

Late Pleistocene temperature patterns in the Western Palearctic: insights from rodent associations compared with General Circulation Models

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20 Abstract word count: 384

Main text word count: 10713

Figures: 13

Tables: 2

Appendices: 6

25 Supplementary material: 1

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30 **Abstract.** Since rodent fossils are preserved in many low and high latitude archaeological and paleontological sites from a wide variety of environments, their associations are a commonly useful proxy for inferring past local climate and environmental conditions. Such a frequent and widespread geographic distribution can help us to better understand past climate evolution by providing access to high spatiotemporal resolution at large geographical scales. The aim of this paper is to develop an approach to generate continental scale temperature maps based on rodent associations and to assess their reliability compared to state-of-the-art General Circulation Models (GCMs). We used the Bioclimatic Analysis, based on fossil and modern rodent associations, to infer climate zone distribution and local temperatures (Mean Annual Temperature, Mean Temperature of the Warmest month and the Mean Temperature of the Coldest month), at the western Palearctic (Europe, Middle East and North Africa) for six different periods: LGM, Heinrich Stadial, Bølling, Allerød, Younger Dryas and present-day conditions. The Bioclimatic Analysis is combined with a spatial generalized linear mixed model to interpolate these surface temperatures across the western Palearctic. We show that the spatial patterns in Mean Annual Temperature and Mean Temperature of the Warmest and Coldest months are very similar between our interpolations and GCMs for both present-day and LGM conditions, but the rodent-based approach provides slightly cooler LGM estimations in western Europe and warmer in eastern Europe. Throughout the Late Glacial oscillations, the rodent-based model infers globally small variations in Mean Annual Temperature and Mean Temperature of the Warmest months and slightly larger changes in Mean Temperature of the Coldest months. Nonetheless, some events show weak but significant regional variations depending of the events and the climate variable. For instance, the most important shifts in mean annual temperature between Allerød and Younger Dryas are observed in northwestern regions. Northeastern regions, on the other hand, experienced relatively stable mean annual temperature, although they did experience considerable warming of the warmest month and cooling of the coldest month. Minor discrepancies appear between GCMs and the rodent-based model, the latter showing colder temperature in northwestern Europe, hence a differential west-east gradient in ice-sheet influence. Our results demonstrate that rodent associations are robust proxies for reconstructing and regionalizing past temperatures at broad scales, offering a readily reproducible approach to be reimplemented in future studies incorporating new rodent data.

Keywords: rodent-based reconstructions, temperature patterns, Last Glacial Maximum, Late Glacial, Heinrich Stadial, Bølling-Allerød Interstadial, Younger Dryas,

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1 Introduction

Understanding past climate changes is necessary for interpreting the evolution of living organisms and their communities in their historical environmental context. Past climate information comes from climate proxy record (in the form of geochemical, physical, geological or biological data) obtained from a natural archive (Markwick, 2007) and/or from General Circulation Models based on thermo-dynamic laws (Randall, 2000). Each proxy has its own set of advantages and limitations. Some are directly correlated to climatic variables (e.g. some isotopes), while others reflect their indirect influence (e.g. pollen, invertebrate or vertebrate associations). Nonetheless, all are complementary, because each proxy provides a piece of information about the global system for a specific sphere (e.g. hydrosphere, biosphere), on particular geographical and time scales, and at a certain resolution. Paleoclimatic inference methods on different climate proxies are constantly improved to overcome their limitations and to provide refined past climate change information. As any single proxy still provides a unique history of the past environment and climate, many studies have emphasized the need for multi-proxy approaches and/or comparisons between data from different proxy natures (e.g. Allen et al., 2008) to have a better understanding of paleoclimate proxy records and climate variations.

Among the many natural archives (e.g. speleothems, chironomids, pollen) available to approximate past climate changes, fossil remains of small mammals (e.g. Rodentia and/or Eulipotyphla) have been used for a long time, because they present several advantages:

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1) their large taxonomic diversity is associated with a wide range of ecological and biological traits that ensure their ubiquitous occurrence in all modern continental biotopes (e.g. Quéré & Le Louarn, 2011; Wilson et al., 2017; Wilson & Mittermeier, 2018);

85 2) their small size, associated with high reproductive rates and fast evolutionary change, makes them particularly sensitive to changes in climate and habitat, which constrain their geographical distributions, biotic interactions and, ultimately, community organization (Wolff & Sherman, 2008);

3) they are regularly found in archaeological and paleontological sites (e.g. Hinton, 1926; Chaline, 1972; Daams et al., 1988; Martin et al., 2000; van den Hoek Ostende, 2003; Cuenca-Bescós et al., 2010; 90 Furió et al., 2011; Minwer-Barakat et al., 2012; Erbajeva & Alexeeva, 2013; Royer et al., 2016; Harzhauser et al., 2017; Markova et al., 2019; Flynn et al., 2023).

As a consequence, small vertebrates and in particular rodents have been recognized as good proxy and regularly used for inferring past local and continental environmental and climatic conditions (e.g. Simar-Pellissier, 1966; Chaline, 1972; Tchernov, 1975; Avery, 1987; van der Meulen & Daams, 1992; Montuire 95 & Desclaux, 1997; Montuire & Marcolini, 2002; Legendre et al., 2005; Hernández Fernández et al., 2007; García-Alix et al., 2008; Cuenca-Bescós et al., 2009; López-García et al., 2010; Royer et al., 2013, 2014; Rofes et al., 2015; Royer et al., 2016; Fernández-García et al., 2016; Mansino et al., 2016; Jeannet, 2018; Stoetzel et al., 2019; López-García et al., 2021; Royer et al., 2021; Linchamps et al., 2023; García-Morato et al., 2024; Piñero et al., 2024; Schürch et al., 2024).

100 In parallel, many different fully coupled General Circulation Models (GCMs) have been developed and used over the past decades to understand past, present-day and future climate variabilities and Earth system changes (e.g. Sloan et al., 1996; Prentice et al., 1998; Salzmann et al., 2008; Haywood et al., 2009; Henrot et al., 2017; Beyer et al., 2020; Kageyama et al., 2020; Kageyama & Paillard, 2021), and to explore their influence on human communities and environment changes (e.g. Allen et al., 2010; Burke et al., 105 2021; Leonardi et al., 2023; Albouy et al., 2024). GCMs use the equations of fluid thermodynamics and integrate biotic and abiotic variables to resolve the space-time changes and dynamics of the Earth climate system. GCMs provide numerical climate information at the global scale, and are therefore not limited by the uneven distribution of sample locations and taphonomic biases. Comparing results from different climate proxies, such as small mammals, to GCM outputs offers considerable potential for gaining a better 110 understanding of the mechanisms driving climate variability (e.g. Emile-Geay et al., 2016; Carré et al., 2021). It also provides unique opportunities for evaluating model performance and proxy applicability (e.g. Kageyama et al., 2001; Jost et al., 2005; Allen et al., 2010; Latombe et al., 2018; Comas-Bru et al., 2019). Although small mammal associations are generally compared with other proxy data at a local scale, such as pollen or stable isotope compositions, combining paleoclimate inferences based on their 115 assemblages with GCM paleoclimate simulations has been rarely tested for refining environmental and chronological context (e.g. Terray et al., 2023). The integration of such data sources into a general approach to paleoclimatic research yields the potential to attain major advances in the understanding of climate change at large spatial scales.

