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Late-Glacial palaeotemperatures and palaeoprecipitations in the Aubrac Mountains (French Massif Central) reconstructed from multiproxy analyses (Coleoptera, chironomids and pollen)

Philippe Ponel ^{a,*}, Frédéric Guiter ^a, Emmanuel Gandouin ^a, Odile Peyron ^b, Jacques-Louis de Beaulieu ^a

^a Aix Marseille University, Avignon University, National Center for Scientific Research, National Research Institute for Sustainable Development, Mediterranean Institute for Marine and Terrestrial Biodiversity and Ecology (CNRS, IRD, IMBE), Aix-en-Provence, France

^b Institute of Evolution Sciences Montpellier, University of Montpellier, National Center for Scientific Research, National Research Institute for Sustainable Development, Practical School of Higher Studies (ISEM, CNRS, IRD, EPHE), Montpellier, France

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ABSTRACT

New investigations performed with a multi-proxy approach provide a robust climate reconstruction for the Late-Glacial in the Massif Central, France. The temperature reconstruction from Coleoptera is obtained from the Mutual Climatic Range Method, or “MCR” method, based on the range of climates corresponding to the area occupied today by the species identified in fossil assemblages. The Weighted Averaging Partial Least Squared (WA-PLS) method is used to produce mean July temperature estimates from Chironomid assemblages. Climate reconstruction from pollen data is performed using an assemblage approach, the Modern Analogue Technique. During the Late-Glacial the July temperature (Tmax) reconstructed from beetles (Coleoptera) was lower than the current Tmax of 18.9 °C. Summer conditions were close to the present at the beginning of the Oldest Dryas (17400–14600 cal. BP), and during most of the Allerød (13900–12800 cal. BP). During the Younger Dryas (12800–11700 cal. BP) Tmax estimates ranged from 12 to 13 °C, much lower than today. The Tmax increased at the onset of the Holocene (11700 cal. BP), reaching values close to the modern conditions from the beginning of the period. Tmax reconstructed from chironomids shows an initial warming around 15000 cal. BP, with a Tmax rise from 7 °C to 11 °C. A maximum (13.5 °C) was reached around 13800 cal. BP. A second optimum of 16 °C occurred after 10800 cal. BP. The Late-Glacial Interstadial (LGI) is marked by temperature decreases (from 13 to 12 to 10–9 °C) around 13200–12900 cal. BP. A second climate minimum was reached around 12600 cal. BP, during the Younger Dryas (Tmax about 10 °C). The end of the Younger Dryas seems to have been warmer, with a Tmax of about 13 °C, just before the early Holocene climate improvement. Pollen-inferred results showed that the Late-Glacial climate at Roustières was characterized by colder and drier winter and summer seasons than today, and by conditions close to the modern ones around 11700 cal. BP, at the onset of the Holocene. Climate conditions comparable to the modern ones were also evidenced at the end of the Allerød, with colder than today conditions evidenced from both Tmax and Tmin (January temperature). During the Oldest and Younger Dryas the coldest month showed a temperature of –13 °C, while summers appeared more moderate (warmest month around 16 °C). Cold conditions were also reconstructed during the Bølling, while temperatures comparable to present-day values were reached during the Allerød. A cold oscillation occurred around 13400 cal. BP. Particularly dry conditions were reconstructed during the Oldest Dryas (17000–15800 cal. BP). From 15800 to the end of the Younger Dryas, the precipitation oscillated around 750 mm, but increased during the Allerød and the Holocene periods. These climatic trends reconstructed by the three proxies allowed identifying the temperate periods (LGI and the Holocene) and the cold events (Younger Dryas) of the Late-Glacial period. However, difficulties due to different sampling resolutions emerged, and several discrepancies linked to the proxy or the methods used are discussed.

* Corresponding author.

E-mail address: philippe.ponel@imbe.fr (P. Ponel).

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1. Introduction

The Late-Glacial (ca. 18000–11700 cal. BP) is a period of special climatic interest characterized by abrupt climatic changes (strong warm and cool events), associated with the successive steps of the deglaciation and changes in atmospheric and ocean circulation (e.g. Walker et al., 2012; Rehfeld et al., 2018). These rapid and marked climate oscillations (Greenland Interstadial-1a to Greenland Interstadial-1e (GI-1a to GI-1e), Greenland Stadial-1 (GS-1)) were observed in ice records of Greenland (Rasmussen et al., 2014) as well as in Europe from various proxies such as pollen, oxygen isotopes, molecular biomarkers, beetles, and chironomids (e.g. Coope and Lemdahl, 1995; Ammann et al., 2000; Coope, 2004; Peyron et al., 2005; Coope and Rose, 2008; Lotter et al., 2012; Millet et al., 2012; Blaga et al., 2013; Moreno et al., 2014; Heiri et al., 2015).

The Late-Glacial temperature evolution in Europe and the Mediterranean area is still a matter of active research and debate (e.g. Heiri et al., 2014). The syntheses of Coope and Lemdahl (1995) based on coleopteran records, of Heiri et al. (2014) based on chironomid records, and of Moreno et al. (2014) based on pollen, chironomids and other proxies show diverging temperature trends in Europe, depending on the studied region. The coleopteran-based reconstructions show considerable regional differences during the Late-Glacial interstadial, but a close agreement during the Younger Dryas (Coope et al., 1998). The chironomid-based reconstructions suggest that temperature variations during the Late-Glacial tended to be more pronounced in Western Europe (British Isles, Norway) than in the South Central/East (South-western Europe, Central and Southeastern regions). This is particularly true for the Younger Dryas cooling which was not evidenced in East and Central Southern Europe (Heiri et al., 2014). Diverging temperature trends were also reconstructed from pollen data and other proxies for the Allerød period, which seems to have been warmer than the Bølling in the Alpine Region, South-western Europe and the Mediterranean area (Moreno et al., 2014).

More reliable temperature reconstructions, especially from Western Europe and Mediterranean regions, are necessary to confirm or not such diverging trends during the Late-Glacial. Temperature reconstructions inferred from multi-proxy approaches including both pollen and chironomids were carried out for several regions of Europe (e.g. Birks and Ammann, 2000; Lotter et al., 2012; Birks et al., 2014; Pawlowski et al., 2015). These studies showed that substantial discrepancies might appear depending on the proxies, especially chironomids and pollen (Millet et al., 2008; Samartin et al., 2017). In France, reconstructions of temperature variations derived from both pollen and chironomids on the same record are scarce (Peyron et al., 2005; Magny et al., 2006; Millet et al., 2008) and – to our knowledge – there is still no temperature reconstructions inferred from pollen, chironomids and coleopteran records.

Coleoptera, chironomid and pollen assemblages have largely been used to quantitatively reconstruct past climatic changes, most often in single proxy approach (e.g. Ponel et al., 2005; Coope, 2010; Heiri et al., 2015; Peyron et al., 2017; Duprat-Oualid et al., This Issue). Among biological proxies from lake sediments, coleopteran fossils may be considered as one of the most sensitive palaeoecological and palaeoclimatic indicators (Coope, 1998, 2004). Palaeoclimatic studies based on Coleoptera are rare in France, but useful data were obtained from Eastern France for the last climatic cycle (Ponel, 1995), from the Paris Bassin for the Late-Glacial (Ponel et al., 2005), from the Massif Central (La Taphanel) for the Late-Glacial and the early Holocene (Ponel and Coope, 1990). Chironomid assemblages are also promising climatic indicators because the temperature was identified as one of the key factors affecting their distribution (Walker, 2001). Chironomids were successfully used to reconstruct major and minor climatic oscillations during the Late-Glacial period in the Swiss Alps (e.g. Ilyashuk et al., 2009; Larocque-Tobler et al., 2010). Palaeoclimatic studies based on chironomid records remain rare in Western Europe: the synthesis of Heiri et al.

(2014) was based on few chironomid records (two for Southwestern Europe and two for East and Central Southern Europe). Only three reconstructions of summer temperatures are available in France, more precisely for the Pyrenees (Millet et al., 2012), the Jura Mountains (Heiri and Millet, 2005) and the Massif Central (Gandouin et al., 2016). Pollen assemblages are often used to reconstruct past climate during the Late-Glacial, because temperature and precipitation changes are identified as major determining factors for shifts in pollen assemblages (Birks and Birks, 2014). However, in French mountains such reconstructions are still lacking except for the Jura (Peyron et al., 2005), the Alps (Ortu et al., 2009) and the Massif Central (Duprat-Oualid, This Issue; Cubizolle et al., 2021; Dendievel et al., 2021).

This calls for the development of multiproxy approaches on the same sedimentary record in order to reconstruct independently past climate variations, and to help identify potential biases of currently used proxies and thus improve the reliability of each proxy-inferred climate record. Here we bring our contribution to this debate with a multiproxy study including Coleoptera, chironomid and pollen data applied to a Late-Glacial sequence in the Massif Central (France).

