1					2	0.21
Lonicera	Honeysuckle					1			4				5	0.52
Maloideae	Apple subfamily	4	8	13		6	2	6	74	4	11	3	131	13.72
Pinus type *sylvestris*	Scots pine type					4		6	38		10		58	6.07
Populus/Salix	Poplar/Willow	1						1	16				18	1.88
Prunus avium/padus	Wild/Bird cherry		3	14		1		5	29				52	5.45
Prunus mahaleb/padus/spinosa	Mahaleb/Bird cherry/Blackthorn	1	12	7	1	4	1	4	66				96	10.05
Prunus amygdalus/spinosa	Almond tree/Blackthorn			1		20	1		9			1	32	3.35
Prunus			6	6		4		1	17			1	35	3.66
Quercus subg. *Quercus*	Deciduous oak					1		21	35	63	62	60	242	25.34
Phillyrea/Rhamnus type *alaternus*	False olive tree/Mediterranean buckthorn								1				1	0.10
Rhamnus cathartica/saxatilis	Buckthorn	10	5					1	9	2			29	3.04
Sambucus	Elder	4							5				9	0.94
Ulmus	Elm								1			1	2	0.21
Viburnum	Viburnum			5		2	1	2	14				24	2.51
Angiosperm	Broad-leaved	3	1	11		11	2	5	12	2	6	5	58	6.07
Unidentifiable				1									1	0.10
Total		28	36	87	1	70	10	67	370	82	110	95	956	100

In lesser proportions, we find birch (*Betula*), hazel (*Corylus*), and pine (*Pinus*), while buckthorn (*Rhamnus*), poplar or willow (*Populus/Salix*), and viburnum (*Viburnum*) represent between 1 and 3% of the assemblage. The rest of the taxa show proportions below 1%: maple (*Acer*), alder (*Alnus*), dogwood (*Cornus*), honeysuckle (*Lonicera*), *Phillyrea/Rhamnus*, elder (*Sambucus*), elm (*Ulmus*), fir (*Abies*), and juniper (*Juniperus*).

At La Tourasse, alterations of the microanatomical wood structure such as FA or RC, which sometimes highly compromise the taxonomical determination, occur in relatively low frequencies (Figure 5).

FA were observed sporadically on a very small part of the corpus (on average less than 4%) and are mostly of low intensity (Figure 6). Thus, there are no indications of the use of degraded wood at La Tourasse even though this is more difficult to assess for the layers in which oak is dominant as this taxon is highly resistant to fungi (Henry, 2011).

RC occur more frequently than FA and show higher variability between levels. While they are quite rare in the Y levels, they reach much higher proportions in the H and G levels (ca. 25% in level G). This does not seem related to differential preservation patterns between the Late Glacial and the Early Holocene levels (for example, higher fragmentation rates of the Late Glacial assemblage inducing smaller observation surfaces). On the contrary, the highest proportions of big charcoals (>4 mm) are found in the Younger Dryas levels, where the percentage of RC is the lowest, while in the Post Glacial levels, the charcoals are smaller on average. This could reflect the fact that RC weaken charcoals and create breakage points, which may have been even more pronounced within an assemblage dominated by deciduous oak whose morphology is naturally more prone to fragmentation than other species (Badal García, 1990; Chabal, 1991; Chrzavzez, 2013; Chrzavzez, Théry-Parisot, Fiorucci, Terral, & Thibaut, 2014). Thus, these results suggest higher frequencies of RC in the Mesolithic levels rather than a poor preservation of RC in the older layers. The fact that among all the samples recorded, RC were numerous and quite small (Figure 6), may reflect the burning of green wood (Caruso Fermé et al., 2018; Théry-Parisot & Henry, 2012). However, as no detailed
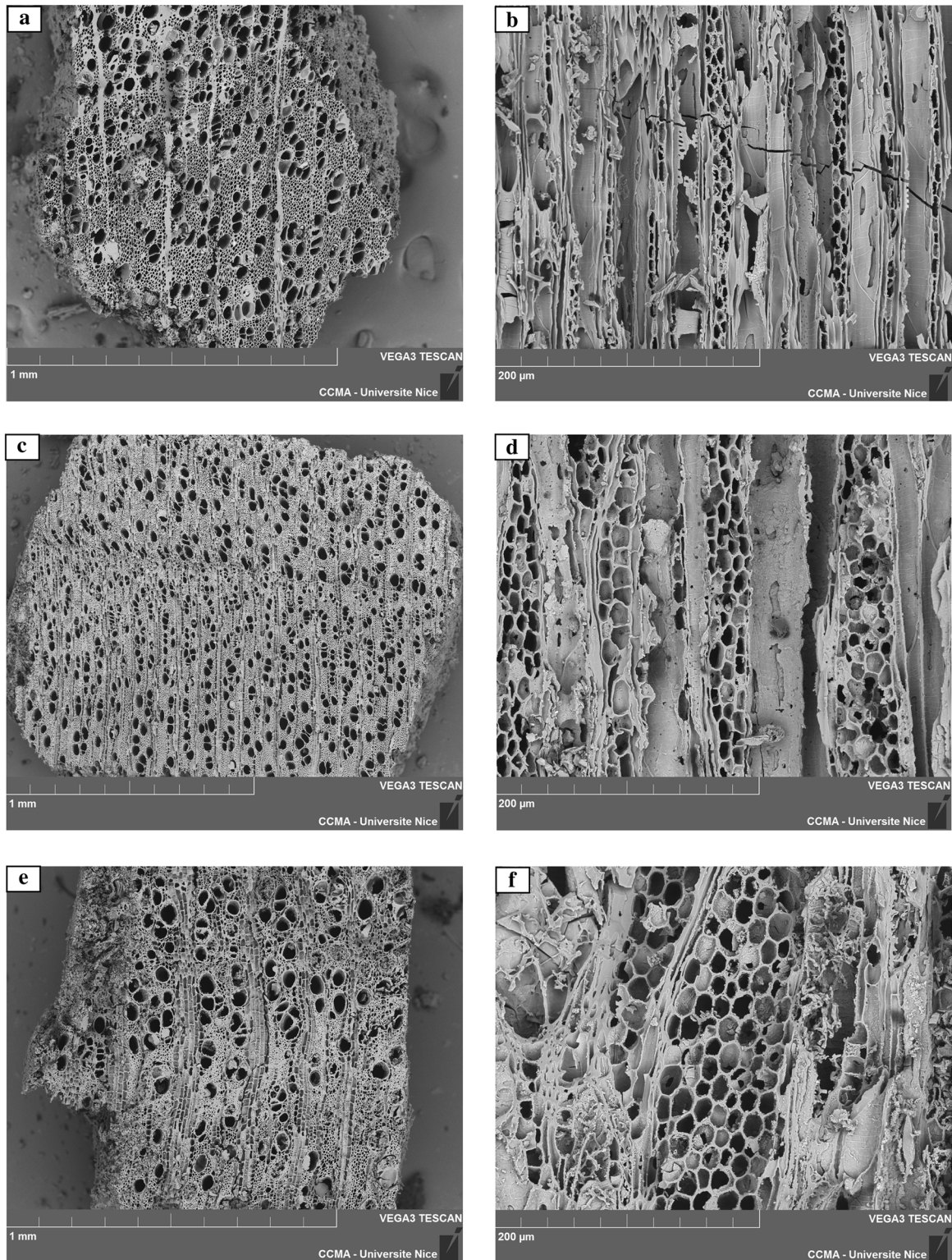
Figure 4: Scanning electron micrographs – Rosaceae Prunoideae. *Prunus* type 1 (*P. avium/padus*): (a) cross-section and (b) tangential section. *Prunus* type 2 (*P. mahaleb/padus/spinosa*): (c) cross-section and (d) tangential section. *Prunus* type 3 (*P. amygdalus/spinosa*): (e) cross-section and (f) tangential section.
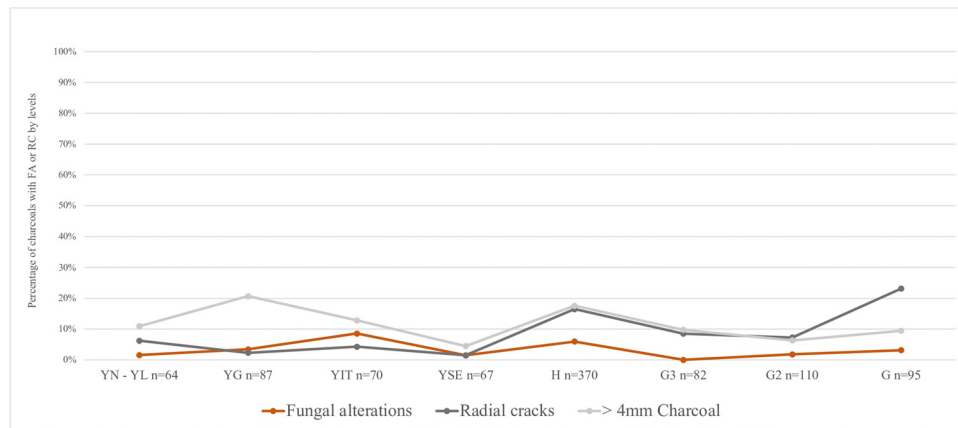
Figure 5: Percentage of FA and RC observed per archaeological level. Some levels were regrouped by time period.

reference frame exists for most of the taxa present at La Tourasse, more information is needed to validate this hypothesis.

Table 2 also shows that there are significant disparities between the number of fragments retrieved from each depositional context. For most levels, it has been impossible to carry out a quantitative approach as each archaeological level yielded less than 100 fragments, except for H and G2 (for the taxonomic accumulation curves of these two levels, see Supplement 3, Figures 1 and 2). Note that the number of identified taxa is not a direct function of the number of analyzed fragments (Figure 7). This relation is complex as it results from several factors that are sometimes difficult to dissociate such as past vegetation structure and human preferences, differential preservation, and archaeological field methodology (e.g., Allué, Expósito, Tumung, Ollé, & Bazgir, 2018; for detailed results regarding flotation vs hand-picked samples, see Supplement 3).

4.2 Statistical Treatment of the Charcoal Data: Looking for Correspondences

At a significance level of 0.05, the results of the CA are highly significant (*p*-value <0.0001); therefore, the null hypothesis (H_0) must be rejected.

The CA (Figure 8) clearly dissociates three main clusters within the first two axes F1 and F2 (cumulated inertia 68%), and four within F1–F3 (cumulated inertia 61.25%). The heaviest contributors to F1 are *Quercus*, *Corylus*, and the three G levels, dated to the Boreal (G3–G) and the very beginning of the Atlantic (G). Most of the remaining individuals and significant contributors are separated by axes F2 (Figure 8a) and F3 (Figure 8b). Axis F2 is mainly defined by the association of *Betula* and *Prunus* type *amygdalus/spinosa* (associated to levels YIT and YG attributed to the Younger Dryas), which show negative correspondences (separated by axis F1) with *Rhamnus* and level YN (and YL to a lesser extent; both levels are dated to the Allerød interstadial). YN is an even higher contributor to axis F3, where the high weight of *Sambucus* and *Rhamnus* is noticeable, but also the weight of the Preboreal level H and *Prunus* type *mahaleb/padus/spinosa* (separated by axis F1).