Rodent fossil remains are abundant at many sites throughout Europe, from the Mediterranean region to 120 high latitudes. This abundancy allows us not only to use their assemblages to reconstruct local climate

conditions, but also to access continental-scale paleoclimate reconstructions under a wide range of environments and time intervals (e.g. Hernández Fernández, 2006; Puzachenko & Markova, 2019, 2023). In this paper, we use rodent associations to infer surface temperature under different climate conditions. We compare their inferences with GCM outputs to better elucidate faunal community signatures and refine climate reconstructions. We focus on large spatial scales, over the western Palearctic (Europe, Middle East and North Africa), where a large amount of fossil data is available from the Last Glacial Maximum (LGM) to the end of the Late Glacial, from 23,000 to 11,700 years before present. This period of major climate changes is characterized by a succession of short warm (Greenland Interstadial) and cold (Greenland Stadial) events leading to the so-called Bølling, Allerød, and Younger Dryas pollen chronozones (e.g. Björck et al., 1998; Peyron et al., 2005; Rasmussen et al., 2014). These climatic events have strongly shaped Palearctic environments and faunal communities.

The aim of this study is twofold:

- First, we propose a new approach to interpolate surface temperature derived from species composition of rodent associations by combining the Bioclimatic Analysis (Hernández Fernández & Peláez-Campomanes, 2003, 2005; Royer et al., 2020) to a spatial generalized linear mixed model. This approach is used to reconstruct mean annual temperature (MAT), as well as mean temperature of the warmest (MTWA) and coldest months (MTCO), in the present-day context and for successive events within the LGM – Late Glacial interval.
- Second, we compare these reconstructions with GCM simulations integrated over the same time periods, to determine the degree of spatiotemporal agreement between those approaches.

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2 Data and method

2.1 Rodent associations from modern localities

145 A total of 157 modern localities covering northern Africa and western Eurasia (north of 25° N and west
of 60° E) were used to reconstruct spatial variation in present-day climate (Figure 1; Table C1). Most of
the sites (n=152) are located at low altitude (below 1000 m above current sea level) to focus on large-
scale signal with no interference of local topography; only five localities are at an altitude higher than
1000 m above sea level. [For each locality, we compiled a rodent faunal list \(Table C2\) by identifying all](#)
150 [rodent species whose geographic range polygons, sourced from the IUCN Red List spatial data \(IUCN,](#)
[2021\), intersect with a 50 km radius buffer around the locality coordinates.](#)

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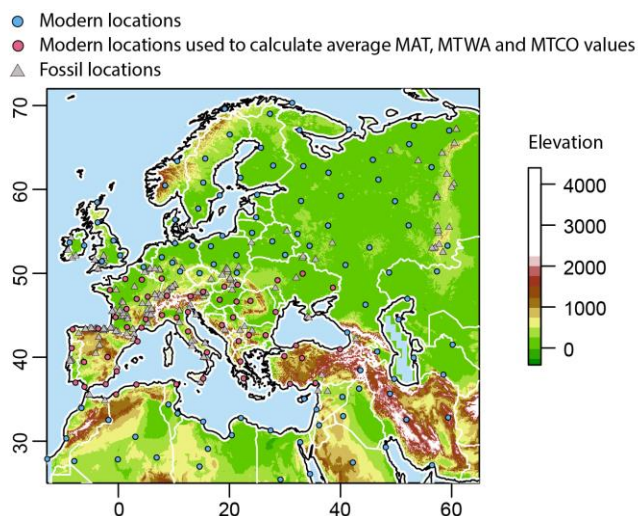


Figure 1: Geographical distribution of modern (circles) and fossil (triangles) rodent associations studied in this work. Pink circles show the modern assemblages used to calculate area-averaged MAT, MTWA and MTCO values.

2.2 Temporal framework and rodent associations from fossil localities

We focused on rodent associations from the Last Glacial Maximum (LGM) to the end of Late Glacial, *i.e.* between 23,000 and 11,700 years before present (BP), compiling a database that includes 279 associations coming from stratigraphic units in 168 archaeological and paleontological sites located from Morocco to the Ural mountains (Fig. 1, Table C2). These fossil associations do not represent a synchronous ensemble. To maximize fossil data availability, we grouped them into six time intervals that correspond to major climatic events and pollen chronozones: LGM (GS2.1bc: 23,000 – 18,000 years BP;

170 65 fossil associations), Heinrich Stadial 1 (GS2.1a: 18,000 – 14,900 BP; 93 ass.), Bølling (GI-1de: 14,900 – 13,900 BP; 47 ass.), Allerød (GI-1abc: 13,900 – 12,900 BP; 41 ass.) and Younger Dryas (GS-1: 12,900 – 11,700 BP ; 33 ass.).

Reconstructing paleoenvironmental and paleoclimatic conditions from faunal remains requires specific analytical and taphonomical considerations (Lyman, 2019) to ensure high data quality. As such data is
175 derived from biological communities, the quality of faunal data depends on accurate taxonomic identifications. Many species are indeed highly difficult to identify due to strong similarity, high morphological variability or extremely low local abundance (e.g. Nadachowski, 1982; Markova et al., 2010; Escudé et al., 2013; Navarro et al., 2018; Arbez et al., 2021; Stoetzel et al., 2023). Faunal remains primarily come from field data, which are regularly re-evaluated to verify the data integrity that may have
180 gone unnoticed during the fieldwork or initial study, in relation to stratigraphic formation, palimpsest processes, and excavation unit definition (e.g. Lyman, 2008; Royer, 2014; Discamps et al., 2023), as well as bioturbation (e.g. Pelletier et al., 2017). To select the stratigraphic units, we ensured that the associated rodent assemblages were detailed, and representative, maintaining good taphonomical integrity of small mammal remains within the archaeological and paleontological stratigraphic units. Sites that did not meet
185 these criteria were not included, despite their contributions, such as the presence of the collared lemming (*Dicrostonyx torquatus*) in Croatia (Lenardić, 2013; Lenardić et al., 2018) or the striped field mouse (*Apodemus agrarius*) in France (Aguilar et al., 2008) during the LGM. Both are found in sites for which unfortunately the associated rodents are unknown. Since each fossil association should be included in a particular time interval, we selected mainly stratigraphic units associated with radiocarbon dates restricted

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to a single time interval (Table C2). Radiocarbon dates were calibrated at 2σ (95.4%) using the *oxcAAR* v1.1.1 R package (Hinz et al., 2018) and IntCal20 calibration curve (Reimer et al., 2020).

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2.3 The Bioclimatic Analysis

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Many methods have been developed to estimate climatic variables from rodent communities (e.g. Hokr, 1951; van de Weerd & Daams, 1978; Daams & van der Meulen, 1984; Chaline & Brochet, 1989; Sesé, 1991; Montuire et al., 1997; van Dam, 2006; Jeannet, 2010; Fagoaga et al., 2019). We used here the Bioclimatic Analysis approach, originally developed by Hernández Fernández (2001) and Hernández Fernández & Peláez-Campomanes (2003, 2005) and updated by Royer et al. (2020). This approach, detailed in these studies, is a commonly used technique in paleoclimatic studies of fossil sites (e.g. Hernández Fernández, 2006; Hernández Fernández et al., 2007; Pérez-Crespo et al., 2013; Socha, 2014; Laplana et al., 2016; Piñero et al., 2016; López-García et al., 2017; Berto et al., 2019b; Fernández-García et al., 2020; Lemanik et al., 2020; Álvarez-Vena et al., 2021; Izvarin et al., 2022; Jovanović et al., 2022; Luzi et al., 2022b; Arbez et al., 2023; Domínguez-García et al., 2023, 2024; Lebreton & López-García, 2023; Rey-Rodríguez et al., 2024; Stoetzel et al., 2025). It skilfully assesses multiple past climate variables (e.g. temperature and precipitation) from mammal communities and provides reliable estimations as well as their associated uncertainties.