In the Massif Central, many palaeoecological investigations were carried out in the Aubrac region (e.g. de Beaulieu et al., 1985). Among the several sites studied, only three present lacustrine deposits spanning the end of the Pleniglacial and Late-Glacial (Bonnecombe 2, La Chaumette and Les Roustières). In the Roustières sequence, Coleoptera, chironomid, pollen and diatom data were analysed for the Late-Glacial period by Ponel et al. (2016) and Gandouin et al. (2016). Chironomid data have been used to reconstruct the July temperature (Gandouin et al., 2016) but no attempt was made to produce temperature estimates inferred from fossil pollen or coleopteran assemblages (Ponel et al., 2016).

The aim of these new investigations is to provide a robust climate reconstruction for the Late-Glacial period in the Massif Central, inferred from a multi-proxy approach based on the Roustières record. More precisely, the purpose of the present study is 1) to establish a reliable quantitative climate reconstruction based on coleopteran and pollen data, 2) to compare the reconstructions obtained there with chironomid-inferred temperature reconstruction, and 3) to discuss these results in a regional context and in the light of other European records and diverging climate patterns. The climatic signal reconstructed with these different proxies is particularly interesting to compare because Coleoptera and chironomids provide usually more reliable reconstruction of July temperature, whereas pollen data perform better in the reconstruction of annual temperature/precipitation and winter temperatures (Peyron et al., 2005; Birks and Birks, 2014).

2. Regional settings

2.1. Geomorphology, extant vegetation and climate

Ponel et al. (2016) and Gandouin et al. (2016) provided a detailed description of the Roustières peatbog (3°5'18"E, 44°42'48"N) and its surroundings; therefore, only a short summary is given here.

The Roustières peatbog is a large peat bog located at 1196 m a.s.l. in the Aubrac region (Fig. 1), a large granitic and basaltic plateau located to the south of the French Massif Central. The peatbog occupies a former glacial niche surrounded by low hills and drained by a small rivulet. According to Poizat and Rousset (1975), two moraine ridges close the depression to the S-W, determining a palaeolake occupied today by the bog. The site is located in the montane zone, potentially occupied by *Fagus sylvatica* forests on volcanic soil, but a long history of intense pastoral activities has deeply modified this vegetation, which is today dominated by *Calluna vulgaris* and *Cytisus purgans* heathlands, and by summer pastures. At lower altitudes oak forests (*Quercus pedunculata*, *Q. sessiflora*, *Q. pubescens*) are present. The climate on the plateau is cold and wet in winter, with heavy rain and snow falls ($T_{min} = -5^{\circ}\text{C}$ – 0°C , average annual rainfall = 1100–1800 mm) (www.meteofrance.com). In

the study area, the mean July temperature is about 18.9 °C (www.worldclim.org).

2.2. Palaeoecological background

Ponel et al. (2016) and Gandouin et al. (2016) reconstructed past landscape dynamics from pollen and insect assemblage successions in the Roustières region. Here we present a brief summary of the palaeoecological successions evidenced at Roustières.

2.2.1. Late Pleniglacial (17700-17300 cal. BP)

The Late Pleniglacial is characterized by herbaceous pollen assemblages with significant percentages of reworked mesophilous taxa, such as *Abies* and *Fagus* but more importantly with occurrences of reworked *Pterocarya* pollen (this exotic tree is a palynostratigraphical marker of the Middle Pleistocene in Europe). In this context, it remains speculative to propose any detailed landscape reconstruction for this period, and, by extent, to infer any climate reconstruction. The coleopteran assemblages during this period are very poor and correspond to a periglacial environment.

2.2.2. Oldest Dryas (17300-14600 cal. BP)

The Oldest Dryas was marked by the disappearance of reworked pollen grains along with a sharp increase of herb percentages, while the *Pinus* curve is significantly declining. Cold steppic grasslands were developing close to the site. It is also marked by regular occurrences of beetles associated with open environments, of aquatic beetles associated with running water, and of cold adapted taxa from that period until the end of the Late-Glacial Interstadial. The chironomid taxa associated with the cold and deep zone of lakes decreased drastically during the Oldest

Dryas and were replaced by littoral and eutrophic taxa at the onset of the Late-Glacial Interstadial.

2.2.3. Late-Glacial Interstadial (14600-12800 cal. BP)

The Late-Glacial Interstadial, which corresponds to the general warming observed at the global scale, is marked by a progressive decline of steppic herbs while shrubs such as *Juniperus* and *Salix* progressively recolonized the area. At the same time, *Pinus* reaches its lowest percentages. It must be noticed that, in other sequences from the Aubrac and the Massif Central (Marais de Limagne in the Velay region), *Juniperus* presents quite higher pollen percentages, suggesting that a hiatus could hide a part of the juniper optimum at the Roustières peatbog. After the juniper phase, *Betula* and rapidly *Pinus* became predominant, while *Artemisia* reached its lowest percentages for the Late-Glacial period. At the same time, beetles from open/cold environments were also present. The abundances of cold-adapted diatoms and chironomids over the Late-Glacial Interstadial seem to indicate relatively moderate but unstable summer temperatures. Regular occurrences of deciduous *Quercus* throughout the LGI may suggest that oak woodlands were developing at lower altitudes, but oak was certainly absent from the Aubrac plateau, considering the low values of *Quercus* percentages during the whole Late-Glacial.

2.2.4. Younger Dryas (12800-11700 cal. BP)

A reversal in the vegetation dynamics marked the beginning of the Younger Dryas, which is well recorded at Roustières contrary to most sites in the Massif Central. Steppic taxa reached a second optimum while *Pinus* and *Betula* were poorly represented. The very cold spell of the Younger Dryas is also clearly indicated by the abundance of cold adapted beetles, a decrease of running water taxa, and a good

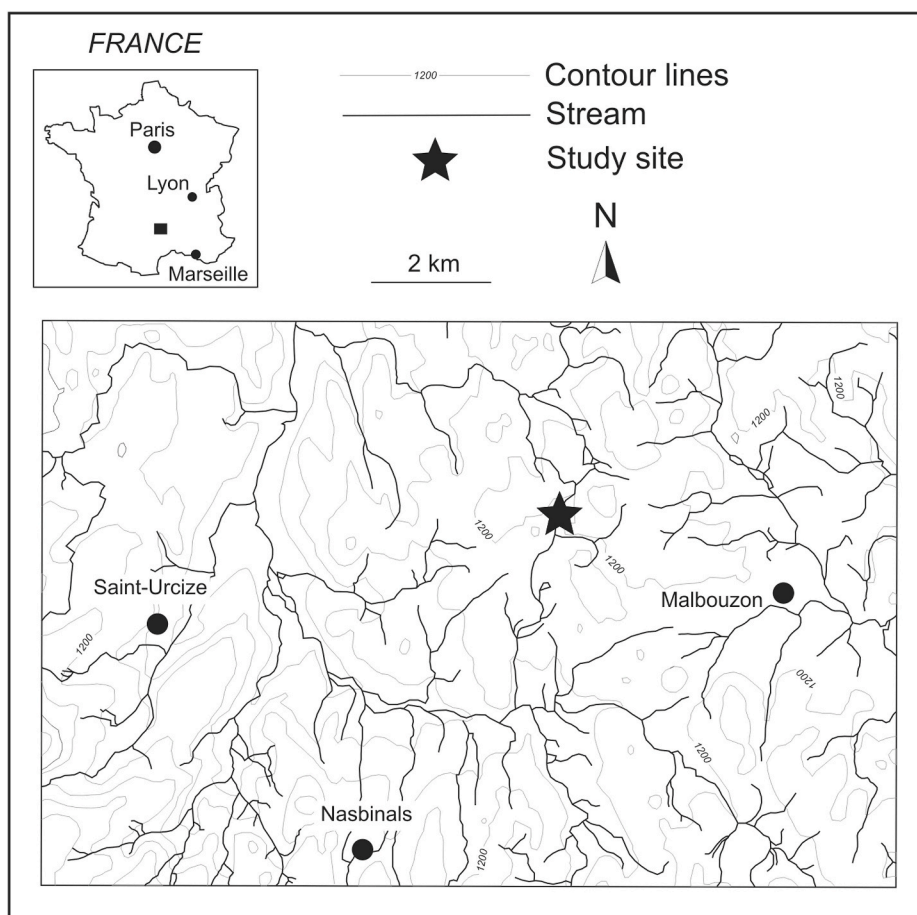


Fig. 1. Location of the Roustières peatbog (star) in the Aubrac Mountains (Massif Central, France; Black Square on the top left inlet).

representation of taxa associated with open environments. The absence of beetles adapted to trees and shrubs, and occurrences of cold stenothermic insects (beetles and chironomids together) provided evidence for a treeless and cold Late-Glacial, certainly due to the relatively high altitude and the harsh continental conditions prevailing in the region even today. An interesting feature is the strong transitory peak of running water Coleoptera at the transition Younger Dryas/Holocene (around 11700 cal. BP), which enables us to better understand the hydrological changes at this transition: the rapid warming at the end of the Younger Dryas lead to a rapid melting of the snow cover, triggering a simultaneous rise of the activity of small streams in the area, and consequently to a strong increase in the number of beetles from running waters. The strong input of water into the depression of Roustières induced also a lake water level rise.