The automatic truncation of the dendrogram generated by the AHC shows that the different levels are regrouped roughly according to the chronostratigraphical units; however, there are some exceptions that involve the Allerød layers YN and YL (Figure 9). YN is the only object in its class and can be considered as an outlier. Due to its high values of *Rhamnus* and *Sambucus*, the taxonomic hierarchy found within YN does not match that of the other levels. Nevertheless, the results are possibly highlighting a bias linked to too low charcoal counts and reduced taxa diversity (MNT: 6 for 26 fragments). The other Allerød level YL has been classified with the Preboreal levels H and YSE, forming the least homogeneous class (intra-class variance 1.28)
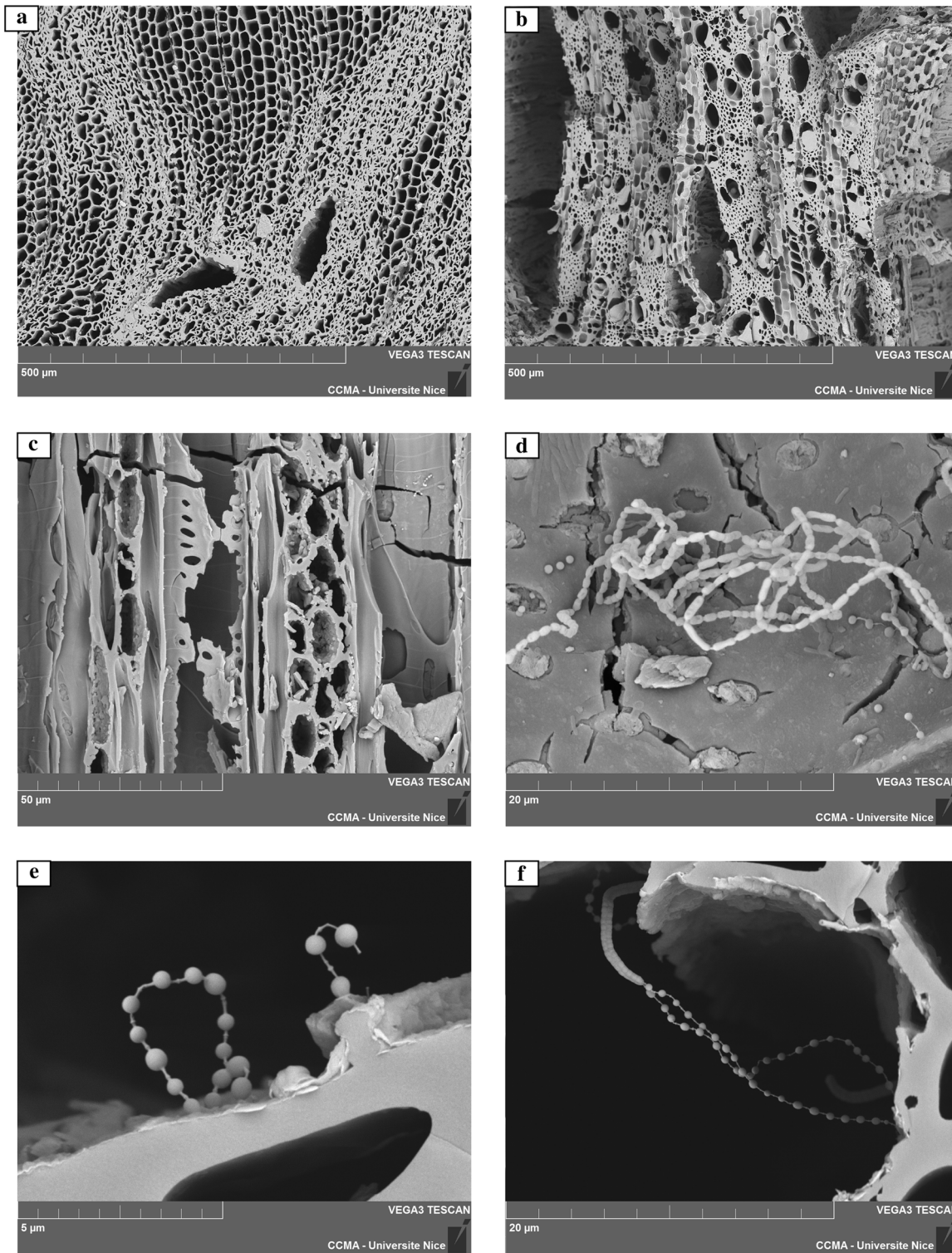
Figure 6: Scanning electron micrographs. (a) Pinus type *sylvestris*, cross-section: example of FA. (b) *Prunus* type 2, cross-section: example of RC. (c) *Prunus* type 1., tangential section: example of FA. (d, e, f) Examples of micro-organisms: tangential section of Acer (d), cross-section (e) and tangential section (f) of *Viburnum*.
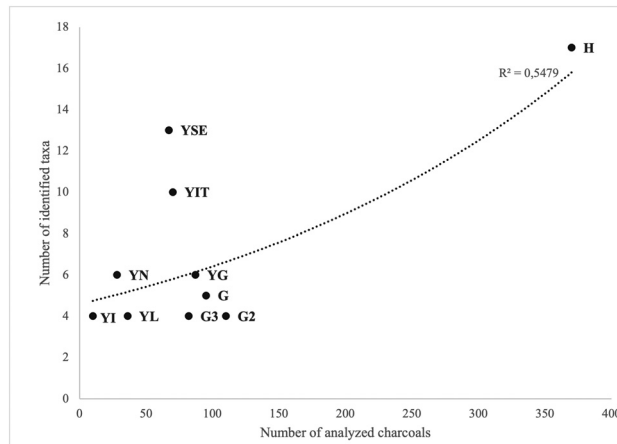
Figure 7: Scatter graph: number of analyzed charcoals vs number of identified taxa (expressed in MNT).

characterized by the importance of Prunoideae (*P. avium/padus/mahaleb*). The five taxa (expressed in MNT) identified in YL are present both in H and YSE (except for *Juniperus*, absent from H), but the reduced effectives and low taxa counts prevent us from going further. While these issues clearly limit our understanding of the Allerød levels, we have however three partially overlapping ^{14}C dates and no clear evidence of a rupture from a floristic viewpoint between YN and YL, which leads us to regroup these two levels. H and YSE show less variability and more similarity, which is in agreement with the initial hypothesis of YSE being originally a part of H and allows us to regroup these two units. Levels YIT, YI, and YG make up the third class characterized by the significant role of *Betula* and a relatively low heterogeneity (intra-class variance 0.63). On the basis of the ^{14}C date obtained on YG and the results of the AHC, we propose to regroup the Younger Dryas YIT and YI with level YG, whose status was unclear on the sole stratigraphic evidence. Finally, the last class is composed of the three least dissimilar levels G, G2, and G3 (intra-class variance 0.12) which share extremely homogeneous and rather poor floristic contents (MNT: 6) and high *Quercus* values. Even though we know from the ^{14}C dates that the occupations span at least 500 years and that G3 and G2 are chronologically closer to one another, all G levels seem to document the same vegetation type which justifies considering them as a whole.

Pearson's adjusted residuals, calculated on the basis of the chi-square results by cell, confirm the statistical significance of the variations in the main taxa within the archaeological levels of La Tourasse (Supplement 4, Table 5). These coincide with well-known ecological processes, namely, the development of forest ecosystems at the Late Glacial–Holocene transition (Figure 10).
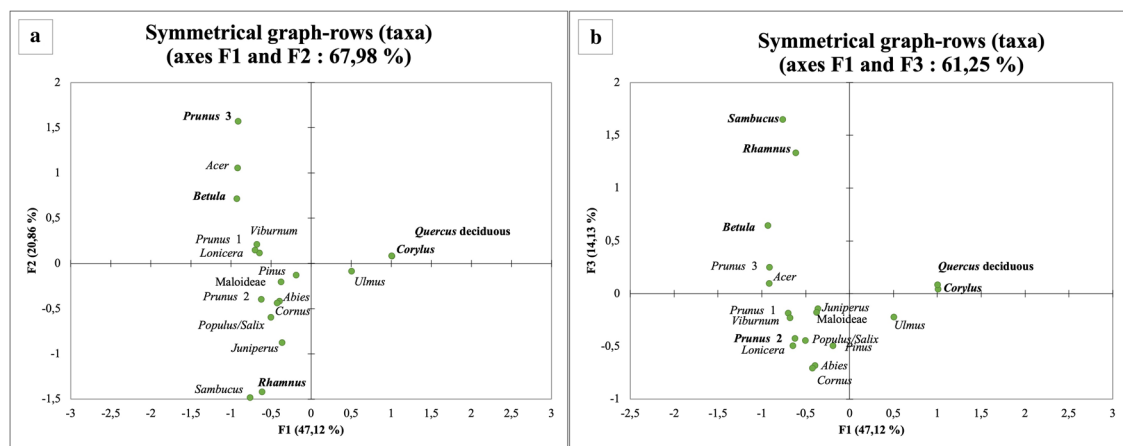

Figure 8: CA: taxa identified by archaeological level. a: axes F1 and F2. b: axes F1 and F3. Labels in bold indicate the most important contributors (more than 10% of each axis).
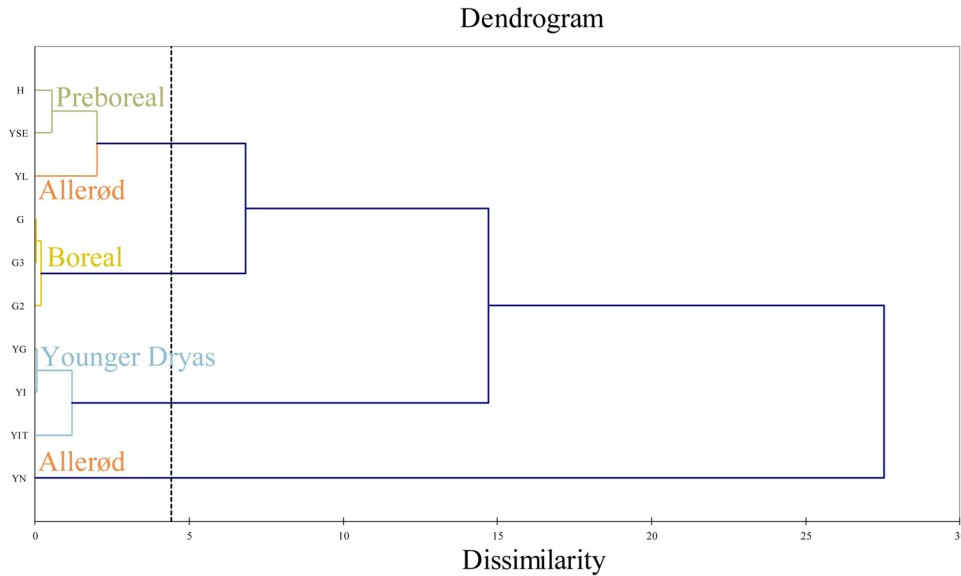
Dendrogram

Figure 9: AHC results: Dendrogram showing the similarity between archaeological levels.

4.3 Vegetation Dynamics at La Tourasse

The statistical pre-treatment of the data has led us to obtain coherent chronostratigraphical units that are quantitatively more robust, except for the Allerød chronozone whose floristic results appear in gray in the anthracological diagram and can be discussed mostly from a qualitative viewpoint (Figure 11).