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The original models for the Bioclimatic Analysis (Hernández Fernández & Peláez-Campomanes, 2003, 2005) were based on 50 modern localities at global scale and successfully validated by using an additional set of different localities from the ones used to develop them. The current models constructed by Royer

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et al. (2020) were based on a new set of 49 modern communities distributed throughout the Palearctic, in order to be representative of the different climate zones (seven localities for seven climate zones). In that paper, the models were also validated based on Leave-One-Out Cross Validation (LOOCV).

220 This approach is based on the bioclimatic breath of each species (assessed through the Climatic Restriction Index, CRI; Hernández Fernández, 2001), which is based on the presence of each species in different climate zones (Table 1), as defined by the combination between monthly precipitation and temperature mean values (Walter, 1970). For this study, we added CRI values for more than one hundred species not defined in the original model, including some extinct species and some “chimeric” species,

225 which are taxa only identified at genus levels or not distinguished from morphological sibling species. These CRI values were defined as in the original model, following the recently updated taxonomic and geographical range information (Wilson et al., 2017). All these added CRI values are detailed in the Table C3.

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Climate		Zonobiome (mainly vegetation type)
I	Equatorial	Evergreen tropical rain forest
II	Tropical with summer rains	Tropical deciduous woodland
II/III	Transition tropical semiarid	Savanna

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III	Subtropical arid	Subtropical desert
IV	Subtropical with winter rains and summer drought	Sclerophyllous woodland–shrubland
V	Warm-temperate	Temperate evergreen forest
VI	Typical temperate	Nemoral broadleaf–deciduous forest
VII	Arid-temperate	Steppe to cold desert
VIII	Cold-temperate (boreal)	Boreal coniferous forest (taiga)
IX	Polar	Tundra

Table 1: Climate zone typology (from Walter, 1970) and its relationships with world vegetation types.

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The bioclimatic spectrum of a locality consists of ten bioclimatic components (BC) values (Hernández Fernández, 2001), calculated on the basis of the CRI values for each climate zone across the entire faunal assemblage and detailed in the Table C2. The use of BCs helps to address the problem of classifying paleoecological records by reducing the number of entities considered (only 10 BCs) and by providing an ecological basis for treating mammals from different regions in a compatible way.

The Bioclimatic Analysis is composed of two parts. The first one relies on linear discriminant functions deduced from the bioclimatic spectra of modern mammalian communities. These linear discriminant functions are subsequently used to classify additional observations (extinct communities in our case) in each climatic zone, with an associated posterior probability (Hernández Fernández & Peláez-Campomanes, 2003). We used posterior probability values to assess the robustness of the climate classifications obtained by the discriminant functions, and considered robust probabilities above 0.95. A prediction error was estimated around 12% for estimating bioclimatic zone with linear discriminant functions on rodent communities (Royer et al., 2020). The second part of the Bioclimatic Analysis is built from transfer functions by means of multiple linear regression analyses of climatic parameters and modern

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bioclimatic spectra. Most predictive equations generated by multiple linear regressions for each climatic factor, produced highly significant determination coefficients (Hernández Fernández & Peláez-Campomanes, 2005), and rarefaction analysis revealed these new models to be reliable even when a substantial percentage of species from the original community was removed (Royer et al., 2020). These models are ultimately used to infer climatic variables for additional observations (*i.e.* extinct communities). Although the Bioclimatic Analysis gives the possibility to estimate eleven climatic variables from fossil faunal assemblages (Hernández Fernández & Peláez-Campomanes, 2005; Royer et al., 2020), in this paper, we focus only on three of them: the Mean Annual surface Temperature (MAT), the Mean surface Temperature of the WArmeSt month (MTWA) and the Mean surface Temperature of the COldest month (MTCO), which are characterized by coefficients of determination of 0.94, 0.92 and 0.85, respectively (Royer et al., 2020).

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2.4 Building interpolation maps

Once temperature data for individual localities were calculated, interpolation maps for the whole western Palearctic at each time interval were built using the ‘isofit’ and ‘isoscape’ functions from the R package *IsoriX* v.0.9.2 (Courtiol & Rousset, 2017; Courtiol et al., 2019), which is based on the *spaMM* v.4.4.16 (Rousset et al., 2016), *rasterVis* v.0.51.6 (Perpinan Lamigueiro et al., 2023) and *terra* v.1.7 (Hijmans et al., 2022) R packages. Interpolations of the three climatic variables estimated from rodent associations were inferred through a spatial generalized linear mixed model (GLMM), using latitude and longitude as covariates. Although the GLMM can include the effects of altitude, the number of high altitude fossil

sites is too limited per period to obtain sufficiently robust correlations to reproduce adiabatic effect, leading to erroneous models for geographical areas at middle and high altitudes. We therefore prefer to apply an average vertical drift rate, to reflect this effect in geographical and temporal terms. Elevation effects were accounted for by applying a temperature lapse rate of -0.5 °C/100 m on rodent association

280 Bioclimatic Model results, and by reinjecting it after the spatial interpolation. The original functions of *IsoriX* were slightly modified to (1) better assess local prediction and uncertainties from the Bioclimatic Model and (2) account for ocean and ice sheet masks:

1) Initially, the *IsoriX* package required aggregated data at each locality to directly calculate the mean and variance before building the interpolation maps. We modified the ‘isoscape’ function to use the inferred

285 data and predicted variance derived from applying the Bioclimatic Model instead of aggregated data. The original Bioclimatic Analysis script was also slightly modified to extract the standard error, the residual scale and the degree of freedom of the residuals generated for each locality, to calculate the variance of inferred data used by the *isoscape* function;

2) In order to obtain approximate boundaries for accessible areas, we generated ocean masks using mean

290 bathymetry variations (Lambeck et al., 2014; Benjamin et al., 2017) of -130 m for the LGM, -120 m for the Heinrich Stadial 1, -100 m for the Bølling, -80 m for the Allerød and -60 m for the Younger Dryas. We also used ice sheet masks derived from the global ICE-6G_C (VM5a) model (Argus et al., 2014; Peltier et al., 2015), with values at 21.0 ky for the LGM, 17.0 ky for the Heinrich Stadial 1, 14.5 ky for the Bølling, 13.5 ky for the Allerød and 12.5 ky for the Younger Dryas. The generated maps have a

295 resolution of 0.1° x 0.1°.

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The quality of the models produced and sites used was evaluated using standard deviation calculated from leave-one-out cross validation (LOOCV) to identify potential outliers to remove (Fig. B1). Three outliers (Bouârfa, Achgabat and Birjand) were detected and excluded for present day simulations, and one outlier impacting sizably temperature reconstructions was observed with the Younger Dryas Belarussian site of Volosovo.

2.5 General Circulation Model simulation of modern and past periods

An essential assessment for any method used in paleoclimatic reconstruction involves comparing inferred climate estimates with observed data. Even though the Bioclimatic [Analysis](#) has previously been tested on several occasions (Hernández Fernández & Peláez-Campomanes, 2003, 2005; Royer et al., 2020), we took the opportunity to evaluate its application by including the spatial dimension. To discuss similarities and differences between our rodent-based reconstructions and state-of-the-art GCMs from modern and past climatic conditions, we used ERA5 reanalysis, GCM simulations from the PMIP4 project and GCM simulations published by Beyer et al. (2020).