2.2.5. The early Holocene (11700-9650 cal. BP)

The beginning of the Holocene was marked at Roustières by a complex succession of mesophilous trees (*Betula*, *Quercus*, *Ulmus*, and *Corylus avellana*). It was also marked by the total disappearance of cold adapted plant and animal taxa and the progressive establishment of standing water and wetland taxa, and by the diversification of phytophagous taxa in response to the diversification of hygrophilous and helophytic plants, which was also recorded by the macrophytic chironomid fauna and epiphytic diatom species. Probably, the Roustières basin was largely filled-in at that time.

3. Material and methods

3.1. The Roustières sediment core and the age-depth model

Ponel et al. (2016) described the Roustières sedimentary profile. The lithology of the sampled sedimentary sequence is made of clay (approximately 1000-900 cm depth), clay-gyttja (900-600 cm), and homogeneous peat (600 cm to the surface). A 4.45 m sedimentary profile (from 9.95 to 5.50 m depth) was selected to record the Late-Glacial oscillations, in agreement with the age model and a previous pollen study (de Beaulieu et al., 1985).

In order to work in a well-constrained chronological context, 22 radiocarbon dates were obtained (Table 1). The age-depth model is based on the first published in Ponel et al. (2016) and updated with the non-marine (IntCal20) radiocarbon calibration (Reimer et al., 2020) (Fig. 2). The dates were calibrated using the Clam software (Blaauw, 2010) associated with the statistical software R (version 3.0.1) (R Core Team, 2012). The dates were calculated at two standard deviations (95% probability density). The age-depth model was developed using a smooth spline interpolation (spar = 0.3 and 10000 iterations) between dated levels with the same software (see also Ponel et al., 2016). The upper and lower sections of the age-depth curve were represented by a dashed line and were extrapolated beyond dated levels. The 2-sigma envelop of the age-depth model encompasses 18 radiocarbon ages; the four remaining dates were excluded from the age-depth model. Three (in red) must be rejected as “too young”; one (in green) is also excluded from the model since it induces a reversal in the age-depth curve if included. A high sedimentation rate occurred at ca. 13000 cal. BP, due to rapid biogenic sedimentation without any detrital input, certainly in response to a lake productivity increase.

3.2. Subfossil data

Coleoptera. 22 sediment slices were extracted from the profile for insect macrofossil analyses (each 20 cm thick, on average, and about 1300 cm³ in volume). Fossil arthropod remains were extracted from each sample and concentrated using the standard method described by Coope (1986): the samples were disaggregated by hand in water and washed over a 300- μ m sieve. The residue was mixed by hand with paraffin, and then submitted to a flotation in order to separate the insect

Table 1

Radiocarbon dates performed on bulk sediments for the Roustières stratigraphy in the Aubrac Mountains (Massif Central, France). Radiocarbon Laboratory abbreviations: SacA = Gif sur Yvette (Saclay), France; Poz = Poznan, Poland.

Lab-code	Depth (cm)	Nature of sample	$\delta^{13}C$ (‰)	Age uncal. BP (1 σ)	Age cal. BP (2 σ)
Poz-16151	600–601	Peaty gyttja	−26	8800 ± 45	9610–10153
SacA 10451	607–608	Gyttja	−24.5	8770 ± 30	9634–9906
SacA 10452	615–618	Gyttja	−24.8	8605 ± 30	9526–9628
SacA 10453	620–622	Gyttja	−23.2	8830 ± 35	9706–10150
SacA 10454	637–640	Gyttja	−23.5	8785 ± 35	9633–10114
SacA 10455	650–653	Gyttja	−23.2	9405 ± 35	10557–10731
SacA 10456	660–664	Gyttja	−22.8	9585 ± 45	10745–11128
SacA 10457	680–681	Gyttja	−22	9705 ± 35	10888–11218
SacA 10458	690–692	Gyttja	−20	9615 ± 35	10782–11166
SacA 10459	715–720	Gyttja	−20.7	10090 ± 35	11404–11957
Poz-16152	730–735	Clayey gyttja	−19.6	10200 ± 60	11628–12108
SacA 10460	745–750	Clayey gyttja	−19.7	10635 ± 40	12446–12682
Poz-16155	755–760	Clayey gyttja	−18.8	10950 ± 60	12648–13063
SacA 10461	760–765	Gyttja	−19.8	10965 ± 40	12657–13054
SacA 10463	810–815	Gyttja	−19.3	10225 ± 40	11769–12086
SacA 10464	820–825	Gyttja	−23.5	11190 ± 40	12902–13234
Poz-16154	835–840	Gyttja	−22.3	11020 ± 60	12705–13092
SacA 10465	855–860	Gyttja	−20.1	11530 ± 40	13268–13477
SacA 10466	870–875	Gyttja	−22.6	12090 ± 45	13789–14081
Poz-16153	885–891	Gyttja	−18.1	12810 ± 60	14909–15841
SacA 10468	930–935	Clay	−20.8	13800 ± 50	16742–17075
SacA 10469	970–975	Clay	−19.2	14360 ± 50	17148–17803

fragments from the vegetative and minerogenic fractions. After washing with detergent, water and alcohol, the fragments were sorted, and identified under a binocular microscope by direct comparison with specimens from a modern reference collection.

Chironomids. Forty-seven samples were analysed from the depths between 995 and 600 cm, at a minimum of 5 cm intervals. The extraction of chironomid remains consisted of successive treatments of KOH (10%, 70 °C) and water-washing over a 100 μ m sieve (Hofmann, 1986), combined with paraffin flotation (Coope, 1986). Head capsules that included at least half the mentum were counted. The larval head capsules were identified with reference to Wiederholm (1983), Schmid (1993), Rieradevall and Brooks (2001), Klink and Moller Pillot (2003), and Brooks et al. (2007).

Pollen. Pollen analysis was made every 5 cm on the same samples set aside for Coleoptera and chironomid analyses. Chemical treatment of pollen samples follows Goehry and de Beaulieu (1979). Pollen grains were identified using standard keys and atlases (Faegri et al., 1989; Moore et al., 1991; Reille, 1992–1999), and compared with a modern reference collection preserved at the IMBE, Aix-en-Provence.

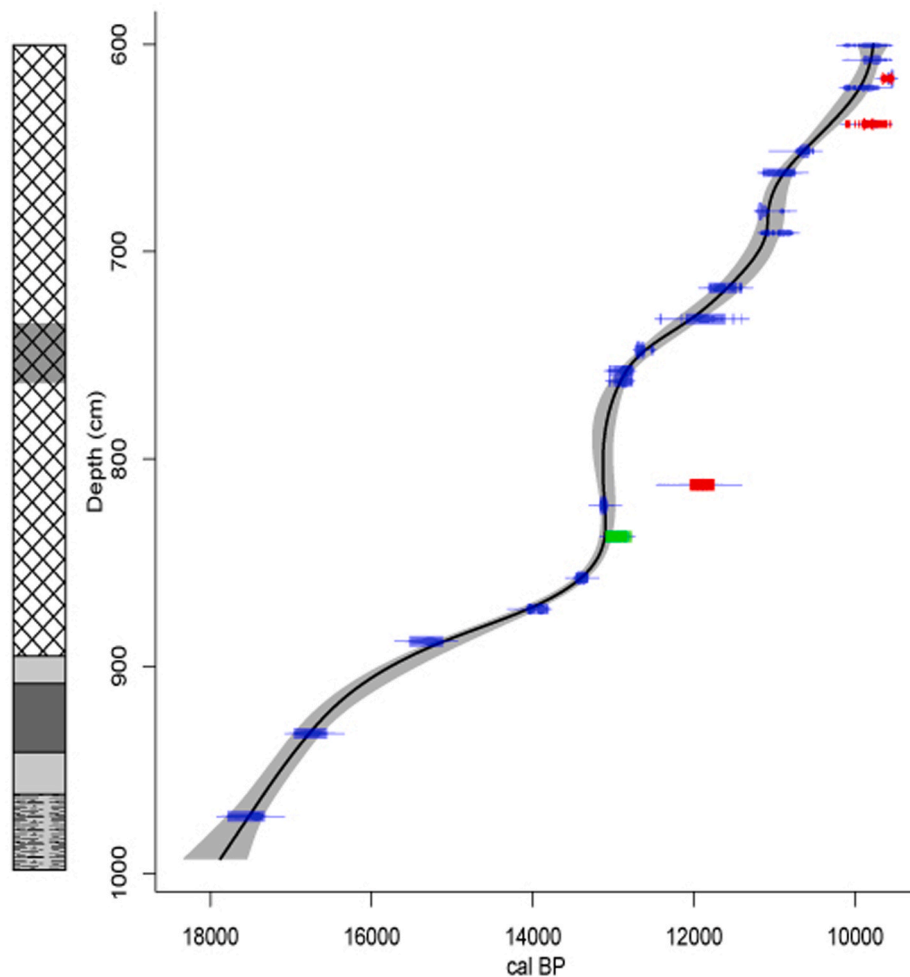


Fig. 2. Age-depth model for the Roustières basin stratigraphy in the Aubrac Mountains (Massif Central, France) computed and based on 22 radiocarbon dates (95% probability density represented in blue). The two-sigma envelop of the model is represented by a grey area. Four dates were excluded from the age-depth model; three (in red) must be rejected as “too young”, one (in green) is also excluded from the model since it induces a reversal in the age-depth curve if included. A dashed line represents the “best” age-depth curve. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. Climate reconstruction methods