The last interstadial is characterized by the clear dominance of heliophilous taxa; almost all of them are Eurasian, cold-resistant taxa (e.g., *Betula*, *P. padus*, *Sambucus*, or capable of tolerating dry conditions (*P. spinosa*, *Rhamnus*, *Juniperus* (Rameau et al., 2008). Some of them can also be shade or half-shade species (*Sambucus* and *P. avium*). However, they are essentially taxa that will colonize open, disturbed, or unstable environments with rapid development (growth and reproduction). Therefore, the floristic assemblage can be interpreted as an open shrubby landscape established in dry conditions, with a riverine vegetation that
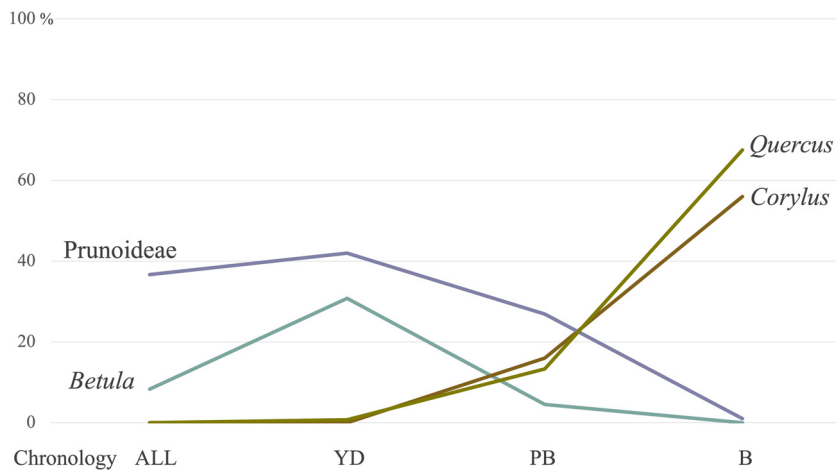

Figure 10: Relative frequencies of the dominant taxa (whose variations are statistically significant) throughout the studied sequence correlated with the associated chronozone.
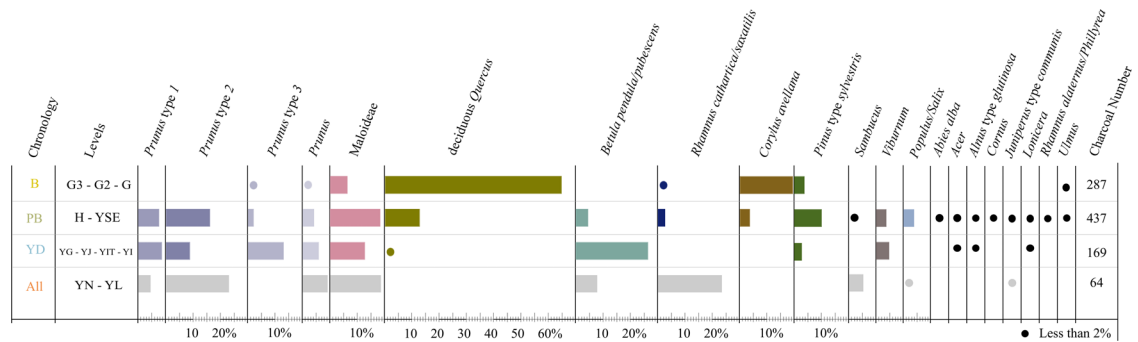
Figure 11: Interpretive anthracological diagram of Y, H, and G layers of Tourasse Cave.

was probably more diversified taxonomically including *Populus/Salix, P. avium, Sambucus, Maloideae* and *Betula pro parte*.

Even though the Younger Dryas is still characterized by the strong dominance of heliophilous and Eurasian taxa, the vegetation seems to slightly shift toward more xeric and/or cold-adapted associations, with increasing proportions of birch, Scots pine, almond, and blackthorn while alder, honeysuckle, bird cherry, viburnum, and Maloideae are also present, reflecting again at least partly a riverine origin. The predominance of *P. amygdalus/spinosa,* a charcoal morphotype regrouping two highly drought-tolerant species, may indicate drier conditions. In temperate Europe today, Rosaceae are usually subordinate species in the vegetation and dominate only as reconquest species of the forest. Thus, it can be assumed that the Tourasse landscape during the Younger Dryas was an open, xeric, Rosaceae-dominated shrubland, with a parallel development of scattered pine-birch stands, while birch may also have grown on the banks of the Garonne.

During the Preboreal (levels YSE and H), we still find a majority of heliophilous species, although many half-shade species appear (*Abies alba, Acer, Corylus, P. avium, P. padus, Cornus*), which reflects a closing of the woody environment through the formation of different forest strata, with secondary species developing in the understory. Finally, several more meso- to thermophilous taxa are identified (*Cornus, Lonicera, P. mahaleb*, deciduous *Quercus, Rhamnus/Phillyrea*), indicating temperate climatic conditions.

The YSE and H assemblage may therefore reflect a mosaic landscape with, on one hand, the persistence of open vegetation types (pine-birch forest, Rosaceae shrublands) and, on the other hand, the development of the Holocene deciduous forest taxa (*Quercus, Corylus*, and *Ulmus*) as well as a whole procession of half-shade undergrowth taxa (*Cornus, Lonicera, Sambucus, Viburnum, Prunus* spp., Maloideae). The high proportions of Rosaceae in the assemblage suggest that only a portion was subordinated to the oak forest, while the other part contributed to open shrublands and, probably, to the riverine vegetation with poplar/willow, elm, birch, and viburnum. The clear reduction in the proportions of *Prunus amygdalus/spinosa* in favor of *Prunus* type *mahaleb/padus/spinosa* may indicate that the shrubland took on a more thermophilous character. Finally, the appearance of fir provides evidence for the presence of more mature and closed woodlands around La Tourasse.

Finally, during the Boreal and the beginning of the Atlantic period, the surrounding environment mainly consisted of deciduous oak forest. Oak appears dominant and probably grew above an understory in which hazel was well-developed while Prunoideae do not seem to have played an important role in the vegetation. The few fragments of Prunoideae found along with *Rhamnus* in these layers probably reflect their changing status as part of the oak forest's undergrowth or edges. Limited percentages of pine indicate the persistence of areas with drier and/or poorer soils, such as the rocky outcrops above the cave, which would have been less favorable to oak. Finally, except for the presence of a few elm fragments, there is no clear exploitation of riverine species.

4.4 Seed Remains

497 carpological remains were recovered throughout the sequence of La Tourasse. 480 have been taxonomically identified, yielding five taxa: *Corylus avellana*, *Prunus*, *Prunus* cf. *spinosa*, and cleavers (*Galium aparine*, *Galium*) (MNT: 3). Six remains were classified as fragments of an indeterminate fleshy fruit and the preservation state of eleven remains hindered their botanical identification (Figure 12, Table 3).

Manual sampling typically boosts the recovery of large carpological remains which, in this study, would be hazelnut shell fragments and *Prunus* fruits. Most of the documented *hazel* remains were collected manually (390 fragments), but the flotation allowed the recovery of a greater proportion of small fragments (182 out of 185 fragments). Moreover, we should highlight that half of the carpological assemblage was recovered due to the flotation of a few sediment samples (Table 4). Because of this method, carpological data from the Younger Dryas levels are available, adding to the floristic list the presence of *Galium*.

The distribution of the carpological remains throughout the sequence shows a clear division between the levels attributed to the Allerød and the YD (YN, YL, YG, YIT, and YI) and the Holocene layers, including level YSE. In the first part of the sequence, cleaver remains dominate the assemblage along with an endocarp fragment of blackthorn (*Prunus* cf. *spinosa*). In levels YN and YL, only some fragments of an indeterminate fleshy fruit were recovered, but this composition is biased due to the unavailability of samples for flotation. Only four remains of hazel nutshells were recovered for level YIT, but their low
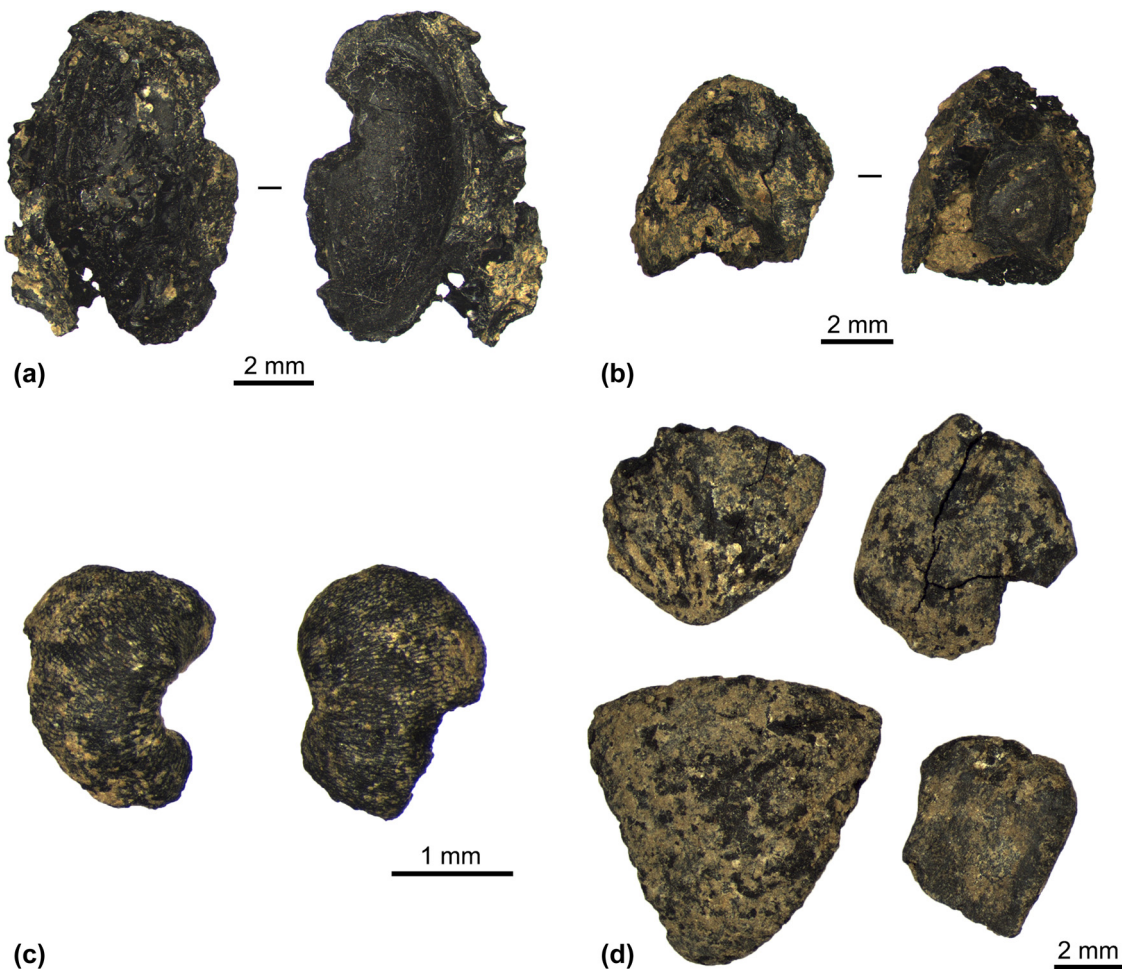

Figure 12: Seed remains from La Tourasse: (a) *Prunus* sp. fruit fragment (level H), (b) indeterminate fleshy fruit fragment (level YN), (c) *Galium aparine* seed fragments (level YIT), (d) *Corylus avellana* shell fragments (level G).

Table 3: Carpological analysis results

Taxa	Vernacular name	Type of remain	YN	YL	YG	YIT	YI	YSE	H	G3	G2	G	Total
Corylus avellana	Hazel	Fr. shell					4		118	161	3	130	48	464
Galium aparine	Cleavers	Fr. seed			2	5	1						8
Galium		Fr. seed			2								2
Prunus		Fr. fruit						5					5
Prunus cf. *spinosa*	Blackthorn	Fr. endocarp					1						1
Unidentified fleshy fruit		Fr. fruit	5	1									6
Unidentifiable		Fr. endocarp			4	2							6
		Fr. seed			1					2	2		5
		Total	**5**	**1**	**9**	**11**	**2**	**118**	**168**	**3**	**132**	**48**	**497**

frequency and the absence of hazel remains in the anthracological assemblage of this layer points to an intrusive character from the overlying levels. The small size of the fragments, together with the low MNI that does not represent even one hazelnut (Table 5), supports this hypothesis.

The composition of the carpological assemblage shows significant changes from level YSE onwards: hazelnut shell fragments become the most frequent remains with level H being the richest. In contrast with previous levels, *Galium* spp. remains were not documented, and the presence of *Prunus* is restricted to level H. In these levels, where hand-collected and flotation remains are analyzed, there are no significant differences in terms of taxonomic diversity between both methods of retrieval, although flotation allows the retrieval of much larger quantities.