By combining model and large amounts of observations (e.g. weather stations, satellite and airborne measurements, buoys, radiosonde data), the state-of-the-art ERA5 global reanalysis (Hersbach et al., 2020) provides a spatially and temporally accurate climate dataset at 0.25° resolution, in particular in Europe (e.g. Johannsen et al., 2019). Here, we used ERA5 here as the reference for the modern climatic context for assessing the quality of our rodent-based model and GCMs. We have extracted monthly air temperature values 2-meters above the surface over land from the 1979-2008 period, from an area

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bounded by the 25° N latitude and the 55° E longitude (which is therefore slightly less extensive than the
320 rodent model).

The PMIP4 project regroups a large ensemble of GCM simulations built for different time periods, including the current present-day and the LGM (Kageyama et al., 2021). For the modern climatic context, we used six PMIP4 simulations for the 1976-2005 period: CCSM4 (Gent et al., 2011), CNRM-CM5 (Voldoire et al., 2013), IPSL-CM5A-LR (Dufresne et al., 2013), MIROC-ESM (Sueyoshi et al., 2013),
325 MPI-ESM-P (Giorgetta et al., 2013) and MRI-CGCM3 (Yukimoto et al., 2012). For the LGM, we used the same six PMIP4 simulations plus the COSMOS-ASO (Stepanek & Lohmann, 2012) and FGOALS-g2 (Zheng & Yu, 2013) simulations. For conciseness, we consider the PMIP4 ensemble mean for spatial mapping.

Beyer et al. (2020) published 2m air temperature estimations combining medium and high resolution
330 GCM (HadCM3 and HadAM3H) simulations and modern-era instrumental data (Beyer et al., 2020). This product, hereafter called Beyer2020, provides monthly bias-corrected 2 m air temperature and many other parameters at the 0.5° spatial resolution and 1,000-2,000-yr temporal resolution for the last 120,000 years, giving the possibility to compare the different periods of the Late Glacial. We extracted here the Beyer2020 simulations at -21.0, -17.0, -15.0, -13.0, -12.0 and 0 ky BP.

335 Finally, to quantify global changes between current and past climatic contexts, we selected 55 of the 157 localities as anchors to calculate average MAT, MTWA and MTCO values from our rodent-based reconstructions and the GCMs. These 55 localities cover the 35° N - 50° N / 15° W - 40° E domain (Fig. 1; Table C1), which was not impacted by ice sheet development (allowing a comparison between past

and present periods) and includes a large part of the archaeological and paleontological sites used in this study, thus limiting the inferences extrapolation in data-free areas.

All the above analyses were performed using the R software (R core team, 2023). R scripts and raw data are available in Supplementary Material 1, in order to be fully reproducible.

3 Results and discussion

3.1 A simple approach from a complex system

Caution must always be exercised when working with reconstructions based on fossil faunal associations (e.g. Lyman, 2017). As any methodological approach based on biotic associations recorded in fossil sites, rodent-based paleoenvironmental reconstructions have limitations induced by multiple ecological assumptions. Knowing these assumptions remain essential to remember the limits of our interpretation, and using the Bioclimatic [Analysis helps](#) to partially overcome these limitations (Hernández Fernández, 2001; Hernández Fernández & Peláez-Campomanes, 2003, 2005; Royer et al., 2020).

The first limitation is the application of the principle of uniformitarianism, *i.e.* suggesting similar ecological tolerances between past and present (Lyman, 2017; Pineda-Munoz et al., 2021). This principle is the first to be used when studying faunal remains. We do know, however, that many species have a high degree of behavioral and ecological plasticity, or high level of endemism. Thus, some species may have changed and their ecological tolerances shifted. This is the reason why current paleoclimatic inference methods avoid considering only one species as a unique indicator of one specific climate, and

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360 approaches use multiple taxa as a better means of reconstructing past environments. Using multiple species, as the Bioclimatic [Analysis](#) does, avoids then the overinterpretation related to one specific single taxon and allows then for a more nuanced understanding of climatic and environmental changes.

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Second, the distribution pattern of modern biotic communities is the result of the combination of many factors (e.g. Jackson & Overpeck, 2000; Williams & Jackson, 2007; FAUNMAP, 1996), including
365 geography (e.g. orography, refugia), biotic interactions (e.g. facilitation, competition) and history (e.g. climatic and/or geographic changes that cause populations expansion or contraction, isolation, extirpation/extinction and eventual speciation). This might lead to the development of past communities in which lived several species from contrasting environments, the so-called disharmonious faunas (Lundelius, 1989; Graham, 2005). The contrary effect is also found in modern assemblages, with some
370 rodent species unexpectedly found in climatically very different environments, as the snow vole (*Chionomys nivalis*), which inhabits very high mountainous regions (e.g. the Alps and the Pyrenees) and lives equally in Mediterranean rocky inlets (Quéré & Le Louarn, 2011). In the same way, past refugia have played a fundamental role in the evolution of species, providing sites to survive extinction and to initiate colonization of new areas when environmental conditions became favorable (e.g. Tougard et al.,
375 2008; Stewart et al., 2010; Royer et al., 2016; Baca et al., 2023a). The current period is a particular period when compared to all past periods, being the result of past history (Jackson & Overpeck, 2000; Graham, 2005; Williams & Jackson, 2007) plus anthropogenic activities. Anthropogenic activities strongly impact some rodents by offering opportunities to synanthropic species to develop, strongly modifying the realized niches of many other species (e.g. Pineda-Munoz et al., 2021), both by constraining or facilitating
380 their expansion. For instance, anthropogenic activities in Europe have favoured species inhabiting open

environments through deforestation, such as the common vole, *Microtus arvalis* (e.g. Baca et al., 2023b), but have contracted significantly the range of the common hamster (*Cricetus cricetus*) in central Europe due to agricultural activities and landscape fragmentation (Surov et al., 2016). The Bioclimatic [Analysis](#)

385 was established based on faunal associations from several typical distinct regions representing the
different biomes found on Earth today and the bioclimatic characterization of the rodent faunas remains largely unbiased, since considering the ecology of each species at biome scale limits the species dependence effect to a particular environment. The combination of species interactions and their biomes also opens up the possibility of identifying special cases, related to taphonomical issues, possible
390 particular ecotones that have occurred in the past, or biomes that were not similar to present ones.

Using faunal associations implies large prediction errors in climatic reconstructions since, like plants, rodents are directly and indirectly (through the resources they use) dependent on multiple “bioclimatic” variables (e.g. temperature fluctuation throughout the diurnal cycle, insolation, seasonal distribution of temperature and precipitation, snow cover, etc.) that influence their behavior and life cycle. For instance,
395 lemmings inhabit environments where MTCO values can easily go down -15 °C, but this variable has a reduced impact on these arctic rodents, because they live under the snow. The critical factors for them are then the quality of the snow cover and the protection it provides from air surface temperature. More importantly, in comparison with plants, rodents belong to an upper trophic level, being also highly dependent on vegetation, which serves as food source and protection from climate and predators. Some
400 species are very restrictive on one type of vegetation, such as the wood lemming (*Myopus schisticolor*), which inhabits exclusively coniferous forest with a thick moss cover (Eskelinen, 2002; Calandra et al., 2015). Such links between vegetation and rodents, imply that all abiotic (e.g. climate, CO₂ concentration)

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and biotic (e.g. pest distribution, other consumers) parameters that affect vegetation subsequently impact rodents. Since the Bioclimatic [Analysis](#), is based only on correlations, and not causations, between faunal components and climate variables, all these interrelations are indirectly taken into account.