Coleoptera. The July temperature reconstruction was obtained from the Mutual Climatic Range Method, or “MCR” method (Atkinson et al., 1986), based on the range of climates corresponding to the area occupied today by the species identified in each fossil assemblage. The palaeotemperature estimate proposed for the whole assemblage corresponds to the overlap of the climatic ranges of the species identified in this assemblage. To avoid any bias, the selected species used and included in an International database (Buckland, 2007) are predatory or scavenger insects and are not associated with plants. It was assumed that their distributional range is driven by climatic factors and not by the distribution of any plant or group of plants. The database includes 436 taxa of Coleoptera (Buckland, 2007), 33 of which are present in the Roustières profile, and can so be used to produce the MCR reconstruction. The MCR reconstruction for Roustières was obtained using the MCR software included in the BugsCEP package (Buckland and Buckland, 2006; Buckland, 2007).

Chironomids. The Weighted Averaging Partial Least Squared (WA-PLS) method was used to produce mean July temperature estimates and was described in details in Gandouin et al. (2016) and summarized here. We used a weighted-averaging partial least squares, 2-component, chironomid-based mean July air temperature inference model. The fossil data were square-root transformed, and the C2 program was used (Juggins, 2003). This inference model is based on a modern calibration set of 274 lakes from Norway and Switzerland (Heiri et al., 2011), including 151 chironomid taxa, spanning a mean July air temperature range of 3.5–18.4 °C. The model has a Root Mean Square Error of

Prediction (RMSEP) of 1.40 °C and a bootstrapped r^2 of 0.87. Because of the dominance of both *Corynocera ambigua* during the Oldest Dryas and unresolved *Tanytarsini*, the statistical significance of the temperature reconstruction was tested using the Telford and Birks (2011) test. In addition, the Goodness-of-fit to temperature was evaluated by passively positioning the fossil samples on a CCA of the modern training set constrained solely against July temperature. The Modern Analogue technique (MAT) was also used to detect fossil samples that lacked good analogues in the modern calibration dataset using squared chord distance as a measure of dissimilarity (Velle et al., 2005).

Pollen. Pollen-inferred climate reconstruction was performed using the Modern Analogue Technique (Guiot, 1990). This method is not a transfer function such as the WA-PLS used with chironomid data. The MAT is an assemblage approach largely used to reconstruct past climates in Europe (e.g. Cheddadi et al., 1997; Peyron et al., 2011; Mauri et al., 2015). This method uses a squared-chord - distance to calculate the degree of dissimilarity between modern and fossil pollen assemblages. The smaller the distance, the greater the degree of analogy between the two pollen samples. MAT is easy to use by requiring no calibration or transformation of the pollen/climate datasets. The optimal number of analogues for each climate parameter – annual amount of precipitation (PANN, in mm), mean temperature of the coldest month (MTCO, in °C) and of the warmest month (MTWA, in °C) – is previously determined with the bootstrap cross-validation method on the basis of obtaining the lower Root Mean Squared of the Errors of Predictions. We retained here five analogues for estimating independently MTCO, MTWA, and PANN. Finally, past climate values are calculated as the weighted mean of the present-day climate values of the closest modern pollen analogues

selected. The method is based on a large data set of modern pollen samples (more than 3100 pollen spectra), mostly located in Europe and Eurasia (Peyron et al., 2017). Please notice that the Aubrac Mountain plateau is close to slopes facing Mediterranean plains, which may also explain the presence of rare thermophilous taxa blown upwards from glacial refuges lower in altitudes. Small occurrence of temperate taxa such as *Quercus* were recorded during the Oldest Dryas in the Roustières pollen diagram. These low percentages were excluded here given that the occurrence of these mesophilous taxa during cold periods is probably linked to regional to long-distance pollen transport and would have biased the climate reconstruction leading sometimes to an over-evaluation of the temperatures. For all these tests we used the package Rioja (R) (Juggins, 2014).

4. Results

4.1. Coleoptera

All the samples, but one (995–990 cm), included MCR beetle species, 33 species in total (Table 2). In the faunal assemblages, a small group of Coleoptera bears a strong climatic significance since they are associated with very cold conditions (Ponel et al., 2016): *Agabus arcticus* (Payk.), **Aphodius mixtus* Villa, **Bembidion (Testediolum)* sp., *Bembidion bipunctatum* (L.), *Eucnecosum brachypterum* (Grav.), *Helophorus glacialis* Villa, **Helophorus schmidti* Villa, *Potamonectes griseostriatus* (Geer), *Tachinus elongatus* Gyll. It is important to note that some of them (indicated by (*)) are not included in the BugsCEP package (Buckland, 2007) which was developed for British, Scandinavian and Central European faunas, and not for more southern regions such as the Massif Central, the southern Alps and Pyrenees, where the percentage of endemic Coleoptera is high. This is the case for *Aphodius mixtus* (today an endemic scarabeid restricted to high altitude grasslands in the French mountains, cf. Ponel et al., 1995, Lumaret et al., 1996), for *Bembidion* subgenus *Testediolum* (a ground beetle typical of melting snow patches, with an ecology similar with that of *Bembidion bipunctatum*), and for *Helophorus schmidti* (living in French mountains, but also at high altitudes in central Europe and in the Mediterranean peninsulas). As a consequence, the number of MCR species present in each assemblage is relatively low, ranging from 1 to 7 (the lowermost sample does not contain any MCR species), but the samples from 790 to 700 cm are well documented, with 4–7 MCR species, and should provide realistic temperature estimates for a period of major climatic changes straddling the Younger Dryas, from the termination of the LGI to the onset of the Holocene.

The area of maximum overlap of species thermal envelopes reaches 100% for almost all the assemblages, but not for the two samples (950–930 and 730–720 cm) where it reaches 66.6% and 80% only,

Table 2

Coleoptera fossils from the Roustières stratigraphy in the Aubrac Mountains (Massif Central, France) included in the Mutual Climatic Range Method (MCR) software programme.

<i>Acidota cruentata</i> (Mannh.)	<i>Agabus arcticus</i> (Payk.)
<i>Agabus bipustulatus</i> (L.)	<i>Agonum thoreyi</i> Dej.
<i>Amara equestris</i> (Duft.)	<i>Aphodius haemorrhoidalis</i> (L.)
<i>Bembidion bipunctatum</i> (L.)	<i>Berosus signaticollis</i> (Charp.)
<i>Cicindela campestris</i> L.	<i>Coelambus novemlineatus</i> (Steph.)
<i>Coelostoma orbiculare</i> (F.)	<i>Colymbetes fuscus</i> (L.)
<i>Erichsonius cinerascens</i> (Grav.)	<i>Eucnecosum brachypterum</i> (Grav.)
<i>Gymnusa brevicollis</i> (Payk.)	<i>Halipilus confinis</i> Steph.
<i>Helophorus glacialis</i> Villa	<i>Hydrobius fuscipes</i> (L.)
<i>Hydroporus palustris</i> (L.)	<i>Hygrotus inaequalis</i> (F.)
<i>Hyphydrus ovatus</i> (L.)	<i>Lesteva longelytrata</i> (Goeze)
<i>Noterus crassicornis</i> (Müll.)	<i>Notiophilus aquaticus</i> (L.)
<i>Ochtheophilum fracticorne</i> (Payk.)	<i>Odacantha melanura</i> (L.)
<i>Olophrum fuscum</i> (Grav.)	<i>Potamonectes elegans</i> (Panz.)
<i>Potamonectes griseostriatus</i> (Geer)	<i>Pterostichus diligens</i> (Sturm)
<i>Serica brunnea</i> (L.)	<i>Tachinus elongatus</i> Gyll.
<i>Tachinus signatus</i> (Geer)	

respectively. Buckland (2007) states that “the lower the percentage overlap, the greater the probability that the sample represents a period of time in which there was a degree of climatic change greater than the tolerance levels of the individual species found”. Results from Roustières are in agreement with this postulate since the two assemblages with less than 100% overlap correspond to two periods of major climatic changes: the beginning of the Oldest Dryas in the lowermost part of the sequence, and the transition Younger Dryas–Holocene at about 11.7 ka cal. BP, which announces a major disruption in the composition of successive coleopteran assemblages (Ponel et al., 2016).