Regarding the hazelnut remains, despite their abundance in some levels, such as YSE (118 fragments), H (161), and G2 (130), most of them are small-sized which, in this case, makes the calculation of the MNI

Table 4: Manual vs flotation sampling of carpological remains

Layers	Manual	Flotation (12L)	Total
YN	5		5
YL	1		1
YG		9	9
YIT		11	11
YI		2	2
YSE		118	118
H	139	29	168
G3	3		3
G2	79	53	132
G	17	31	48
Total	**244**	**253**	**497**

Table 5: *Corylus avellana* carpological remains

	Corylus avellana	YIT	YSE	H	G3	G2	G	Total
	Total fragments	4	118	161	3	130	48	464
	Weight (g)	0.03	0.26	0.73	0.2	1.17	1.21	3.41
	Fr. ≥ 16	1	2	9		20	8	40
	Fr. < 16	3	116	152	3	110	40	424
MNI	Bouby and Surmely (2004) (0.383 g/hazelnut)	0.07	0.67	1.92	0.05	3.05	3.15	8.91
	Mithen et al., (2001) (0.42 g/hazelnut)	0.06	0.61	1.75	0.05	2.79	2.87	8.12
	Berihuete-Azorín and Antolín (2012) (formula)	0.31	7.50	10.63	0.19	9.38	3.50	31.50

essential. Different methods have been used and discussed in a previous work (see Berihuete-Azorín & Antolín, 2012) to overcome the potential overrepresentation of the hazelnut shells. We have applied three of them (Table 5), and they provided dissimilar results. This was especially found for the richest levels – such as YSE or H – depending on the basis of the method, weight or surface of remains. Although a thorough taphonomic analysis is required to evaluate which of these methods is more accurate in our case, since the size of some remains is significantly small enough to suggest the need for another size group, the calculation of MNI is the key when we compare different levels. For instance, in level G, the number of remains is low (48) compared with the underlying levels; however, if we consider the MNI based on the weight of fragments (2.87–3.15), the presence of hazel would be similar to that of level G2 (2.79–3.05) or even higher than in level H (1.75–1.92), which concur with the results of the anthracological assemblage, where hazel wood charcoal has similar abundance in levels G2 and G, and higher than in level H. In any case, the presence of hazel is significant from the Preboreal onwards, except for level G3, where the absence of samples for flotation could have biased the composition of the assemblage.

Hazelnuts can be gathered during the end of the summer and the beginning of autumn. The gathering season is similar for *Prunus* fruits, which ripen from September to November. However, both hazelnuts and *Prunus* drupes can be preserved and stored for some months. Therefore, these taxa are rather mediocre seasonal indicators. On the other hand, we consider that cleaver could be a good marker of seasonality, regardless of whether it was introduced accidentally or intentionally. As cleaver seeds ripen from August to September, we propose that the Younger Dryas occupations of level YG happened at the end of the summer.

5 Discussion: The Archaeobotanical Potential of La Tourasse

What is the potential of the archaeobotanical data from La Tourasse whose long and complicated history caused the irrevocable loss of most macroremains? The assemblages retrieved for this study suffered to some extent from representativeness biases linked to the sampling methods used. The main limitation encountered was the subsequent paucity of macrobotanical remains which affected some levels more than others. Nevertheless, the anthracological and carpological spectra from La Tourasse are ecologically compatible and the floristic data appear coherent from a biostratigraphical and biochronological viewpoint. The data thus allowed a partial reconstruction of local vegetation and plant use. The robustness of our paleoecological and -economical data can be further discussed through a comparison with already published archaeo- and paleobotanical sequences evidencing comparable vegetation dynamics.

5.1 Paleoecological Reliability of La Tourasse Sequence

5.1.1 Late Glacial Rosaceae Shrubland

At La Tourasse, the most remarkable feature of the Late Glacial vegetation is the major role played by Rosaceae (Prunoideae and, to a lesser extent, Maloideae), whereas conifers are present but lower in abundance. The history of the key-taxa found in the Allerød levels –Rosaceae, *Rhamnus*, *Sambucus* – is particularly difficult to track through other paleobotanical proxies such as palynology, as they are entomogamous and thus systematically underrepresented or even absent from the pollen record (Allué, Nadal, Estrada, & García-Argüelles, 2007; Guitian, Guitian, & María-Sanchez, 1993).

These specificities have thus to be kept in mind when establishing comparisons with the regional pollen record. The northern slope of the Pyrenees has benefitted from many palynological studies (Jalut & Turu i Michels, 2006) and some sequences are particularly suitable for comparison with La Tourasse as they come from lower altitude peat bogs and lakes. One of these sequences is Barbazan, which is located at 450 masl and less than 40 km away from La Tourasse (Andrieu, et al., 1988; Andrieu-Ponel, 1991) (Figure 13).
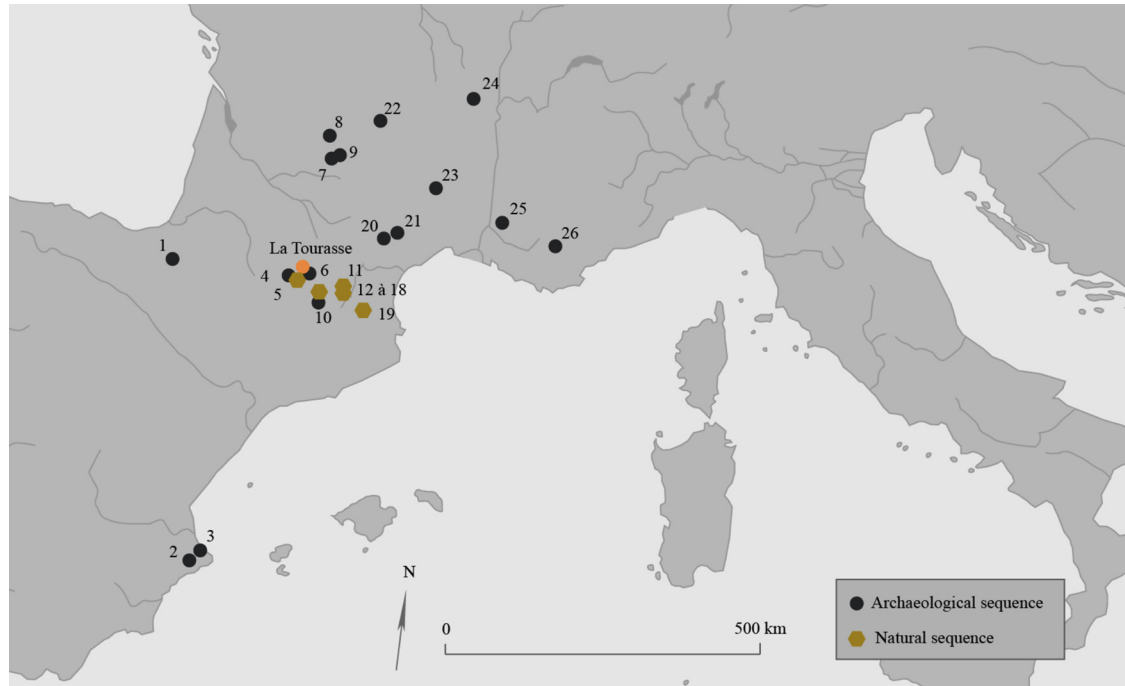
Figure 13: La Tourasse in its regional archaeologcial and paleoenvironmental context: (1) Aizpea, (2) Abric de la Falguera, (3) Cova Fosca, (4) Grotte du Moulin, (5) Lac de Barbazan, (6) Buholoup, (7) Grotte du Sanglier, (8) Les Fieux, (9) Les Escabasses, (10) Balma de la Margineda, (11) Pinet, (12) Balcère, (13) Les Bassettes, (14) La Borde, (15) Le Gourg Nègre, (16) Laurenti, (17) La Moulinasse, (18) Les Sagnes, (19) Freychinède, (20) Grotte du Gazel, (21) Abeurador, (22) Les Baraquettes, (23) La Poujade, (24) Al Poux, (25) Abri Jérôme, and (26) Fontbrégoua (For more details, see Supplement 5).

Some low- to mid-altitude sites show that the Allerød is marked by the development of pine-birch forests, while pioneer heliophilous taxa such as juniper, willow, and buckthorns (*Hippophae rhamnoides*, *Rhamnus*) that were already identified during the previous phase are still frequent (Jalut & Turu i Michels, 2006). This ecological signal is coherent with that provided by the charcoal assemblage of La Tourasse, where taxonomic correspondences between palynology and anthracology can be observed (*Betula*, *Rhamnus*, and *Juniperus*). As the proportions of pine throughout the anthracological sequence of La Tourasse (Figure 11) hint at its continuous but minimal presence, the absence of pine in the Allerød levels would thus be related to insufficient sampling rather than reflect an ecological reality. However, it should be noted that the palynological records from Barbazan also show low percentages of pine, suggesting that this taxon played a minor role there compared to adjacent areas (Andrieu-Ponel, 1991; Barbaza & Heinz, 1992). There are few and mostly discreet charcoal evidences for the Late Glacial development of elder in southwestern France. At Troubat, a rockshelter located at 541 masl and only 20 km from La Tourasse (e.g., Barbaza & Heinz, 1992), elder frequencies do not exceed 0.5%, which leads us to hypothesize that this taxon may be overrepresented at La Tourasse. The reasons for this are likely linked to insufficient sampling and illustrate one or several firewood gathering episodes in the Garonne riparian area. However, a Late Glacial spread of elder in soils with favorable hydric conditions is suggested at Bouyssonie (South-Central France), where two elder remains yielded dates around 12.7 ka cal. BP (Langlais et al., 2019). This taxon was found to represent more than 40% of the charcoal remains from the Azilian archaeological units (Chrzavzez, 2016; Henry, 2021).

La Tourasse is currently the only site we know of to record a change in *Prunus*-types between the Allerød and the Younger Dryas, hinting at a shift in plant communities with *P. amygdalus/spinosa* developing at the expense of *P. avium/padus*. The presence of other floristic indicators suggests a change toward drier and/or colder conditions (*Betula/Pinus*), making this scenario plausible. However, the representativeness issues encountered at La Tourasse make it difficult to completely discard a change in wood gathering areas over time, i.e., from the riparian area where *P. avium/padus* can be found to the rocky outcrops near the cave more

adapted to *P. spinosa* (the presence of this species rather than the one of *P. amygdalus* is suggested both by the charcoal and the carpological data). As very few sites excavated recently in the area have yielded Younger Dryas occupations, new research is indispensable to confirm the existence of such a trend. In any case, the palynological data from the Northern Pyrenees show an interruption in the development of the tree cover and a return of steppic herbaceous communities during the Younger Dryas (Jalut & Turu i Michels, 2006). These changes are more marked within the Mediterranean climatic domain due to increasing aridity (Jalut et al., 1998). Nevertheless, the development of oak which began during the interstadial follows its course, with very low but persistent contributions recorded in the pollen diagrams (Jalut & Turu i Michels, 2006; Reille, 1990). Deciduous oak also appears at La Tourasse with other mesothermophilous taxa that could have been associated with the oak patches such as *Lonicera* and *Acer*. Although they are only represented by a few fragments that could thus be intrusive, the presence of such taxa has been reported regarding other contemporary contexts. For instance, oak charcoal was identified in the Younger Dryas levels of Abeurador, Buholoup, Gazel, and Troubat (Barbaza & Heinz, 1992; Heinz, 1999; Heinz & Barbaza, 1998; Heinz, Ruas & Vaquer 1992; Vernet, 1980).

5.1.2 Almond, Blackthorn, or Cherry?

The remarkable dynamism of Rosaceae within the Late Glacial–Early Holocene forest reconquest process in Southern Europe is documented by charcoal data (from natural sequences included: Delhon, Thiébault, Brochier, & Berger, 2010) from around the Mediterranean basin, its hinterlands, and adjacent biogeographical regions (Allué et al., 2007; Asouti, Ntinou, & Kabukcu, 2018; Bazile-Robert, 1980; Fiorentino & Parra, 2015; Heinz, 1999; Heinz & Thiébault, 1998; Henry, Valdeyron, Bouby, & Théry-Parisot, 2013; Starkovich & Ntinou, 2017; Théry-Parisot, 2001b; Thiébault, 1999; Vernet & Thiébault, 1987; Vernet, Thiébault, & Heinz, 1987; Zapata, Cava, Iriarte, Baraybar, & De La Rua, 2002).