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3.2 Modern climate

3.2.1 Climate zone classification

The climatic classifications obtained using modern rodent associations almost perfectly capture the distribution of climatic regions of the western Palearctic (Fig. 2). Only 15.9 % (n=25) of localities were not well predicted, which is in agreement with the apparent error (13 %) published by Royer et al. (2020). Nevertheless, most wrong predictions tend to be concentrated around ecotonal areas between different climate zones (Fig. 2), particularly in the transition regions between the temperate area (VI) and the boreal climate zone (VIII) in southern Scandinavia or between the desert (III) and the Mediterranean climate (IV) along the northern African coast and Middle-East. Few of these localities show posterior probability values below 0.95, suggesting that the model has difficulties in distinguishing the mixed faunal associations between two climatic zones. A number of classification errors comes from regions with ample climatic variations and highly diverse environments at local and regional scales, such as the Anatolian and Iranian plateaus. They include mountainous areas home to a very wide range of rodents with distinct ecological affinities, from deserts and semi-deserts (*Rhombomys*, *Meriones*) to steppes (*Ellobius*, *Cricetulus*) and woodlands (*Apodemus*), which leads to mixed rodent communities. The classification posterior probabilities do not systematically detect these mix associations, although some

425 were found in northern Anatolia and in the Balkans. Similarly, mountainous regions may also be associated with classification errors (e.g. the Apennines), due to the mixture of lowland species (several species easily survive up to 2,000 m) and the relatively few species typical of high mountain environments (*Marmota*). Finally, some errors may be associated with insularity, where faunal associations are the result of the process of Holocene island isolation and the introduction of species by humans. For instance, 430 in Ireland the absence of many vole species and the only presence of wood mouse and squirrel represent a clear case of out-of-equilibrium communities that act to bias climate classifications. Nonetheless, despite all these potential sources of errors (communities from ecotonal, highly heterogeneous or areas with peculiar biogeography history), the climate of 84 % of the modern rodent assemblages was correctly classified.

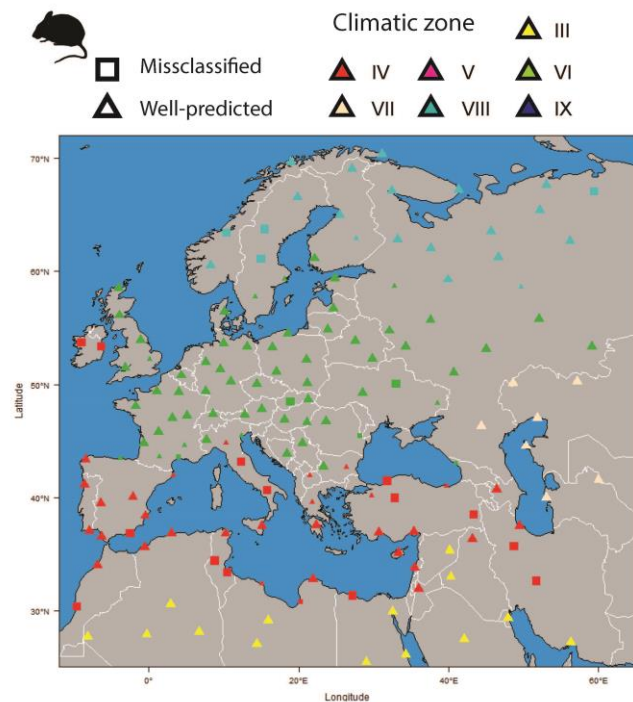
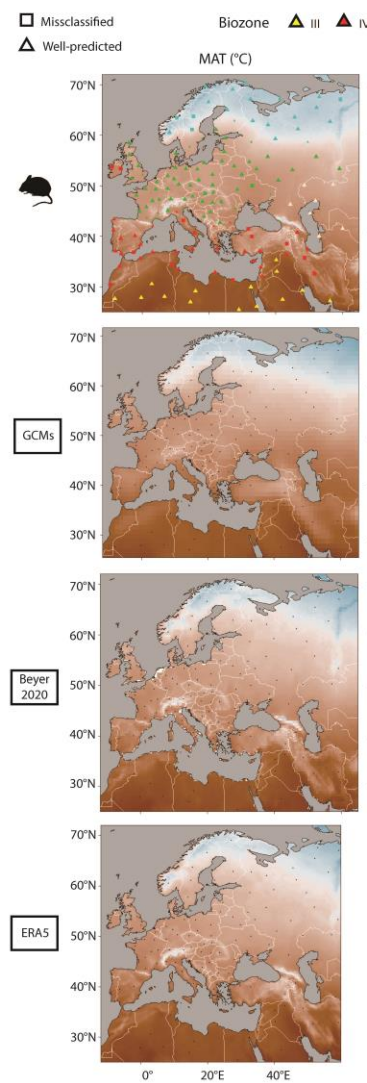
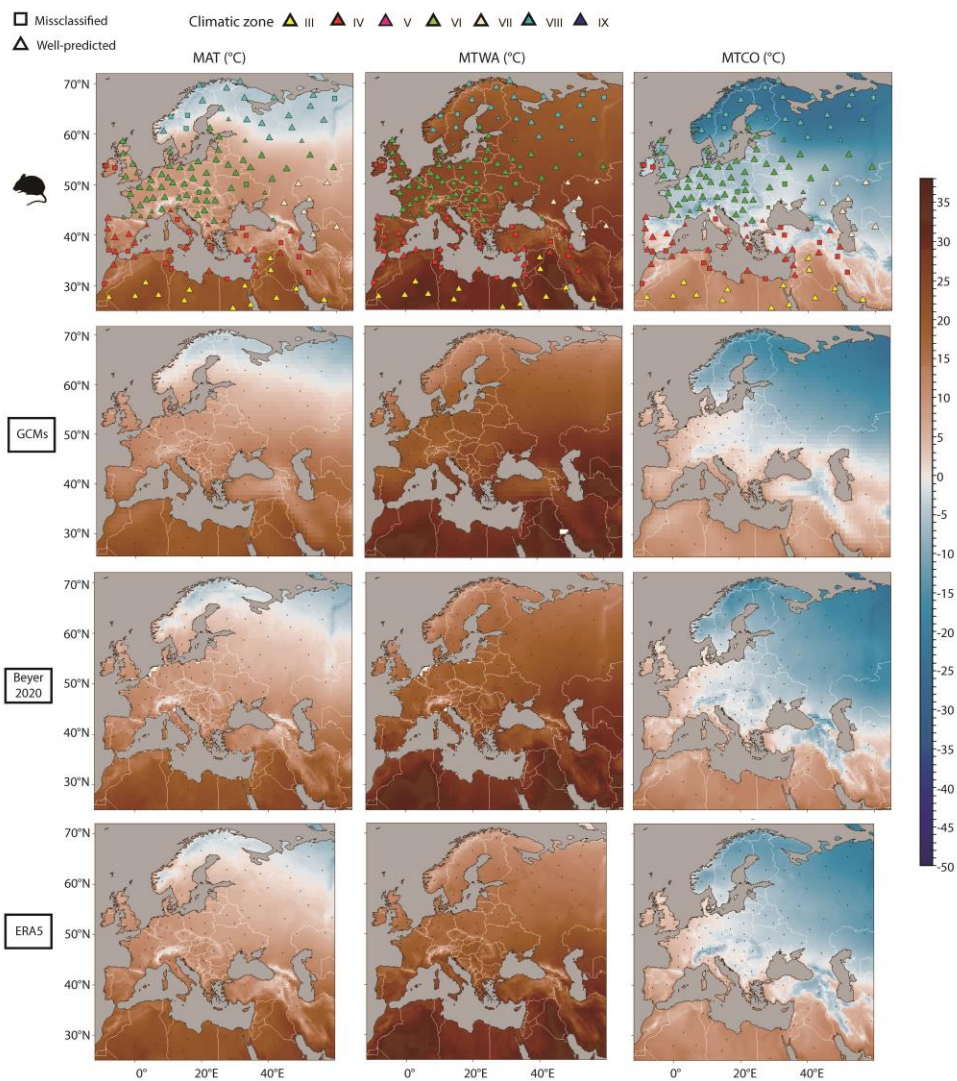


Figure 2: Present-day climatic classifications obtained using modern rodent associations. Colors represent the climatic zone estimated by the Bioclimatic Model (see Table 1). Triangles represent well-classified localities, while squares depicts not well-classified localities in comparison with their modern situation (see Table C1). These last symbols show two sizes, the larger one representing the well-established localities by Bioclimatic Model with a posterior probability values higher than 0.95 while the small one presents localities with a posterior probability values obtained smaller than 0.95 by the Bioclimatic Model.