The mean temperatures of the warmest month (Tmax July) obtained from the MCR reconstruction for beetles are presented on Fig. 3. These estimates are usually more reliable than the mean temperatures of the coldest month, since, for Coleoptera, summer is the main period of activity involving in particular crucial phases of development and mating, whereas most of the beetles enter diapause in winter and thus are able to stand very low temperatures. For this reason, we only used Tmax values in this paper (Fig. 3), showing that Tmax reconstructed from beetle assemblages for most of the period before the Holocene is much below the current Tmax of 18.9 °C, with the exception of the beginning of the Oldest Dryas (but as indicated above, the area of maximum overlap for this sample 950–930 cm is low) and most of the Allerød period (which suggests that at that time the summer thermal conditions were close to the present conditions). During the Younger Dryas, Tmax estimates are precise and ranged from 12 to 13 °C, much lower than at present. These values are particularly reliable since for this period the MCR method is based on a substantial number of MCR species. Tmax increased strongly at the onset of the Holocene, reaching values close to the modern conditions from the beginning of the period onwards.

4.2. Chironomids

Gandouin et al. (2016) provided a detailed description of the Chironomid-inferred temperature results. To summarize, and based on the results of the Telford and Birks (2011) test ($p < 0.05$), they clearly show that the temperature of the warmest month (July) is the major driver of change in the chironomid assemblages of the Roustières basin for the Late-Glacial period. Nevertheless, these authors also showed that temperature before 17000 and after 11700 cal. BP have no close analogue in the modern calibration data set. Therefore, temperature reconstruction for the Oldest Dryas should be treated with caution, while Younger Dryas samples with a “good” fit may be more consistent. The reconstruction of the temperature of the warmest month (Tmax) reveals several thermal fluctuations (Fig. 3). The initial climate warming occurred around 15000 cal. BP when Tmax rose from 7 °C to 11 °C. A maximum of about 13.5 °C was reached around 13800 cal. BP. A second thermal optimum of 16 °C occurred after 10800 cal. BP. The Late-Glacial interstadial (LGI) seems to be marked by temperature decreases (−3 °C/−2 °C: from 13/12 to 10/9 °C) around 13200 cal. BP and 12900 cal. BP. A second climate minimum was reached when the temperatures reached about 10 °C around 12600 cal. BP during the Younger Dryas period. The end of the Younger Dryas seems to have been warmer with summer temperatures of about 13 °C, just before the early Holocene climate improvement.

Reliability of the chironomid-based temperature reconstruction was discussed in detail in Gandouin et al. (2016). Variables other than temperature may have been influencing the response of the chironomid assemblages at this time. Other variables known to influence chironomid distribution and abundance include water depth, pH oxygen conditions, and trophic levels (Juggins, 2013; Brooks et al., 2016). This is especially important for taxa such as *Corynocera ambigua*, which has a strong influence on the temperature reconstruction during cold episodes, but presents an ambiguous response to temperature according to Brodersen and Lindegaard (1999) since it may respond also to the natural infilling of the site and to lake level fluctuations.

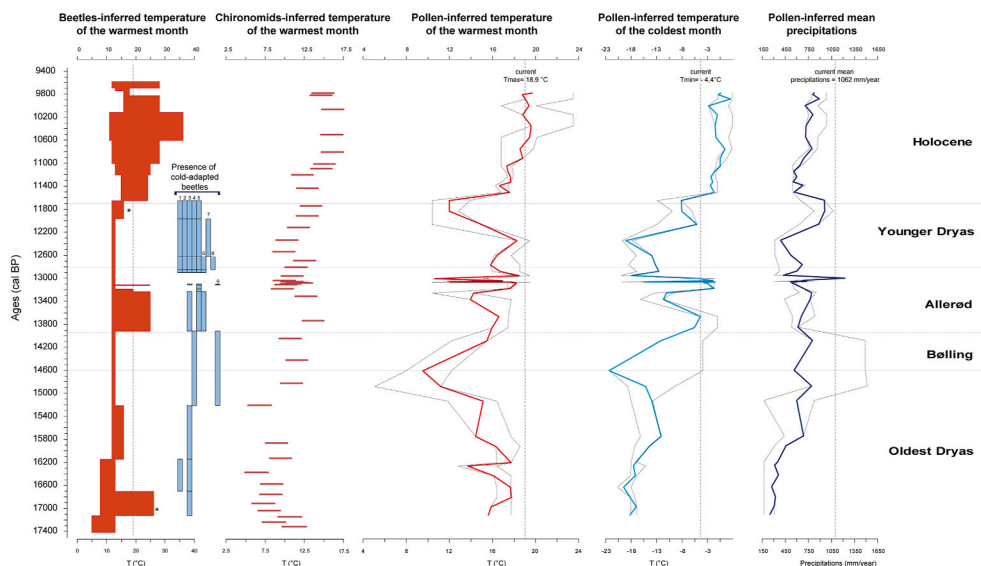


Fig. 3. Synthetic diagram for the Roustières basin stratigraphy in the Aubrac Mountains (Massif Central, France) with – from left to right – 1) the temperature of the warmest month (July) inferred from Coleoptera, chironomids and pollen, 2) the temperature of the coldest month (January) and 3) the annual precipitation inferred from pollen data. The dotted lines on the beetle- and pollen-inferred temperature of the warmest month (histogram) corresponds to the current Tmax of 18.9 °C (www.worldclim.org), the pollen-inferred temperature of the coldest month corresponds to the current Tmin of –4.4 °C, and the pollen-inferred annual precipitation corresponds to the current 1062 mm/yr.

4.3. Pollen

The Modern Analogues Technique was used to reconstruct mean temperatures of the warmest (July), coldest (January) months, and the annual precipitation. Results shows that during the Late-Glacial the climate at Roustières was characterized by colder and drier conditions than today in winter and summer, and by conditions close to the modern ones around 11700 cal. BP, at the onset of the Holocene (Fig. 3). Climate conditions comparable to the modern ones are also evidenced at the end of the Allerød. Conditions colder than today are evidenced from both the temperature reconstructions of the warmest and the coldest month. However, these two temperature signals suggest different patterns: the cooling is particularly strong in winter during the Oldest and Younger Dryas (coldest month around –13 °C, *i.e.*, 8 °C less than today) while it appears more moderated in summer for the same time periods (warmest month around 16 °C, *i.e.*, 3 °C less than today). Cold conditions were also reconstructed for the Bølling, while temperatures comparable to present-day values were reached during the Allerød period. There, a strong cold oscillation is depicted around 13400 cal. BP. After the cold event of the Younger Dryas, the temperatures increased again to reach values slightly above the modern ones.

Results also suggest high summer temperature during the Oldest Dryas. However, the reconstruction of summer temperatures for cold periods such as the Oldest and Younger Dryas must be treated with caution. The reconstruction of the temperature of the warmest month inferred from pollen data is less reliable than the reconstruction of the two other climate parameters (winter temperature and annual precipitation), particularly in regions where summer temperature does not limit vegetation (Bordon *et al.*, 2009; Bartlein *et al.*, 2011; Duprat-Oualid, This Issue). This is also true for Scandinavia, where July temperature alone seems not to be a good predictor of the broad-scale vegetation changes through the Late-Glacial. Precipitation is an extremely important climatic component and had a large impact on the Late-Glacial vegetation in NW Europe (Birks and Birks, 2014). At Roustières, particularly dry conditions were reconstructed for the Oldest Dryas (17000–15800 cal. BP) with precipitation around 300 mm, *i.e.*, 700 mm less than today. From 15800 to the end of the Younger Dryas, the precipitation oscillated around 750 mm (*i.e.*, 300 mm less than today). Precipitation also increased during the Allerød and the Holocene periods.

5. Discussion

To discuss these results in a regional context (Fig. 4) we present a comparison between Tmax reconstructed by beetles and chironomids at the Roustières basin (the orange zones represent the common range values reconstructed by both proxies), the Tmax inferred from Coleoptera at La Taphanel (Ponel and Coope, 1990), and the North-GRIP oxygen isotope record (North Greenland Ice Core Project members, 2004). The green bars (a) represent the occurrences of tree-dependent beetles, and asterisks (*) mark MCR bars with overlap <100%. Fig. 5 presents a focus on the three Tmax reconstructions for the interval 15400–11000 cal. BP. This focus allows a comparison according to the depth and temporal resolution of each insect sample with respect to the 2-sigma confidence interval of the age/depth model (Ponel *et al.*, 2016).

5.1. General comments

The general climatic trend reconstructed by both beetles, chironomids and pollen (Figs. 3 and 5) allows identifying the temperate periods at Roustières (LGI and the Holocene) and the cold event (Younger Dryas) of the Late-Glacial period. However, some difficulties due to different sampling resolutions emerge and several discrepancies linked to the proxy or the method used need to be discussed.