The results from La Tourasse reopen the debate regarding the physiognomy of the Late Glacial–Early Holocene Prunoideae shrubland, presented by Bazile-Robert (1980) as a vegetation developing alongside pine-juniper woodlands composed of Rosaeae, Rhamnaceae, and Oleaceae, in which *Amygdalus* plays an important role. To our knowledge, this author was the first to evidence these specific associations for the French northwestern Mediterranean, cautiously putting forward their possible link with the Near and Middle Eastern Irano-Turanian *Amygdalus*, *Pistacia*, and *Juniperus* steppe-vegetation (*Ibid.*). The data acquired since then lead to question these interpretations both from a microanatomical and ecological viewpoint. First, the anatomical criteria put forward by Bazile-Robert (*op. cit.*) to distinguish the different *Prunus* species (*P. amygdalus*, *P. avium*, *P. mahaleb*, and *P. spinosa*) were very tenuous and are no longer in use. While Bazile-Robert presented *P. amygdalus* as a diffuse-porous species (semi-ring porous at the most), it is generally acknowledged today that *P. amygdalus* has mostly ring-porous wood (Allué et al., 2007; Henry et al., 2013; Schweingruber, 1990; Vernet et al., 2001). Thus, as most microanatomical characteristics of *Prunus* spp. overlap, charcoal analysts currently tend to use or adapt the anthracotypes 1 (*P. avium/padus*), 2 (*P. mahaleb/spinosa*), and 3 (*P. spinosa/amygdalus*) based on ray-width proposed by Heinz (Heinz & Barbaza, 1998). Yet, the *P. amygdalus* identified in the 1980's is usually diffuse-porous with wide rays (Bazile-Robert, 1980; Krauss-Marguet, 1980) and could thus correspond to *P. spinosa*. It is important to note that the types identified in the Allerød levels of Troubat (Barbaza & Heinz, 1992), Le Sanglier (Théry-Parisot, 2001b), and La Tourasse correspond mainly to *Prunus* type 1 and 2, *de facto* excluding *P. amygdalus*. As already observed by Heinz (Barbaza & Heinz, 1992), the floristic composition of the Allerød contexts we just mentioned resembles a vegetation type that has been qualified as "altimontane," which develops today in the Pyrenees between the mountain and the subalpine vegetation belts (Cantegrel, 1986) that are characterized by the presence of *P. padus* and Maloideae and their association with Rhamnaceae and juniper. As *P. padus* contributes both to *Prunus* anthracotypes 1 and 2, it could actually be the main taxon found during the Allerød. This seems also more coherent from an ecological viewpoint, as this Eurasian taxon is more cold-tolerant than *P. mahaleb*. With the exception of Heinz's work, *P. padus* has been overlooked by the anthracologists working in the area.

Finally, the brief review presented here leads to question the status of *P. amygdalus* within Late Glacial–Early Holocene assemblages from Southwest Europe. It is either absent or identified only in very

small proportions (less than 2–3% in SW France). This suggests that almond never played a significant role in the vegetation (Allué et al., 2007; Bazile-Robert, 1981; Fiorentino & Parra, 2015; Heinz, 1999; Heinz & Thiébault, 1998; Ruiz-Alonso, Uzquiano Ollero, & Zapata Peña, 2014; Théry-Parisot, 2001a). This contrasts with the important Pleistocene contribution of *Amygdalus* spp. in the Eastern Mediterranean (e.g., Asouti et al., 2018; Ntinou, 2021; Starkovich & Ntinou, 2017) and Central Asia (e.g., Allué et al., 2018), where almond originated (Fernández et al., 2015; Grasselly, 1976; Zeinalabedini, Khayam-Nekoui, Grigorian, Gradziel, & Martínez-Gómez, 2010). Therefore, our hypothesis is thus that the importance of *Prunus* type 3 in some Late Glacial assemblages relates to a spread of *P. spinosa* that is particularly well-adapted to dry conditions and superficial soils. This has also already been hypothesized for Early Holocene contexts (e.g., Henry et al., 2013; Zapata et al., 2002). In any case, a systematic reexamination of the microanatomical characteristics of the genus *Prunus* and their variability is needed to move forward on this matter.

5.1.3 Spread of the Holocene Oak Forest

As suggested by our analysis of the differences between level H (manual sampling) and YSE (flotation), oak is likely slightly underrepresented (Supplement 3). However, the paleoecological signal obtained for the Preboreal at La Tourasse, in a context of very Early Mesolithic occupations, is particularly coherent with the regional paleobotanical data.

The high taxonomic richness of the levels dated to the end of the Preboreal at La Tourasse shows a mosaic landscape, which is a well-documented feature found at several sites of equivalent altitude, such as Buholoup or Troubat, at Abeurador or in the Middle Rhône valley (Delhon et al., 2010). The Tourasse data are also consistent with palynology, where the Preboreal is characterized by the spread of oak and hazel (at the expense of birch) accompanied by low frequencies of elm (Andrieu-Ponel, 1991; Jalut, 1973; Reille & Lowe, 1993). Pine reaches its optimum development at middle and high altitudes (Reille, 1990). The presence of fir is characteristic of the Preboreal, where it appears in Pyrenean charcoal assemblages around 10200–10000 cal. BP (Heinz, 1999; Jalut, 1977), at a time where palynological records document a spread of this taxon out of its Pyrenean refugia (Beaudouin et al., 2007).

Finally, the deciduous oak forest documented at La Tourasse from the levels of the Preboreal–Boreal transition onwards is a wide-spread and well-known vegetation type. According to palynology, the Boreal is still characterized by the oak-hazel-elm triad, and above all by the continuous development of hazel (Andrieu-Ponel, 1991; Jalut, 1973; Reille, 1990), which is entirely consistent with our anthracological and carpological results. The charcoal data from Troubat levels that are contemporary with the Tourasse G ensemble are remarkably comparable, with the same taxa showing an identical hierarchy (*Quercus, Corylus*, Rosaceae, and *Pinus*) (Barbaza & Heinz, 1992; Heinz & Barbaza, 1998).

5.2 Plant Use at Tourasse Cave

5.2.1 Gathering of Edible Plants

The carpological analysis of La Tourasse provides information regarding the use of plant resources. Bearing in mind their carbonized state, the abundance of some of the taxa and their fragmentation, criteria referred by Dietsch (1996) and Bouby and Billaud (2005), we consider that the carpological assemblage was probably introduced into the site by humans. During the Allerød, fleshy fruits from the abundant Maloideae and *Prunus* spp. thriving in the surroundings of the site were available. These fruits are rich in vitamins and sugars and, usually, they can be eaten raw. Their gathering is simple, and they can be preserved dry for some months (Rivera Núñez & Obón de Castro, 1991), as documented in some sites of the Iberian Peninsula (Pérez Jordà, 2010; Zapata, 2001). The recovered fragments of fleshy fruits of La Tourasse may have accidentally fallen into the fire during their drying. Unfortunately, we were unable to identify most of the remains taxonomically.

In the levels dated to the YD, the assemblage is basically composed of cleaver seeds. This taxon has been documented in different Epipaleolithic and Mesolithic sites from Turkey (Oküzini) (Martinoli & Jacomet, 2004) to France (Al Poux à Fontanes, Baraquettes IV, Fontbrégoua) (Bouby, 2002; Bouby & Surmely, 2004; Savard, 2000), but its interpretation remains uncertain: were the seeds intentionally gathered or accidentally introduced into the site stuck to the clothes? Ethnobotanical works reported the use of cleaver seeds as "coffee" and leaves and stems as greens in Europe (Rivera Núñez & Obón de Castro, 1991).

With the beginning of the Holocene, hazel remains dominate the carpological assemblages of La Tourasse and other Mesolithic sites of the Eurosiberian region, such as in Duvensee (Holst, 2010), Baraquettes IV (Bouby & Surmely, 2004) or different sites of Scotland (Bishop, Church, & Rowley-Conwy, 2013), and of the Iberian Peninsula (Berihuete-Azorín & Antolín, 2012). Most authors point out that hazelnuts became the main energetic source during the Mesolithic, as they are rich in proteins, lipids, vitamins, and minerals (Bishop et al., 2013; Divišová & Šída, 2015; Holst, 2010). Their ubiquity could be explained indeed because of the possibilities of transport and storage for long periods. Even so, this taxon is evidently overrepresented, as its ligneous pericarp resists very well to charring and subsequent deposition and burial. The absence of acorns can be highlighted, considering the abundance of oak wood charcoal in the upper levels. This resource, rich in carbohydrates and proteins (Prado-Nóvoa, Mateos, Zorrilla-Revilla, Vidal-Cordasco, & Rodríguez, 2017), was used during the Mesolithic at many sites, such as Cova Fosca (Antolín et al., 2010), Santa Maira (Aura, Carrión, Estrelles, & Jordà, 2005), or Abric de la Falguera (Pérez Jordà, 2006). Their absence at La Tourasse could be explained by preservation problems, a lack of interest of human groups, or even linked to site functionality or the season of occupation.

5.2.2 Firewood Management

Even though we found that the Boreal-Atlantic levels from La Tourasse were not wholly representative statistically, their floristic poverty is highly surprising when compared to that of the Late Glacial and Preboreal levels and other sites of Southern France, where the average was of eleven taxa/level according to a synthesis published in 2009 (Delhon & Thiébault, 2009). That being said, Mesolithic occupations of several sites show low taxonomic diversity (5–6 taxa) such as L'abri Jérôme (Vaucluse), Troubat (Barbaza & Heinz, 1992; Heinz & Barbaza, 1998), La Poujade (Aveyron; Krauss-Marguet, 1980), Le Cuzoul de Gramat (Bertin, 2021; Henry et al., 2013), or Les Escabasses (Henry, Coli, Valdeyron, & Théry-Parisot, 2020). In the wider context of Mesolithic hunter-gatherer occupations, the recurrent taxonomic paucity could be the result of repeated, short-term occupations, and therefore of insufficient gathering for the vegetation to be accurately represented (e.g., Chabal, 1997; Chabal et al., 1999). It could also result from human selection, with the most abundant taxa being systematically targeted and, thus, be independent from the duration of occupation (on this matter see also Henry et al., 2009, 2020; Henry, Zavadskaya, Alix, Kurovskaya, & Beyries, 2018). From a theoretical viewpoint and given these two possibilities, it seems difficult to associate a limited taxonomic list to short duration occupations (e.g., hunting camps) and taxonomic variety to longer occupations (e.g., base camps). In fact, this limited species list associated with more frequent occurrences of RC could reflect a deliberate fuel wood selection favoring (green?) wood of a limited number of species and a potentially greater investment put in the cutting of live trees than expected from a short-term hunting camp (e.g., Théry-Parisot, 2001a). Ethnographic studies have repeatedly evidenced wood-cutting and firewood selection on the basis of several criteria (i.e., state of the wood, diameter, taxonomy, etc.) even for unspecialized uses of fire and temporary occupations (Dufraisse, Pétrequin, & Pétrequin, 2007; Henry, 2011; Henry & Théry-Parisot, 2014; Picornell Gelabert, Asouti, & Allué Martí, 2011; Shackleton & Prins, 1992; Théry-Parisot, 2002). Collecting green wood can offer several advantages depending on the characteristics of the occupations and the fires (Henry et al., 2018; Théry-Parisot & Henry, 2012). As seasonal indicators are rare at La Tourasse, we can imagine two main scenarios. In the case of a winter occupation, snow would cover a major part of the ground biomass. This would have led the occupants of the cave to use standing wood as it would have been easier to acquire in these conditions. Green wood could have been targeted alongside standing dead wood, as it offers a steadier and longer lasting combustion. On the other

hand, green wood produces smoke. This can be useful particularly if the occupations take place during the spring and/or summer, which is suspected for level YG according to the carpological data. Smudge fires can be put in place to repel insects or other animals. More generally speaking, the production of smoke can also relate to hide and/or meat processing, communication or symbolic activities, and rituals (Alix & Brewster, 2004; Beyries, 2008; Brody, 1981; Hansen, Krawchuk, Trugman, & Williams, 2022; Henry et al., 2018). To test the hypothesis of an early Holocene fuelwood economy in which green wood is a significant element, the development of new experimental datasets is needed on additional taxa.