3.2.2 Temperature interpolations

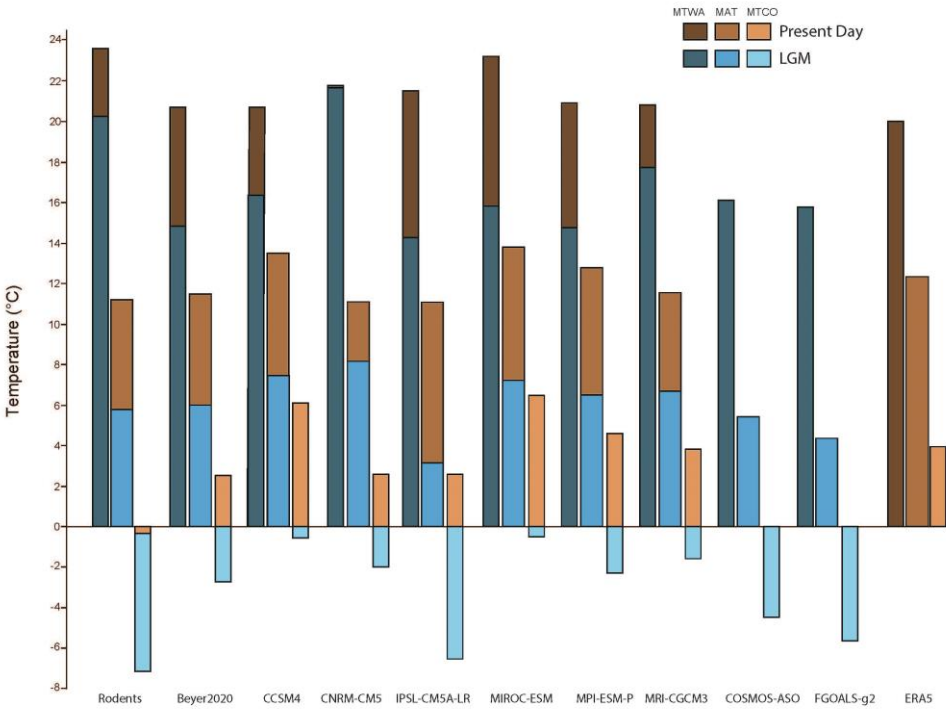
Our rodent-based reconstructions of modern MAT, MTWA and MTCO depict a geographical distribution that is consistent with the spatial pattern shown by GCMs, Beyer2020 and ERA5 (Fig. 3). The area-

averaged temperature values estimated by rodent-based reconstructions reach 11.2 °C for the MAT, 23.6 °C for the MTWA and -0.4 °C for the MTCO (Table 2, Fig. 4).



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450 Figure 3: Mean Annual Temperature (MAT), Mean Temperature of the Warmest month (MTWA) and Mean Temperature of the
 Coldest month (MTCO) estimated from 157 modern rodent associations spatially distributed all over the western part of Europe
 and the northern part of Africa (Fig. 1). For rodent predictions, colors represent the climatic zone estimated by the Bioclimatic
 Model (see Table 1). Triangles represent well-classified localities, while squares depicts not well-classified localities in comparison
 455 with their modern situation (see Table C1). These last symbols show two sizes, the larger one representing the posterior probability
 values higher than 0.95 while the small one presents the posterior probability values obtained smaller than 0.95. For comparison,
 equivalent data are shown for ERA5 (restricted to the 55°E), the PMIP4 GCM ensemble mean and the Beyer et al. (2020) GCM.
 Small black crosses represent the localities with rodent associations.



460 Figure 4: Bar plot of area-averaged MAT, MTWA and MTCO for present-day and the LGM, as estimated from rodent associations,
 ERA5 and multiple GCMs. The area average is based on the 55 locations not affected by maximum ice-sheet extension (see text and
 Table 2).

Model	Period	MAT	MTWA	MTCO	MAT anomalies	MTWA anomalies	MTCO anomalies
Interpolations from rodent association models	Present-day	11.18	23.57	-0.36			
	YD	8.65	23.06	-4.67	-2.53	-0.51	-4.31
	Allerød	8.60	22.12	-3.90	-2.58	-1.45	-3.54
	Bølling	7.58	22.35	-7.62	-3.60	-1.23	-7.26
	Heinrich Stadial	8.08	22.22	-5.29	-3.10	-1.35	-4.93
	LGM	5.91	20.21	-7.16	-5.27	-3.36	-6.80
Beyer2020	Present-day	11.47	20.66	2.51			
	YD	9.76	22.32	0.55	-1.71	1.66	-1.96
	Allerød	9.63	21.76	0.51	-1.85	1.10	-2.00
	Bølling	8.06	18.70	-0.75	-3.41	-1.97	-3.26
	Heinrich Stadial	6.98	17.02	-2.20	-4.49	-3.64	-4.71
	LGM	5.99	14.81	-2.74	-5.49	-5.85	-5.25
ERA5	Present-day	12.28	20.02	3.89			
CCSM4	Present-day	13.48	22.97	6.09			
	LGM	7.44	16.33	-0.58	-6.04	-6.64	-6.67
CNRM-CM5	Present-day	11.07	21.72	2.58			
	LGM	8.15	21.58	-1.98	-2.92	-0.14	-4.56
IPSL-CM5A-LR	Present-day	11.09	21.46	2.59			
	LGM	3.13	14.24	-6.55	-7.96	-7.22	-9.14
MIROC-ESM	Present-day	13.81	23.16	6.46			
	LGM	7.21	15.77	-0.51	-6.60	-7.39	-6.97
MPI-ESM-P	Present-day	12.79	20.87	4.59			
	LGM	6.48	14.73	-2.31	-6.31	-6.14	-6.90
MRI-CGCM3	Present-day	11.56	20.76	3.81			
	LGM	6.67	17.69	-1.60	-4.89	-3.07	-5.41
COSMOS-ASO	LGM	5.41	16.08	-4.43			
FGOALS-g2	LGM	4.35	15.75	-5.66			

Table 2: Area-averaged MAT, MTWA and MTCO in rodent-based estimations, ERA5 and PMIP4 and Beyer2020 GCMs for different time periods covered by the data (present-day, LGM, Heinrich Stadial, Bølling, Allerød and Younger Dryas). The area average includes the 55 locations (see text and Table 2). Anomalies against the present-day conditions are also shown.