5.1.1. Sedimentation rate and temporal resolution of the Coleoptera-inferred Tmax reconstruction

An important issue is the time span covered by each sediment sample with beetle remains. Coleoptera samples 3 to 6 are positioned at the boundary of the Allerød/Younger Dryas (Fig. 5) during which the sedimentation rate was particularly high (Ponel *et al.*, 2016). It is rather difficult to explain such a peak in the sedimentation rate without any detrital input (the sediment is composed of pure gyttja) but it can be assumed that the general warming of the LGI (documented by peak D in Fig. 5) may partly explain an increase of biogenic lake sediment production. At this period (*ca.* 13000 cal. BP), the diatom record was characterized by a transitory increase of the diatom concentration (Gandouin *et al.*, 2016). As a result, changes in MCR values must be interpreted with caution and with respect to the time-resolution of each sample, particularly for the identification of correlations with rapid climatic events (Figs. 4 and 5) such as the GI-1d (Aegelsee oscillation) and GI-1b (Gerzensee oscillation).

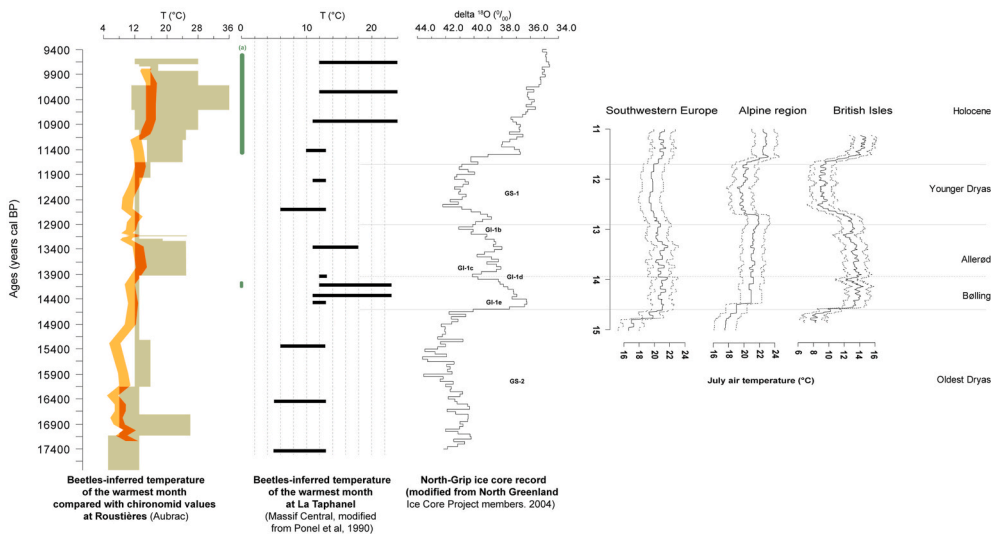


Fig. 4. Synthetic diagram for the Roustières basin stratigraphy in the Aubrac Mountains (Massif Central, France) with – from left to right – 1) the reconstructed temperature of the warmest month (inferred from Coleoptera, green histograms) obtained by the Mutual Climatic Range (MCR) method, and superimposed with the chironomid-inferred temperature of the warmest month (light orange curve); the common Tmax ranges obtained by both methods are represented in dark orange), and 2) the beetle-inferred temperature reconstruction (by the MCR method) of the warmest month at La Taphanel (France), 3) the oxygen isotope curve from the North-GRIP ice core record, and 4) the regional temperature reconstructions from chironomid records from different parts of Europe (modified from Heiri et al., 2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

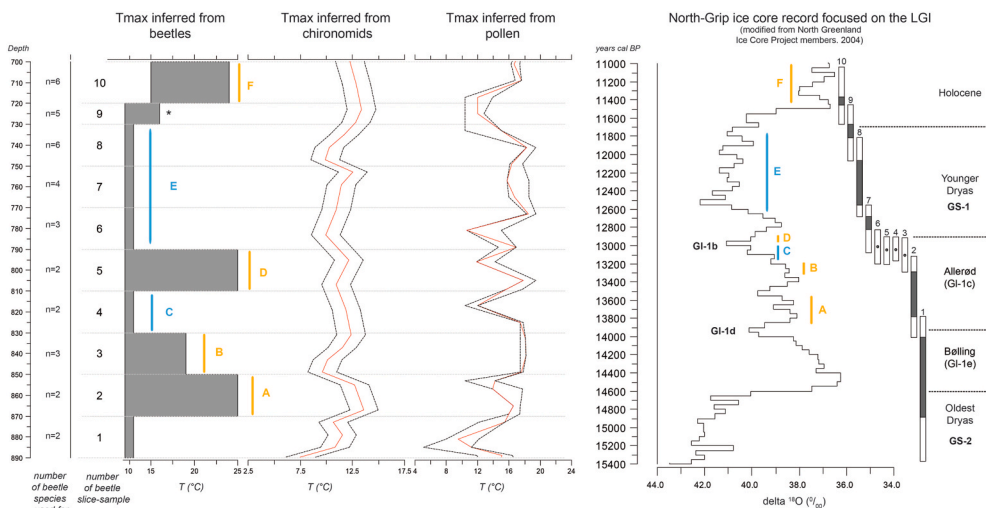


Fig. 5. Focus on the Late-Glacial for the Roustières basin stratigraphy in the Aubrac Mountains (Massif Central, France) with – from left to right – 1) the Tmax inferred from Coleoptera, 2) chironomids, 3) pollen, and 4) the oxygen isotope ($\delta^{18}\text{O}$) record from the North-GRIP ice core. Each numbered rectangle on the right represents these time intervals for the corresponding numbered slice of sediment. The grey rectangles show the minimum time span possibly “covered” by the sample, the grey + white rectangles show the maximum time span, and the grey dots in white rectangles indicate that the sample may cover less than 10 years within the maximum range symbolized by the white rectangle.

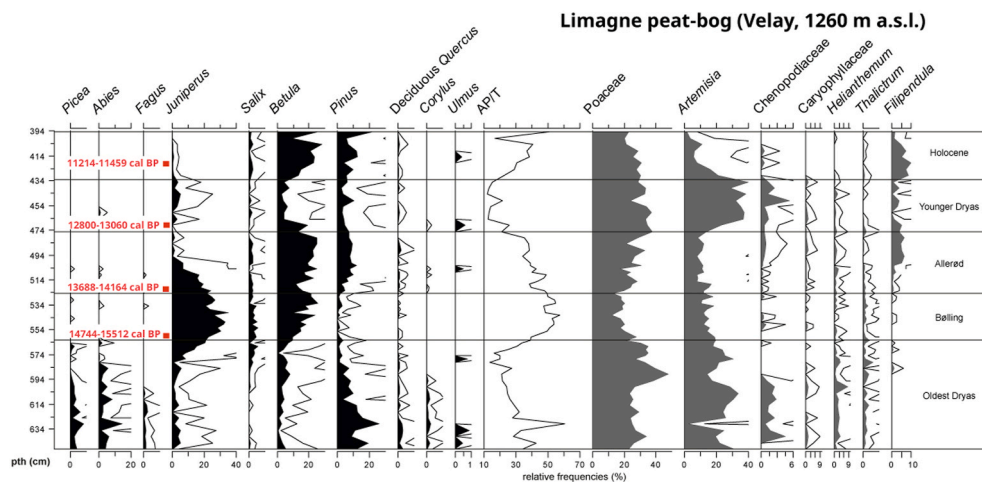


Fig. 6. Simplified palynological diagram from the Late-Glacial interstadial at Limagne (Massif Central, France; from Reille and de Beaulieu, 1988, added with new, formerly unpublished radiocarbon dates). The taxa selected can be compared with those represented in the Roustières diagram (see Poneil et al., 2016).

5.1.2. A hiatus during the Bølling?

As pointed out by Poneil et al. (2016), the classical juniper phase at the onset of the LGI, with a strong optimum followed by a stable phase, is not well-recorded in our data, contrary to a palynological record from Roustières studied by de Beaulieu et al. (1985), or the pollen record from the Limagne peat bog in the Velay region (Fig. 6; Reille and de Beaulieu (1988), and hitherto unpublished radiocarbon dates), or the Lapsou pollen record (Duprat-Oualid et al., This Issue). In the Limagne and Lapsou pollen records, the onset of the Bølling is marked by a strong increase in the *Juniperus* percentages reaching >30%, while at Roustières the increase in *Juniperus* was moderate. Therefore, and together with the absence of any thermal optimum reconstructed by beetles, chironomids and pollen during the Bølling strengthen the hypothesis of a possible hiatus within the Bølling in our new profiles. This hiatus in a section of our pollen record would eventually have been induced by a very high sedimentation rate. As a result, and in agreement with the 2-sigma time intervals of samples 2 and 3, the warming reconstructed by MCR (bars A and B, Fig. 5) may be probably contemporaneous with warm episodes of the GI-1c recorded in the North-GRIP ice core (Fig. 5).

5.1.3. A bias in the reliability of the pollen-inferred temperature of the warmest month reconstruction for cold periods?