6 Conclusion

Despite an archaeobotanical assemblage that presented a certain number of shortcomings, the critical assessment and statistical analyses of our results and their comparison with contemporaneous sequences led us to retrieve valuable data regarding paleoenvironmental history and human practices at La Tourasse. Our research there suggests that the Younger Dryas stadial impacted the shrubby vegetation surrounding the site; furthermore, it documented for the first time a possible shift in *Prunus* species and a possible peak in aridity, while suggesting that the Younger Dryas did not prevent the minimal development of mesothermophilous broad-leaved taxa. We hope that new archaeological sequences covering the Allerød, the Younger Dryas, and the Early Holocene will provide the possibility to further investigate the dynamics of Prunoideae in Southwest Europe. In-depth morphometric and eco-anatomical studies also appear necessary to reassess the accuracy of anthracology for discriminating different anatomical groups within this subfamily. During the Late Glacial and especially the very early Holocene, the human occupants of La Tourasse collected a diversity of woody species. This reflects the gathering of firewood from the surroundings of the rockshelter to the banks of the Garonne as well as the fact that the landscapes consisted of a mosaic of vegetation. This pattern changes with the arrival of the Holocene oak forest, suggesting not only a homogenization of the environment due to increasing temperatures and moisture but also increasing wood selectivity targeting a few taxa from a single vegetation type. The fact that this has been observed at other Mesolithic sites leads us to question if this behavior could be linked to cultural choices or if it is related to the type and function of the occupations, especially as the possible use of green wood use has been highlighted at La Tourasse. Further studies both on new sites with the possibility of high-resolution records and on microanatomical signatures of wood charcoal are needed to fully explore these exciting research avenues.

Data availability statement: All data generated or analyzed during this study are included in this published article and its supplementary information files.

References

Alix, C., & Brewster, K. (2004). Not All Driftwood is Created Equal: Wood Use and Value along the Yukon and Kuskokwim Rivers, Alaska. *Alaska Journal of Anthropology*, *2*(1–2), 48–68.

Allué, E., Expósito, I., Tumung, L., Ollé, A., & Bazgir, B. (2018). Early evidence of Prunus and Prunus cf. Amygdalus from Palaeolithic sites in the Khorramabad Valley. *Compte Rendu Palevol*, *17*(6), 335–345.

Allué, E., Nadal, J., Estrada, A., & García-Argüelles, P. (2007). Los datos antracológicos de la Balma del Gai (Bages, Barcelona): Una aportación al conocimiento de la vegetación y la explotación de los recursos forestales durante el Tardiglaciar en el NE peninsular. *Trabajos de Prehistoria*, *64*(1), 87–97.

Andrieu, V., Hubschman, J, Jalut, G., & Hérail, G. (1988). Chronologie de la déglaciation des Pyrénées françaises. Dynamique de sédimentation et contenu pollinique des paléolacs; application à l'interprétation du retrait glaciaire. *Quaternaire*, *25*(2–3), 55–67.

Andrieu-Ponel, V. (1991). Paysages de la haute Garonne depuis les temps glaciaires. *Revue géographique des Pyrénées et du Sud-Ouest*, *62*(1), 95–99.

Antolín, F., Caruso, L., Mensua, C., Olària, C., Piqué, R., & Alonso, N. (2010). Forest resources exploitation in the Late Mesolithic and Early Neolithic site of Cova Fosca (Ares Del Maestre, Castelló, Spain). In *Des Hommes et des plantes. Exploitation du milieu et des ressources végétales de la Préhistoire à nos jours* (pp. 323–333). Antibes: APDCA.

Asouti, E., Ntinou, M., & Kabukcu, C. (2018). The impact of environmental change on Palaeolithic and Mesolithic plant use and the transition to agriculture at Franchthi Cave, Greece. *PLOS ONE*, *13*(11), 38.

Aura, J. E., Carrión, Y., Estrelles, E., & Jordà, G. P. (2005). Plant economy of hunter-gatherer groups at the end of the last Ice Age: Plant macroremains from the cave of Santa Maira (Alacant, Spain) ca. 12000–9000 B.P. *Vegetation History and Archaeobotany*, *14*(4), 542–550.

Badal García, E. (1990). Méthode de prélèvement et paléoécologie du Néolithique d'après les charbons de bois de « La Cova de les Cendres » (Alicante, Espagne). *Pact, Journal of the European Study Group on Physical, Chemical, Mathematical And Biological Techniques Applied to Archaeology*, *22*, 231–243.

Badal García, E. (1992). L'anthracologie préhistorique: À propos de certains problèmes méthodologiques. *Bulletin de la Société Botanique de France. Actualité Botanique*, *139*(2–4), 167–189.

Badal, E., & Carrión Marco, Y. (2004). La presencia de hongos e insectos xilófagos en el carbón arqueológico : Propuestas de interpretación. *Avances en arqueometría*, 98–106.

Barbaza, M. (2011). Environmental changes and cultural dynamics along the northern slope of the Pyrenees during the Younger Dryas. *Quaternary International*, *242*(2), 313–327.

Barbaza, M., & Heinz, C. (1992). La grotte-abri du Moulin (Troubat, Hautes-Pyrénées). Environnement et Archéologie. *Bulletin de la Société Botanique de France. Actualités Botaniques*, *139*(2–4), 685–695.

Barrière, C. (1959). Grotte de Rouffignac (Résultats des premières fouilles, 1957-1958). *Pallas. Revue d'étude Antiques*, *8*(2), 3–8.

Bazile-Robert, E. (1980). Les groupements à Amygdalus et Prunus de la fin du Tardiglaciaire et du début du Postglaciaire en Méditerranée Nord-Occidentale. *Geobios*, *5*(13), 777–781.

Bazile-Robert, E. (1981). Flore et végétation des gorges du Gardon à la moyenne vallée de l'Hérault, de 40 000 à 9 500 B. P., d'après l'anthracoanalyse. *Paléobiologie Continentale*, *12*(1), 79–90.

Bazile-Robert, E. (1984). Les charbons de bois du Mas d'Azil (Ariège). Étude paléobotanique. *Bulletin de la Société Préhistorique Française*, *81*(4), 109–110.

Beaudouin, C., Jouet, G., Suc, J.-P., Berné, S., & Escarguel, G. (2007). Vegetation dynamics in southern France during the last 30kyBP in the light of marine palynology. *Quaternary Science Reviews*, *26*(7), 1037–1054.

Beaulieu, J. L. de., Pons, A., & Reille, M. (1985). Recherches pollenanalytiques sur l'histoire tardiglaciaire et holocène de la vegetation des Monts d'Aubrac (Massif Central, France). *Review of Palaeobotany and Palynology*, *44*(1), 37–80.

Berihuete-Azorín, M., & Antolín, F. (2012). A Les Avellanes, Foc i Flames: Tafonomia i Quantificació de Les Closques d'avellana Recuperades En Contextos Arqueològics. Revisió Del Registre Documentat a La Península Ibèrica. *Cypsela*, (*19*), 281–294.

Bertin, I. (2021). *Environnement et combustibles à l'aube de la néolithisation. Étude anthracologique des niveaux du second Mésolithique au Cuzoul de Gramat* (*Lot*) (*Mémoire de Master 2, Préhistoire, Paléoenvironnement et Archéosciences*). Nice: Université Côte d'Azur.

Beyries, S. (2008). Modélisation du travail du cuir en ethnologie: Proposition d'un système ouvert à l'archéologie. *Anthropozoologica*, *43*(1), 9–42.

Binney, H., Edwards, M., Macias-Fauria, M., Lozhkin, A., Anderson, P., Kaplan, J. O., … Zernitskaya, V. (2017). Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. *Quaternary Science Reviews*, *157*, 80–97.

Bishop, R. R., Church, M. J., & Rowley-Conwy, P. A. (2013). Seeds, fruits and nuts in the Scottish Mesolithic. *Proceedings of the Society of Antiquaries of Scotland*, 143, 9–72.

Bojňanský, V., & Fargašová, A. (2007). *Atlas of seeds and fruits of Central and East European Flora*. The Carpathian Mountains Region. Spinger.

Bouby, L. (2002). Plantes utilisées sur le site mésolithique d'al poux à fontanes (Lot): Les témoins carpologiques. In *Gisements post-glaciaires en Bas-Quercy. Variabilité des espaces et des statuts de deux occupations mésolithiques sauveterriennes de plein air* (Vol. 1, p. 77–81). Toulouse: Archives d'écologie préhistorique.

Bouby, L., & Billaud, Y. (2005). Identifying prehistoric collected wild plants: A case study from Late Bronze Age settlements in the French Alps (Grésine, Bourget Lake, Savoie). *Economic Botany*, *59*(3), 255–267.

Bouby, L., & Surmely, F. (2004). Les restes carpologiques carbonisés du site mésolithique des Baraquettes IV (Velzic, Cantal). *Bulletin de la Société Préhistorique Française*, *101*(3), 457–462.

Breuil, A. (1950). Lascaux. *Bulletin de la Société préhistorique de France*, *47*(6–8), 355–363.

Brewer, S., Cheddadi, R., de Beaulieu, J. L., & Reille, M. (2002). The spread of deciduous Quercus throughout Europe since the last glacial period. *Forest Ecology and Management*, *156*(1), 27–48.

Brody, H. (1981). *Maps and dreams: Indians and The British Columbia frontier*. Vancouver-Toronto: Douglas & McIntyre.

Cantegrel, R. (1986). Ecological thresholds and biological organization of pinus uncinata ram. Communities: New prospects in Neouvielle (Western Pyrenees). *Bulletin de la Société Botanique de France. Actualités Botaniques*, *133*(sup1), 193–208.

Cappers, R. T. J., Bekker, M., & Jans, J. E. A. (2006). *Digital seed atlas of The Netherlands* (1st ed.). Groningen: Barkhuis.

Caruso Fermé, L., Théry-Parisot, I., Carré, A., & Fernández, P. M. (2018). The shrinkage cracks and the diameter of the log: A experimental approach toward fuel management by Patagonian hunter-gatherers (Paredón Lanfré site. Río Negro Province, Argentina). *Archaeological and Anthropological Sciences*, *10*(2), 1821–1829. doi: 10.1007/s12520-017-0487-4.

Chabal, L. (1991). *L'Homme et l'évolution de la végétation méditerranéenne des âges des métaux à la période romaine; recherches anthracologiques théoriques, appliquées principalement à des sites du Bas-Languedoc*. (Thèse de doctorat en Physiologie et biologie des organismes et populations). Université de Montpellier II, Montpellier.

Chabal, L. (1992). La représentativité paléo-écologique des charbons de bois archéologiques issus du bois de feu. *Bulletin de La Société Botanique de France. Actualités Botaniques*, *139*(2–4), 213–236.

Chabal, L. (1994). Apports récents de l'anthracologie a la connaissance des paysages passés: Performances et limites. *Histoire & Mesure*, *9*(3–4), 317–338.

Chabal, L. (1997). *Forêts et sociétés en Languedoc* (*Néolithique final, Antiquité tardive*): *L'anthracologie, méthode et paléoécologie*. Paris: MHS.

Chabal, L., Fabre, L., Terral, J.-F., & Théry-Parisot, I. (1999). L'Anthracologie. In: La botanique, Errance, Paris, p. 43–104.

Chrzavzez, J. (2013). *Approche expérimentale de la conservation des charbons de bois dans les gisements paléolithiques: Processus post-dépositionnels, fragmentation et représentativité des assemblages anthracologiques*. (Doctoral dissertation). Université Nice Sophia Antipolis, Nice.

Chrzavzez, J. (2016). Échantillonnage charbons pour datation. In *Grotte Bouyssonie, Brive-la-Gaillarde, Corrèze. Rapport de fouille programmée triannuelle, 2013-2015-2016* (pp. 78–81).