The averaged MAT value is 1 °C lower than the ERA5 value and is very close to 4 of the 6 GCMs values (Table 2, Fig. 4). At the site scale, despite the presence of few obvious outliers, the MAT rodent-based reconstruction values are within the GCMs uncertainty range (Fig. 5A). The most sizable pattern for MAT is the abrupt decrease in temperature between climate zones VI and VIII, a pattern captured by our rodent-based reconstruction despite cold biases in the climate zone VIII. The relationship between rodent estimations and ERA5 is strong ($R^2 = 0.92$), comparable with the relationship between ERA5 and the GCMs (with R^2 ranging between 0.87 and 0.97: Fig. 5B). MAT values obtained from Bioclimatic Analysis of rodent assemblages show spatial discrepancies with ERA5 (Fig. 6). There is a tendency towards cold biases ($\sim -3/-4$ °C) all along the Atlantic coast latitudinal gradient, contrasting with positive biases (up to $\sim +3$ °C) over Ukrainian and Russian steppes (Fig. 6). Similar bias patterns are observed when comparing ERA5 with GCMs and Beyer2020 estimations, but with weaker differences, as in Iberian Peninsula or in Scandinavia (Fig. 6).

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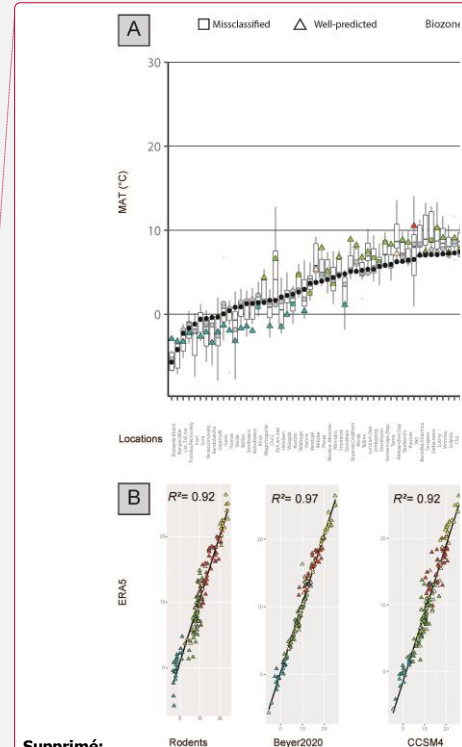
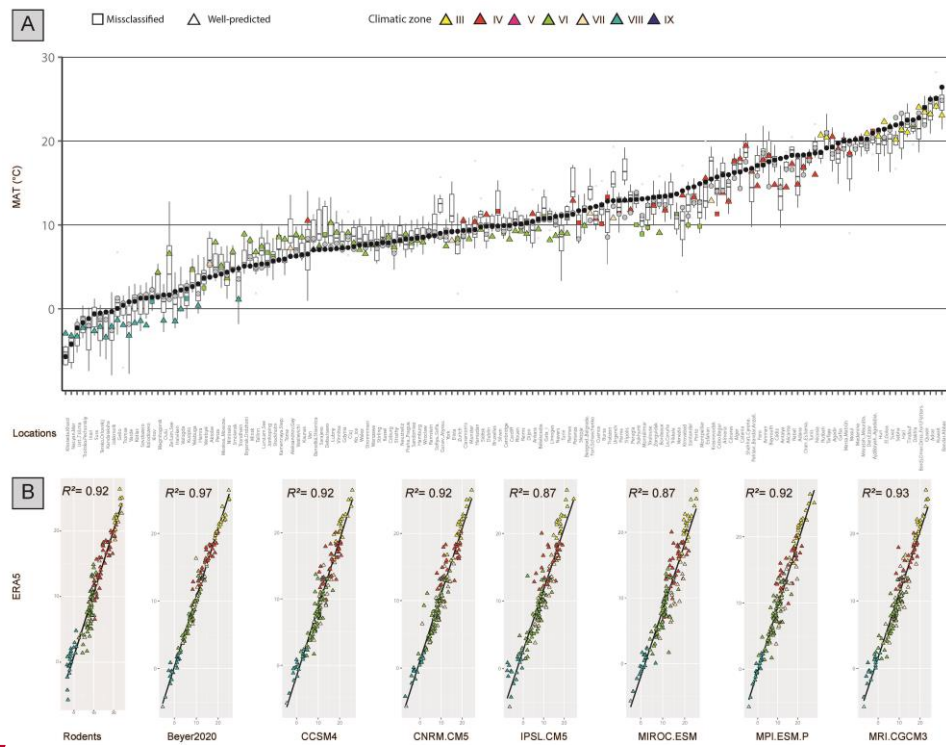


Figure 5: A) Present-day area-averaged MAT estimated from 157 rodent associations. Triangles represent localities whose modern climate zone was correctly classified, while squares are localities wrongly classified. Colors represent the climatic zone estimated by the Bioclimatic Model (see Table 1). MAT estimations from Beyer et al. (2020) (grey circles) and ERA5 values (black circles) are also shown. The boxplots represent MAT estimations from six different PMIP4 GCMs. Localities were ordered according to modern MAT values from ERA5 estimations. B) Scatterplots and linear regressions between present-day MAT from ERA5 and the estimations from rodent assemblages or from the GCMs. All of them are statistically significant ($p < 0.05$) and R^2 is shown.

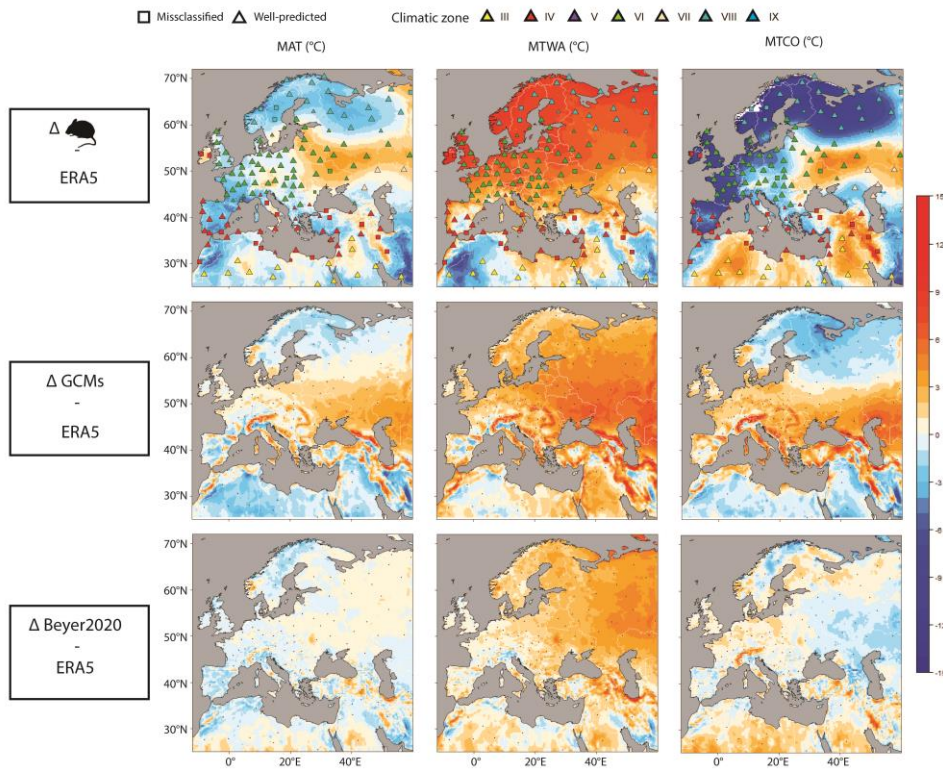
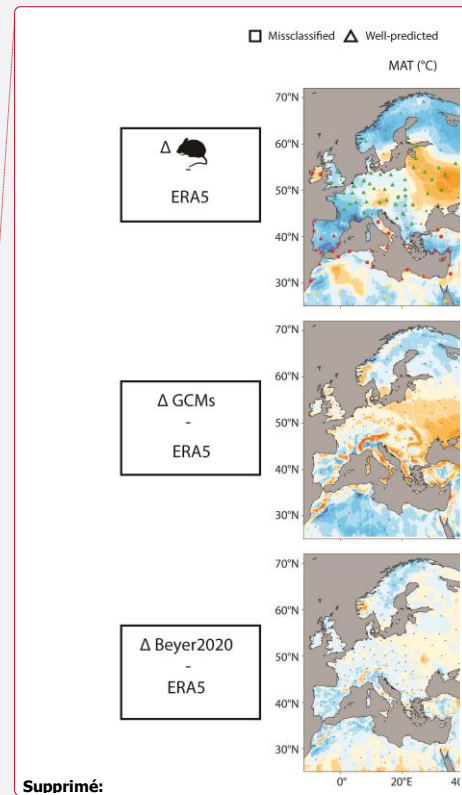