One major concern is the absence of summer cooling reconstructed with the pollen assemblages during the Younger Dryas (Figs. 3 and 5) while such a cooling is evidenced both by beetle and chironomid-inferred T_{max}. If we compare the results with those of the Lapsou peat bog, we can clearly see that the Lapsou reconstruction also does not show cold conditions in summer during the Younger Dryas (Duprat-Oualid et al., This Issue). These results suggest that the reconstruction of summer temperatures based on pollen data, for cold periods such as for the Oldest and Younger Dryas, must be treated with caution. We need to better explore the ability of the MAT to robustly reconstruct summer temperatures during cold periods because the discrepancies observed can be related to the method selected to reconstruct past climate. The choice of another method, classical or newer (Weighted Averaging Partial Least Square (WAPLS), Boosted Regression Tree (BRT), inverse modelling), would probably have led to different results and needs to be tested (Peyron et al., 2005, 2011; Salonen et al., 2014). Recent studies show that a multi-method approach should be chosen to reconstruct past climate with more confidence (Peyron et al., 2005; Brewer et al., 2008; Salonen et al., 2019). Moreover, at a more global scale, Salonen et al. (2019) suggested that several climate parameters considered as primary or secondary climate variables can be reconstructed from European pollen data. For example, in the high latitudes in northern Europe, summer temperature is a primary variable and winter temperature a secondary one. Therefore, summer and winter temperature variables do less correlate than in northern America, allowing both summer and winter temperatures (correlated at $\rho = 0.28$; $p < 0.001$) to be quantitatively reconstructed with high mean R² values (0.79 and 0.72). In southern Europe, the effect of summer temperature is less dominant compared to winter temperature, but the role of the precipitation is important. Birks and Birks (2014) suggested that in North Western Europe, precipitation is extremely important for vegetation changes, and that its interaction with temperature controlled most of the vegetation patterns during the Late-Glacial. To summarize, it appears that July temperature alone is not a good predictor of the vegetation patterns through the Late-Glacial (Birks and Birks, 2014).

Moreover, the role of the modern pollen dataset is important in the results given that the palaeoenvironmental reconstructions are generally based on a modern calibration dataset. Here, we used an extended modern pollen dataset, which covers Europe, Siberia, and Tibetan areas, while the dataset used to calibrate the beetle and chironomid transfer functions is more limited (Britain, Europe, Scandinavia, Alps). The analogues selected for these cold periods are located in the steppes of Russia and Mongolia, which are characterized today by a very

continental climate and would explain the high summer temperature record obtained. Therefore, our discussion about the reconstructed temperatures of the warmest month is based on the results of chironomids and Coleoptera only.

5.2. T_{max} comparisons: chironomid-inferred temperatures versus coleopteran-MCR temperatures

The comparison between the chironomid and coleopteran temperature reconstructions (Fig. 4) is particularly useful for chironomid samples older than 17000 cal. BP and younger than 11700 cal. BP having no close analogues in the modern calibration data set. As recently discussed by Bajolle et al. (2018), this is not surprising since the WA-PLS methods perform well in non-analogue situations because the estimates are based on modelled taxon temperature optima assuming unimodal responses to temperature (Birks and Birks, 2014). This allows the model to infer temperatures outside the range of the calibration set. Nevertheless, some discrepancies occur between 16200 and 15000 cal. BP and between 11700 and 11200 cal. BP. These results suggest that variables other than temperature may have influenced the response of the chironomid assemblages at these times. Poneil et al. (2016) assume that the warming at the end of the Younger Dryas lead to a reactivation of the rivulet network around the lake (indicated by the expansion of running water beetles), in response to rapid melting of the snow cover during increasingly warmer summers (indicated by the sudden disappearance of snow patch beetles). This snow melting is correlated with a strong input of water into the depression of Roustières. We assume that such a cold-water influx could have been favourable for the persistence of taxa with a cold thermal optimum, and thus artificially affected the chironomid habitats and populations. The same phenomena may have happened between 16200 and 15000 cal. BP, and perhaps during all of the LGI, since the recurrent presence of *Helophorus glacialis* over this period is characteristic of melting snow during summer. Unfortunately, the resolution of the coleopteran samples compared to the chironomid one could also skew the MCR results. Indeed, a probable clustering of beetle faunas (of different thermal optima) cannot be ruled out, which leads to the pooling of cold and warm phases and thus an underestimation or overestimation (as the case may be) of the T_{max} values.

5.3. Regional comparisons

5.3.1. From the beetle point of view

Climatic reconstructions based on coleopteran data are rare in France, but in the Massif Central another regional Late-Glacial beetle site is available at La Taphanel (Poneil and Coope, 1990), about 200 m lower in altitude as Roustières and located 70 km to the North-West. This sedimentary profile spans the period from the end of the last glacial period to the Boreal chronozone. Unfortunately, the coleopteran succession of La Taphanel sequence was indirectly dated, only by correlation with the palynostratigraphy and not by direct radiocarbon dating, so that a detailed comparison with the Roustières sequence remains tentative. Poneil and Coope (1990) mentioned that the occurrences of *Agabus arcticus* and *Helophorus glacialis* in the middle of the Late-Glacial Interstadial (LGI) should be attributed to a cold event intercalated between the Bølling and Allerød, the so-called Older Dryas period. However, there is no equivalent episode at Roustières, a continuous record of cold adapted taxa (e.g. *Princidium bipunctatum*, *Helophorus glacialis*, *Eucnecosum brachypterum*, *Aphodius mixtus*, *Potamonectes griseostriatus*, *Tachinus elongatus*) throughout the Bølling and Allerød suggest that the LGI was overall colder here than at La Taphanel, maybe due to its higher altitude. Surprisingly, T_{max} estimates for the early LGI at Roustières are much lower than expected during the Bølling and equivalent with those obtained for the Oldest Dryas and for the Younger Dryas (11–12 °C; Fig. 3). The second half of the LGI, the Allerød, seem to have been warmer according to the MCR estimates, with T_{max} apparently equivalent with the present summer

temperatures. But these results should be treated with caution since cold adapted beetles are present throughout the LGI (although in low numbers), suggesting an overall cold LGI. At La Taphanel, there are two realistic Tmax estimates values for the LGI, with 11–13 °C and 12–13 °C (Fig. 4), the three other estimates for the same period are less precise but are still consistent with these figures. The closest records available with coleopteran-inferred Tmax estimates for the LGI are unfortunately two low altitude sites in the Paris Basin (Ponel et al., 2005). In these two records, Conty and Houdancourt, the very rich fauna identified enabled very precise summer temperature reconstructions, and suggested Tmax around 17–18 °C for several beetle assemblages. At Conty, occurrences of stenothermic species suggested that the climate of the earlier part of the Bølling was warmer than during the latter part of the LGI.

5.3.2. The Late-Glacial Interstadial: common patterns and discrepancies at a regional/global scale

The North-GRIP ice record perfectly illustrates the abruptness of the global warming starting at ca. 14600 cal. BP (Fig. 4) in the North Atlantic region (North Greenland Ice Core Project members, 2004). Thanks to successive palaeoclimatic studies, it was possible to trace in detail the rapid climatic improvement characterizing the beginning of the Bølling in different European areas (e.g. von Grafenstein et al., 1999; van Raden et al., 2013; Heiri et al., 2015). In Europe, the evolution of temperatures during the Late-Glacial is still debated because clearly diverging temperature trends were reconstructed, depending on the studied region (e.g. Heiri et al., 2014). A chironomid-based synthesis (Heiri et al., 2014) suggested that temperature variations during the Late-Glacial and particularly the warming characterising the Bølling were more pronounced in North-Western Europe (British Isles) than in the South-Central/East (South-Western Europe, Central and South-Eastern regions). Diverging temperature trends are also reconstructed for the Allerød period, which seems warmer than the Bølling in the Alpine Region, Southwestern Europe and the Mediterranean area (Heiri et al., 2014; Moreno et al., 2014). Coleopteran-based reconstructions also show considerable regional differences during the Late-Glacial interstadial (Coope et al., 1998). There is still no clear explanation for the causes of these different patterns; however, changes in the North Atlantic overturning and associated latitudinal shifts in sea ice probably explain such diverging trends (Lane et al., 2013; Heiri et al., 2014).

In the La Taphanel record (Fig. 4) this warming also seems to have been marked by high MCR values, while this was not the case at Roustières. In the Roustières record, the Bølling seems to remain relatively cold, with stable beetle-inferred Tmax from the end of the Oldest Dryas to the end of the Bølling. Temperatures reconstructed by chironomids slightly increased at the end of the Oldest Dryas but remained also stable throughout the Bølling (Fig. 4). Moreover, the Allerød is documented at Roustières both by MCR beetle reconstruction with large amplitudes of Tmax and by a slight increase of Tmax inferred from chironomids, suggesting that the Allerød was warmer than the Bølling in the Aubrac region. This progressive rise of Tmax is in agreement with the alpine Tmax synthesis based on chironomids (Heiri et al., 2014) and with the trend reconstructed from chironomids at Maloja Pass (Central Swiss Alps, 1865 m a.s.l., Ilyashuk et al., 2009). This pattern was also observed in the pollen-inferred temperatures reconstruction (Fig. 3). However, the progressive rise in temperature seems opposite to what was recorded in the North-GRIP record, at La Taphanel (Fig. 4), but also in the British Isles (Coope and Lemdahl, 1995). Generally, in Western Europe, continental ecosystems rapidly responded to the general warming of the Bølling, which is supposed to have been superior to what occurred during the Allerød. For example, at Gerzensee (Switzerland), this sudden rise in temperature is recorded by an increase of several thermophilous chironomids (Lotter et al., 2012; Brooks and Heiri, 2013). However, it must be noticed that these taxa remained present throughout the rest of the Late-Glacial (including the Younger Dryas). On this basis, and as already discussed, the hypothesis of a hiatus within

the Bølling must be reconsidered at Roustières.