Chrzavzez, J., Théry-Parisot, I., Fiorucci, G., Terral, J.-F., & Thibaut, B. (2014). Impact of post-depositional processes on charcoal fragmentation and archaeobotanical implications: Experimental approach combining charcoal analysis and biomechanics. *Journal of Archaeological Science*, *44*, 30–42.

Costamagno, S., Barshay-Szmidt, C., Kuntz, D., Laroulandie, V., Pétillon, J.-M., Boudadi-Maligne, M., … Chevallier, A. (2016). Reexamining the timing of reindeer disappearance in southwestern France in the larger context of late glacial faunal turnover. *Quaternary International*, *414*, 34–61.

Costamagno, S., Cochard, D., Ferrié, J.-G., Laroulandie, V., Cazals, N., Langlais, M., … Philibert, S. (2008). Nouveaux milieux, nouveaux gibiers, nouveaux chasseurs? Évolution des pratiques cynégétiques dans les Pyrénées du Tardiglaciaire au début du Postglaciaire. *Bulletin de la Société Préhistorique Française*, *105*(1), 17–27.

Delhon, C., & Thiébault, S. (2009). De la forêt aux foyers paléolithiques et mésolithiques dans le Sud de la France: Une revue des données anthracologiques et phytolithiques. *Actes du XV congrès mondial*, 13, 119–133. Lisbonne: Luiz Oosterbeek.

Delhon, C., Thiébault, S., Brochier, J., & Berger, J. (2010). Dynamiques de végétation au Tardiglaciaire et à l'Holocène ancien en moyenne vallée du Rhône d'après les données anthracologiques. *Quaternaire*, *21*(3), 281–293.

Dietsch, M.-F. (1996). Gathered fruits and cultivated plants at Bercy (Paris), a Neolithic village in a fluvial context. *Vegetation History and Archaeobotany*, *5*(1), 89–97.

Divišová, M., & Šída, P. (2015). Plant use in the Mesolithic period. Archaeobotanical Data from the Czech Republic in a European Context – A Review. *Interdisciplinaria Archaeologica - Natural Sciences in Archaeology*, *VI*(1), 95–106.

Dufraisse, A., Pétrequin, P., & Pétrequin, A.-M. (2007). La gestion du bois de feu: Un indicateur des contextes socio-écologiques. Approche ethnoarchéologique dans les Hautes Terres de Papua (Nouvelle-Guinée indonésienne). *Cahiers d'Archéologie Romande*, *108*, 115–126.

Fat Cheung, C. (2015). *L'Azilien pyrénéen parmi les sociétés du Tardiglaciaire ouest-européen: Apport de l'étude des industries lithiques* (*ED TESC: Préhistoire*). Université de Toulouse - Jean Jaurès, Toulouse.

Fat Cheung, C., Chevalier, A., Bonnet-Jacquement, P., Langlais, M., Ferrié, J.-G., Costamagno, S., … Ballista, S. (2014). Comparaison des séquences aziliennes entre Dordogne et Pyrénées. Etat des travaux en cours. In *Les groupes culturels de la transition Pléistocène-Holocène entre Atlantique et Adriatique* (vol. 3, pp. 17–24). Bordeaux: Bulletin de la Société Préhistorique Française.

Fernández, A., Font i Forcada, C., Kamali, K., Rubio-Cabetas, M. J., Wirthensohn, M., & Socias i Compagny, R. (2015). Molecular analyses of evolution and population structure in a worldwide almond [Prunus dulcis (Mill.) D.A. Webb syn. P. amygdalus Batsch] pool assessed by microsatellite markers. *Genetic Resources and Crop Evolution*, *62*, 205–219.

Fiorentino, G., & Parra, I. (2015). "Lost" postglacial littoral environments in SE Italy: Anthracological evidence at Grotta delle Mura. *Review of Palaeobotany and Palynology*, *218*, 198–203.

Gaussen, H., & Rey, P. (1947). Carte de la végétation de la France, région de Toulouse, feuille 71 [Végétation]. Toulouse: Centre National de Recherche Scientifique.

Grasselly, C. (1976). Les espèces sauvages d'amandier. *Options Méditerranéennes*, *32*, 28–43.

Guitian, J., Guitian, P., & María-Sanchez, J. (1993). Reproductive biology of two Prunus species (Rosaceae) in the Northwest Iberian Peninsula. *Plant Systematics and Evolution*, *185*, 153–165.

Hansen, W. D., Krawchuk, M. A., Trugman, A. T., & Williams, A. P. (2022). The Dynamic Temperate and Boreal Fire and Forest-Ecosystem Simulator (DYNAFFOREST): Development and evaluation. *Environmental Modelling & Software*, *156*, 1–14.

Heinz, C. (1991). Upper Pleistocene and Holocene vegetation in the south of France and Andorra. Adaptations and first ruptures: New charcoal analysis data. *Review of Palaeobotany and Palynology*, *69*, 299–324.

Heinz, C. (1999). Les transformations du paysage végétal pyrénéen au cours de l'Epipaléolithique et du Mésolithique. In *L'Europe des derniers chasseurs - Peuplement et paléoenvironnement de l'Epipaléolithique et du Mésolithique* (pp. 115–123). Grenoble: Editions du CTHS.

Heinz, C., & Barbaza, M. (1998). Environmental changes during the Late Glacial and Post-Glacial in the central Pyrenees (France): New charcoal analysis and archaeological data. *Review of Palaeobotany and Palynology*, *104*, 1–17.

Heinz, C., Ruas, M.-P., & Vaquer, J. (1992). La grotte de l'Abeurador (Félines-Minervois, Hérault): Paléoécologie d'après l'anthracologie et la carpologie. *Bulletin de la Société Botanique de France. Actualités Botaniques*, *139*(2–4), 465–482.

Heinz, C., & Thiébault, S. (1998). Characterization and paleoecological significance of archaeological charcoal assemblages during Late and Post-Glacial phases in Southern France. *Quaternary Research*, *50*, 56–68.

Henry, A. (2011). *Paléoenvironnements et gestion des combustibles au Mésolithique dans le sud de la France: Anthracologie, ethnoarchéologie et expérimentation*. (Doctoral dissertation, Université Nice Sophia Antipolis). Université Nice Sophia Antipolis, Nice. Hal archives ouvertes.

Henry, A. (2021). Recherches archéobotaniques à Bouyssonie: Bilan et perspectives. In *La grotte Bouyssonie. Rapport d'opération de fouilles programmées*. DRAC Nouvelle-Aquitaine (pp. 146–148).

Henry, A., & Boboeuf, M. (2016). Environnement ligneux et gestion du bois de feu au cours du Mésolithique au Clos de Poujol (Campagnac, Aveyron). *Bulletin de la Société Préhistorique Française*, *113*(1), 5–30.

Henry, A, Bouby, L., & Valdeyron, N. (2011). Environment and plant economy during the Mesolithic in the Haut-Quercy (Lot, France): Anthracological and carpological data. *SAGVNTVM EXTRA*, *11*, 79–80.

Henry, A., Coli, V. L., Valdeyron, N., & Théry-Parisot, I. (2020). Old taphonomy issues, new charcoal data for Mesolithic contexts: Impact of fragment size and sampling context on the assemblages of Escabasses cave (SW France). *Journal of Archaeological Science: Reports*, *30*, 1–10.

Henry, A., Liard, A., Oberlin, C., Orliac, M., & Huot, J.-P. (2022). La grotte de la Tourasse (Saint-Martory, Haute-Garonne): Résultats des nouvelles datations. *Bulletin de la Société Préhistorique Française*, *119*(2), 327–331.

Henry A., & Puech E. (2022). Recherches archéobotaniques à Bouyssonie: État des lieux. In Delvigne V., Lesvignes E., Langlais M. (Eds.), *La grotte Bouyssonie. Rapport d'opération de fouilles programmées* (pp. 155–170). DRAC Nouvelle-Aquitaine.

Henry, A., Théry-Parisot, I., & Voronkonva, E. (2009). La gestion du bois de feu en forêt boréale : Archéo-anthracologie et ethnographie (région de l'Amour, Sibérie). *In Gestion des combustibles au Paléolithique et au Mésolithique. Nouveaux Outils, Nouvelles Interprétations*, *13*, 17–37.

Henry, A., & Théry-Parisot, I. (2014). Fuel use and management during the Mesolithic: Recent approaches in archaeobotany. *Maison de la recherche, Proceedings of the Round Table*, *6*, 65–83. Toulouse: P@lethnologie Association.

Henry, A, Valdeyron, N., Bouby, L., & Théry-Parisot, I. (2013). History and evolution of Mesolithic landscapes in the Haut-Quercy (Lot, France): New charcoal data from archaeological contexts. *The Holocene*, *23*(1), 127–136.

Henry, A., Zavadskaya, E., Alix, C., Kurovskaya, E., & Beyries, S. (2018). Ethnoarchaeology of fuel use in Northern forests: Towards a better characterization of prehistoric fire-related activities. *Ethnoarchaeology, Journal of Archaeological, Ethnographic, and Experimental Studies*, *10*(2), 99–120.

Holst, D. (2010). Hazelnut economy of early holocene hunter-gatherers: A case study from Mesolithic Duvensee, Northern Germany. *Journal of Archaeological Science*, *37*(11), 2871–2880.

Huot, J.-P. (1985). *Fouilles de la Tourasse, Rapport d'activités*. Unpublished report.

Huot, J.-P. (1991a). *Fouilles de la Tourasse, Rapport d'activités*. Unpublished report.

Huot, J.-P. (1991b). *Fouilles de la Tourasse, Rapport d'activités. Campagnes 1989-1990-1991*. Unpublished report.

Huot, J.-P., Capdevielle, C., & Christensen, M. (1991). Le Sauveterrien de la Tourasse, Fouilles de 1989. *Revue des Comminges*, *104*(2), 153–163.

Isarin, R., & Bohncke, S. (1999). Mean July temperatures during the Younger Dryas in Northwestern and Central Europe as inferred from climate indicator plant species. *Quaternary Research*, *51*, 158–173.

Jalut, G. (1973). Évolution de la végétation et du climat de l'extrémité orientale des Pyrénées pendant le Tardiglaciaire et le Post glaciaire. *Bulletin de l'Association Française pour l'Étude du Quaternaire*, *10*(2), 55–68.

Jalut, G. (1977). *Végétation et Climat des Pyrénées méditerranéennes depuis quinze mille ans*. Paris: École des Hautes études en Sciences Sociales.

Jalut, G., Galop, D., Belet, J.-M., Aubert, S., Amat, A. E., Bouchette, A., … Fontugne, M. (1998). Histoire des forêts du versant nord des Pyrénées au cours des 30 000 dernières années. *Journal de la Botanique*, *5*, 73–84.

Jalut, G., Marti, J. M., Fontugne, M., Delibrias, G., Vilaplana, J. M., & Julia, R. (1992). Glacial to interglacial vegetation changes in the northern and southern Pyrénées: Deglaciation, vegetation cover and chronology. *Quaternary Science Reviews*, *11*(4), 449–480.

Jalut, G., & Turu i Michels, V. (2006). La végétation des Pyrénées françaises lors du dernier épisode glaciaire et durant la transition Glaciaire-Interglaciaire (Last Termination). In *Els Pirineus i les àrees circumdants durant el Tardiglacial. Mutacions i filiacions tecnoculturals, evolució paleoambiental. Homenatge Georges Laplace*, XIV Colloqui internacionald'arqueologiadePuigcerdá, 10-11X 2006, Institut d'Estudis Ceretans, Gérone, 23.

Kabukcu, C., & Chabal, L. (2021). Sampling and quantitative analysis methods in anthracology from archaeological contexts: Achievements and prospects. *Quaternary International*, *593–594*, 6–18.

Krauss-Marguet, I. (1980). *Contribution à l'Histoire de la végétation Postglaciaire des Grands Causses d'après l'analyse anthracologique du gisement préhistorique de la Poujade* (Commune de Millau-Aveyron) (DES). Université des Sciences et Techniques du Languedoc, Montpellier.