5.4. A too cold Allerød for any afforestation?

The LGI was marked by a general afforestation at a large scale (Ammann et al., 2000; Finsinger et al., 2006; Vescovi et al., 2007), but at Roustières, the presence of tree-dependent Coleoptera is only observed continuously during the Holocene, with exception of a single occurrence at the end of the Allerød, while at La Taphanel, a single Late-Glacial occurrence is also recorded during the Bølling. As already discussed in Ponel et al. (2016) the scarcity of tree-dependent insects suggests the absence of forests at ca. 1000 m a.s.l. in the Aubrac Mountains. This point supports the hypothesis of cool conditions throughout the LGI: it must be noticed that a continuous presence of cold-adapted beetles is recorded from the Oldest Dryas to the Younger Dryas, with two maxima of cold species diversity, during the Allerød and the Younger Dryas (Fig. 3). In particular, the continuous occurrences of *Aphodius mixtus* (an endemic scarabeid restricted to high altitude grasslands in the Alps, the Massif Central and the Pyrenees) almost throughout the Late-Glacial, is a good indicator of these cold and treeless conditions, because 1) its current distribution area is above 1700 m a.s.l. and 50% of its habitats are above 2000 m, and 2) contrary to most of the members of the genus *Aphodius*, *A. mixtus* is not a true dung beetle, since its larvae are found in rotten vegetative matter that accumulates on grounds with a dense cover of Poaceae in alpine grasslands (Ponel et al., 1995; Lumaret et al., 1996). The only Coleoptera sample lacking *A. mixtus* was sample 5, which corresponded to a less cold period according to the MCR reconstruction (bar D, Fig. 5).

5.5. The minor climatic changes during the LGI: which impacts on our records?

As illustrated by the North-GRIP ice core record (Figs. 4 and 5) the warming of the LGI (Bølling and Allerød) was interrupted by minor climatic events, which were also documented in continental records such as from Lake Gerzensee in Switzerland (van Raden et al., 2013). Lake Mondsee in Austria (Lauterbach et al., 2011), or Lake Lautrey in France (Peyron et al., 2005). At Roustières, no proxy allowed us to confirm the presence of a cold episode corresponding to GI-1d (Older Dryas). Later, the very low values of MCR-Tmax at ca. 13000 cal. BP (C, Fig. 5) could be evidence for the climatic reversal called GI-1b in the North-GRIP record, and for the Gerzensee oscillation revealed in several terrestrial records (van Raden et al., 2013). Thanks to the high sedimentation rate at this period, the duration of this cooling event did not exceed ca. 2 centuries at Roustières around 13000 cal. BP, which is consistent with the timing proposed at Gerzensee (van Raden et al., 2013). The pollen-based reconstruction also showed a transient lowering of Tmax, which may correspond to the Gerzensee oscillation, while no lowering was observed in the Tmax values reconstructed with chironomids. However, as discussed in the previous section, rapid climate reversals might have little or no impact on the vegetation and insect communities in a relatively cold and treeless LGI.

5.6. The Younger Dryas: 12 °C summer temperatures for one millennium?

Diverging climate patterns at the scale of Europe are also evidenced for the Younger Dryas event. This cool event is very well depicted in the North-GRIP ice cores, in Norway and the British Isles, but was less evidenced in Eastern and Central Southern Europe and in the Mediterranean area (Heiri et al., 2014; Moreno et al., 2014).

At Roustières, the Younger Dryas appears as a period with a well-marked cooling, documented by beetle-Tmax, chironomid-Tmax (Figs. 3 and 4) and pollen-MTCO curves (Fig. 3). Over the Younger Dryas, Tmax inferred from Coleoptera remained stable around 12–12.5 °C, which is partly consistent with values reconstructed from chironomids. The lowering of the MTCO curve (Fig. 3) inferred from

pollen is consistent with the intense climatic reversal, which characterized the Younger Dryas at a global scale (the mean values of MTCO reached ca. -15°C).

This period also corresponds to the maximum of the diatom ratio *Stauriosirella pinnata*/*S. venter* observed at Roustières, which can be interpreted as an indicator of cold conditions (Gandouin et al., 2016). As a whole Tmax reconstructed from beetles for the Younger Dryas in Northern Europe are very similar, as stated by Coope and Lemdahl (1995). The estimates obtained for this period are slightly above 10°C in the British Isles, in Southern Sweden and in Central Poland (Coope and Lemdahl, 1995). However, studies in Scandinavia suggested that the situation seemed quite different here, since estimates obtained for the Younger Dryas by Lemdahl (2000a) from Kråkenes Lake in Norway showed that mean temperatures of the warmest month were very low: Tmax were probably well below 10°C for summers compared with $12\text{--}13^{\circ}\text{C}$ at Roustières. This very cold Younger Dryas in Norway is supported by the complete disappearance of Coleoptera at this period, as reported by Lemdahl (2000a), suggesting that the conditions were too harsh even for the most cold-tolerant beetles. This is clearly not the case at Roustières, where a rich cold dependent fauna was recorded, with 8 stenothermic species: *Agabus arcticus*, *Aphodius mixtus*, *Bembidion (Testediolum) sp.*, *Bembidion bipunctatum*, *Eucnecosum brachypterum*, *Helophorus glacialis*, *Helophorus schmidti*, *Potamonectes griseostriatus*, *Tachinus elongatus*. In Sweden, the site of Madtjärn (Björck et al., 1996) provided further evidence for an extremely cold Younger Dryas, with MCR producing Tmax around 8°C . In short, the Younger Dryas at the relatively high altitude of Roustières (above 1000 m) was clearly warmer than the Younger Dryas at high latitudes in Scandinavia. Closer to Roustières but located at lower altitude (603 m), the Swiss site of Gerzensee analysed by Lemdahl (2000b) provided estimates for Tmax of about $9\text{--}14^{\circ}\text{C}$ during the Younger Dryas, very similar to the values obtained for the Aubrac Mountains.

6. Conclusions

This study provided the first temperature reconstruction for the Late-Glacial period for the Massif Central inferred by a multi-proxy approach including pollen, chironomid and coleopteran records. The results obtained by the different proxies suggest a climatic trend for the Late-Glacial consistent with the regional climate patterns. In spite of the overall good coherence, there were some obvious discrepancies, especially concerning the comparison between mean July temperature reconstructed from pollen data and from Coleoptera/chironomids. This represents a challenging issue to get through some obstacles. First of all, for our study area, the Mutual Climatic Range Method (based on coleopteran data) is partially “blind”, since it does not include many climatic significant taxa from the Mediterranean area or South Europe. These taxa are not yet included in the MCR database, but are often observed as fossils in sites located in the south of the Alps (or in the Eastern Pyrenees) with sometimes many endemic species, or species located at the limit of their geographical range as this is the case at Roustières.

Secondly, pollen-inferred climate reconstructions specifically for the Late-Glacial period and particularly the reconstruction of the summer temperature may be improved by 1) the choice of a multi-method approach (WAPLS inverse modelling to take into account the CO₂ changes and other methods) is important and would probably have led to different results. The use of a multi-method approach can also be tested on chironomids data. 2) The role of modern pollen datasets used for the calibration both with pollen and chironomid data could also be discussed. And 3) independent proxies such as Coleoptera or chironomids as analysed in this study, as well as the use of molecular biomarkers such as Glycerol Dialkyl Glycerol Tetraethers (GDGTs), are going to becoming a promising tool in paleoclimatology (Martin et al., 2020).

Our contribution must be considered as a milestone in the effort to establish a European network on multiproxy palaeoenvironmental data. This also points out that – beyond the global signal of past climatic

changes provided by $\delta^{18}\text{O}$ from ice cores – it will be imperative to improve our knowledge on their regional expression by improving outputs of general circulation models, by reconstructing regional/local climatic patterns, and by assessing the heterogeneity of palaeoecological responses to Late-Glacial climatic variability.

In such context and as already mentioned, accurate climatic reconstructions from terrestrial archives must necessarily be based on reliable multi-proxy approaches. Such investigations are still scarce in Europe, and much remains to be understood to explain the differences between the signals reconstructed by the different proxies, but multi-proxy approaches represent the only mean to embrace the complexity of climatically unstable periods such as the Late-Glacial.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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