Langlais, M., Delvigne, V., Jacquier, J., Lenoble, A., Beauval, C., Peschaux, C., … Pesesse, D. (2019). Une nouvelle archéo-séquence pour le Magdalénien en Corrèze. Focus sur le Magdalénien moyen ancien de la grotte Bouyssonie (Brive-la-Gaillarde, Corrèze, France). *PALEO. Revue d'archéologie Préhistorique*, *30*(1), 204–229.

Marinval, P. (1988). *Cueillette, agriculture et alimentation végétale de l'épipaléolithique jusqu'au 2ème âge du fer en France méridionale. Apports palethnographiques de la carpologie*. (Doctoral dissertation, Paris, EHESS). EHESS, Paris.

Marinval, P. (2007). Dades Complementàries Sobre l'economia Vegetal de l'Epipaleolític i El Mesolític de La Balma de La Margineda'. In *Les excavacions a La Balma de la Margineda* (*1979-1991*) (Vol. IV, pp. 480–491). Andorra: Edicions del Govern d'Andorra.

Martinoli, D., & Jacomet, S. (2004). Identifying endocarp remains and exploring their use at Epipalaeolithic Öküzini in Southwest Anatolia, Turkey. *Vegetation History and Archaeobotany*, *13*(1), 45–54.

Mithen, S., Finlay, N., Carruthers, W., Carter, S., & Ashmore, P. (2001). Plant use in the Mesolithic: Evidence from Staosnaig, Isle of Colonsay, Scotland. *Journal of Archaeological Science*, *28*(3), 223–234.

Monod, B. (2013). Carte géologique harmonisée du département de la Haute-Garonne [Map]. BRGM.

de Mortillet, G. (1895). 622e séance. —16 Mai 1895. Correspondance. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, *6*(1), 323–327.

Moskal-del Hoyo, M., Wachowiak, M., & Blanchette, R. A. (2010). Preservation of fungi in archaeological charcoal. *Journal of Archaeological Science*, *37*, 2106–2116.

Naughton, F., Sanchez Goni, M. F., Rodrigues, T., Salgueiro, E., Costas, S., Desprat, S., … Abrantes, F. (2016). Climate variability across the last deglaciation in NW Iberia and its margin. *Quaternary International*, *414*, 9–22.

Ntinou, M. (2021). Vegetation change in southeastern Greece during the Late Pleistocene. The wood charcoal record from Klissoura Cave 1 (Peloponnese, Greece). *Quaternary International*, *593–594*, 104–117.

Orliac, M., & Orliac, E. (1972). *Fouilles à la grotte de la Tourasse 1965-1970* (*rapport de fouilles*). Revue de Comminges vol. 34 Saint-Gaudens, 1–37.

Pérez Jordà, G. (2006). *Estudi de Les Llavors i els Fruits. In El abric de la Falguera* (*Alcoi, Alacant*): *8.000 años de ocupación humana en la cabecera del río de Alcoi* (Vol. 2, pp. 111–119). Alicante; Alcoy: Diputación Provincial de Alicante; Ayuntamiento: Caja de Ahorros del Mediterráneo.

Pérez Jordà, G. (2010). Estudio paleocarpológico del cingle del mas cremat. In *Generalitat Valenciana. El Cingle del Mas Cremat* (*Portell de Morella, Castellón*). *Un asentamiento en altura con ocupaciones del Mesolítico Reciente al Neolítico Final: Parque Eólico de las Cabrillas—Zona III del plan Eólica Valenciano* (pp. 147–155). Valencia: Renomar S.A. y Ein Mediterráneo S. L.

Picornell Gelabert, L., Asouti, E., & Allué Martí, E. (2011). The ethnoarchaeology of firewood management in the Fang villages of Equatorial Guinea, central Africa: Implications for the interpretation of wood fuel remains from archaeological sites. *Journal of Anthropological Archaeology*, *30*(3), 375–384.

Piette, É. (1895). Hiatus et lacune. Vestiges de la période de transition dans la grotte du Mas-d'Azil. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, *6*(1), 235–267.

Piette, É. (1907). *L'art pendant l'Age du renne*, Paris: Masson.

Prado-Nóvoa, O., Mateos, A., Zorrilla-Revilla, G., Vidal-Cordasco, M., & Rodríguez, J. (2017). Efficiency of gathering and its archaeological implications for an European early palaeolithic population. *Journal of Anthropological Archaeology*, *45*, 131–141.

Protin, M., Schimmelpfennig, I., Mugnier, J.-L., Buoncristiani, J.-F., Le Roy, M., Pohl, B., … Team, A. (2021). Millennial-scale deglaciation across the European Alps at the transition between the Younger Dryas and the Early Holocene – Evidence from a new cosmogenic nuclide chronology. *Boreas*, *50*(3), 671–685.

Rameau, J.-C., Mansion, D., Dumé, G., Gauberville, C., Bardat, J., Bruno, E., & Keller, R. (2008). *Flore forestière française, guide d'écologie illustré. Région méditerranéenne*. Paris: Ministère de l'agriculture et de la pêche - DGFAR.

Rasmussen, S. O., Bigler, M., Blockley, S. P., Blunier, T., Buchardt, S. L., Clausen, H. B., … Winstrup, M. (2014). A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: Refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews*, *106*, 1–14.

Reille, M. (1990). Recherches pollenanalytiques dans l'extrémité orientale des Pyrénées: Données nouvelles, de la fin du Glaciaire à l'Actuel. *Ecologia Mediterranea*, *16*(1), 317–357.

Reille, M., & Lowe, J. J. (1993). A re-evaluation of the vegetation history of the eastern Pyrenees (France) from the end of the last glacial to the present. *Quaternary Science Reviews*, *12*(1), 47–77.

Rivera Núñez, D., & Obón de Castro, C. (1991). *La guía de Incafo de las plantas útiles y venenosas de la Península Ibérica y Baleares (excluidas medicinales)*. Madrid: Incafo.

Rodet, M. J. (2000). *Les industrie Aziliennes de Grotte de la Tourasse (Saint-Martory—Haute Garonne) (DEA Environnement et Archéologie)*. MAE, Paris.

Ruiz-Alonso, M., Uzquiano Ollero, P., & Zapata Peña, L. (2014). Macrorrestos vegetales de Santa Catalina (Lekeitio, Bizkaia): Carbones y bellotas del Tardiglaciar. *Kobie Serie Excavaciones Arqueológicas en Bizkaia*, *4*, 75–92.

Savard, M. (2000). *Étude de l'assemblage Carpologique de La Baume de Fontbrégoua (Var) Du Paléolithique Final Au Chasséen Récent (D.E.A Environnement et Archéologie)*. Paris I - Panthéon-Sorbonne; Paris X Nanterre, Paris.

Schweingruber, F. H. (1978). *Mikroskopische holzanatomie*. Zürcher: Institut fédéral de recherches forestières.

Schweingruber, F. H. (1990). *Anatomy of European Woods: An atlas for the identification oh European trees, shrubs and dwarf shrubs*. Bern: Paul Haupt.

Shackleton, C. M., & Prins, F. (1992). Charcoal analysis and the "Principle of the least effort"—A conceptual model. *Journal of Archaeological Science*, *19*(6), 631–637.

Starkovich, B. M., & Ntinou, M. (2017). Climate change, human population growth, or both? Upper Paleolithic subsistence shifts in southern Greece. *Quaternary International*, *428*(Part B), 17–32.

Théry-Parisot, I. (2001). Étude anthracologique de la grotte du Sanglier (Reilhac, Lot). In La grotte du Sanglier à Reilhac (Lot). Du Magdalénien au Néolithique ancien. Préhistoire du Sud-Ouest (pp. 93–99) Vol. 4. Cressensac.

Théry-Parisot, I. (2001a). *Économie des combustibles au Paléolithique*. Paris: CNRS éditions.

Théry-Parisot, I. (2002). The gathering of firewood during Palaeolithic time. In *Charcoal analysis: Methodological approaches, palaeoecological results and wood uses* (pp. 243–250). Oxford: Archaeopress.

Théry-Parisot, I., Chabal, L., & Chrzavzez, J. (2010). Anthracology and taphonomy, from wood gathering to charcoal analysis. A review of the taphonomic processes modifying charcoal assemblages, in archaeological contexts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *291*(1–2), 142–153.

Théry-Parisot, I., & Henry, A. (2012). Seasoned or green? Radial cracks analysis as a method for identifying the use of green wood as fuel in archaeological charcoal. *Journal of Archaeological Science*, *30*, 1–8.

Thiébault, S. (1999). Le milieu végétal des derniers chasseurs-cueilleurs en Vercors et Chartreuse. Nouvelles données anthracologiques et proposition d'une biozonation. In *L'Europe des derniers chasseurs: Epipaléolithique et Mésolithique* (pp. 589–602). Grenoble: C.T.H.S.

Triat-Laval, H. (1982). Pollenanalyse de sédiments quaternaires récents du pourtour de l'Étang de Berre. *Ecologia Mediterranea*, *8*(4), 97–115.

Valdeyron, N., Briand, T., Bouby, L., Henry, A., Khedhaier, R., Marquebielle, B., … Bosc-Zanardo, B. (2011). *Le gisement mésolithique des Fieux (Miers, Lot): Une halte de chasse sur le causse de Gramat? Haltes de chasse en Préhistoire. Quelles réalités archéologiques?* (Vol. 3, pp. 335–346). Toulouse: P@lethnologie.

Vaquer, J., & Ruas, M.-P. (2009). La grotte de l'Abeurador Féline-Minervois (Hérault): Occupations humaines et environnement du Tardiglaciaire à l'Holocène. In De Méditérannée et d'ailleurs. Mélange offerts à Jean Guilaine (p. 761–792). Toulouse: Archives d'Écologie Préhistorique.

Vernet, J.-L. (1980). La végétation du bassin de l'Aude, entre Pyrénées et Massif Central, au Tardiglaciaire et au Postglaciaire d'après l'analyse anthracologique. *Review of Palaeobotany and Palynology*, *30*, 33–55.

Vernet, J.-L., Ogereau, P., Figueiral, I., Machado Yanes, C., & Uzquiano, P. (2001). *Guide d'identification des charbons de bois préhistoriques et récents. Sud-Ouest de l'Europe: France Péninsule ibérique et îles Canaries*. Paris: CNRS éditions.

Vernet, J.-L., & Thiébault, S. (1987). An approach to Northwestern mediterranean recent prehistoric vegetation and ecological implications. *Journal of Biogeography*, *14*(2), 117–127.

Vernet, J.-L., Thiébault, S., & Heinz, C. (1987). Nouvelles données sur la végétation préhistorique postglaciaire méditerranéenne d'après l'analyse anthracologique. *Premières communautés paysannes en Méditerranée occidentale*, CNRS éditions, Paris, 87–94.

Vidal Matutano, P. (2016). *Around the Fire: Landscape, Climate and Firewood Management in Hunter-gatherer Groups during the Middle Palaeolithic (Alicante, Spain)*. Ph.D. thesis. Universitat de València.

Zapata, L. (2001). El Uso de Los Recursos Vegetales En Aizpea (Navarra, Pirineo Occidental): La Alimentación, El Combustible y El Bosque. In *Cazadores-recolectores en el Pirineo navarro: El sitio de Aizpea entre 8000 y 6000 años antes de ahora: Volume 10* (Anejos de Veleia: Series maior, pp. 325–360). Univ. del País Vasco/Euskal Herriko Unibertsitatea: Servicio Ed.

Zapata, L., Cava, A., Iriarte, M. J., Baraybar, J. P., & De La Rua, C. (2002). Mesolithic plant use in the western Pyrenees: Implications for vegetation change, use of wood and human diet. In *UCL. Hunter-gatherer Archaeobot- any. Perspectives from the Northern Template Zone* (pp. 96–107). London: Institut of Archaeology.

Zeinalabedini, M., Khayam-Nekoui, M., Grigorian, V., Gradziel, T. M., & Martínez-Gómez, P. (2010). The origin and dissemi-nation of the cultivated almond as determined by nuclear and chloroplast SSR marker analysis. *Scientia Horticulturae*, *125*(4), 593–601.