Figure 6: Differences in MAT, MTWA and MTCO between rodent-based, PMIP4 GCM ensemble mean and Beyer2020 GCM and the ERA5 reanalysis. Warm colors indicate that the models estimate higher temperatures than ERA5, while cold colors indicate the opposite.

Compared to ERA5, MTWA values are overestimated by all models over Europe. The warm bias reaches almost 4 °C for rodent-based reconstructions, 2 to 3 °C for GCMs and less than 1 °C for Beyer2020 (Table

2, Fig. 4). At the site scale, although most rodent-based reconstruction values fall within the range of the



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GCM uncertainty, they are usually in the warmer range of their estimations (Fig. 7A). Rodent associations generally infer warmer conditions than ERA5 and Beyer2020 for most of the climate zones, particularly for climate zones VI and VIII (Fig. 6 and 7A). Climate zones III and VII, on the other hand, show more accurate estimations (Fig. 7A). The regressions between ERA5 and the rodent estimates remain, however, still satisfactory ($R^2 = 0.84$) as GCMs ($R^2 = 0.79-0.93$), which indicates that the rodent-based model captures relatively well the spatial pattern of MTWA variation, although the slope and intercept going significantly away from 1 and 0 respectively (Fig. 7B). Discrepancies between rodent-based estimations and ERA5 show a similar pattern to GCMs biases, although somewhat more pronounced. It generally consists of higher temperature estimates, especially at latitudes above 50°N and lower estimation under 40°N (Fig. 6).

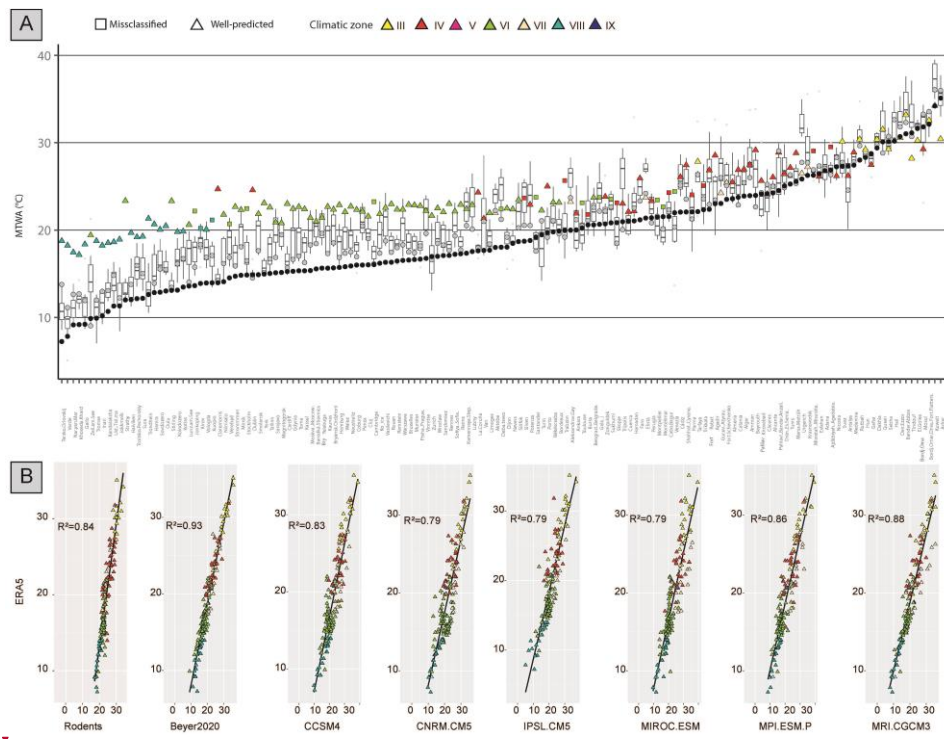
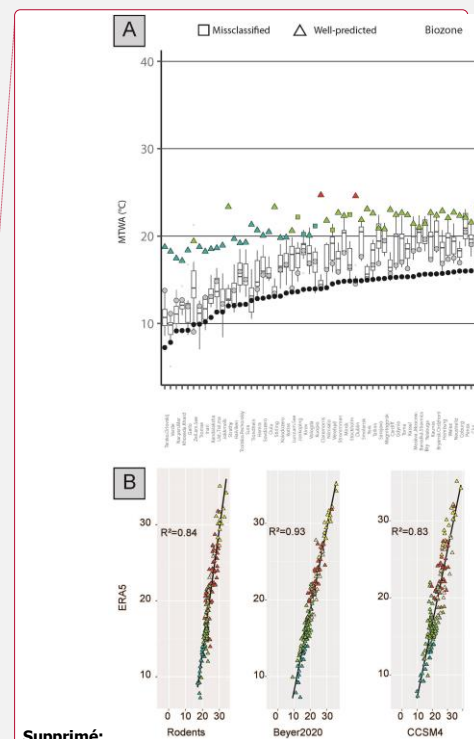


Figure 7: A) Present-day area-averaged MTWA estimated from 157 rodent associations. Triangles represent localities whose modern climate zone was correctly classified, while squares are localities wrongly classified. Colors represent the climatic zone estimated by the Bioclimatic Model (see Table 1). MTWA estimations from Beyer et al. (2020) (grey circles) and ERA5 values (black circles) are also shown. The boxplots represent MTWA estimations from six different PMIP4 GCMs. Localities were ordered according to modern MAT values from ERA5 estimations. B) Scatterplots and linear regressions between present-day MTWA from ERA5 and the estimations from rodent assemblages or from the GCMs. All of them are statistically significant ($p < 0.05$) and R^2 is shown.

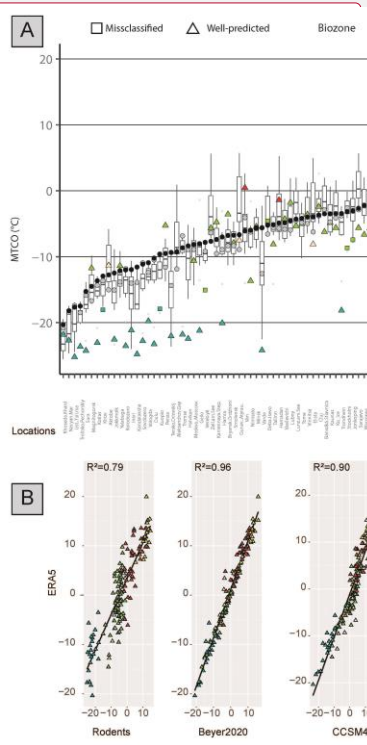
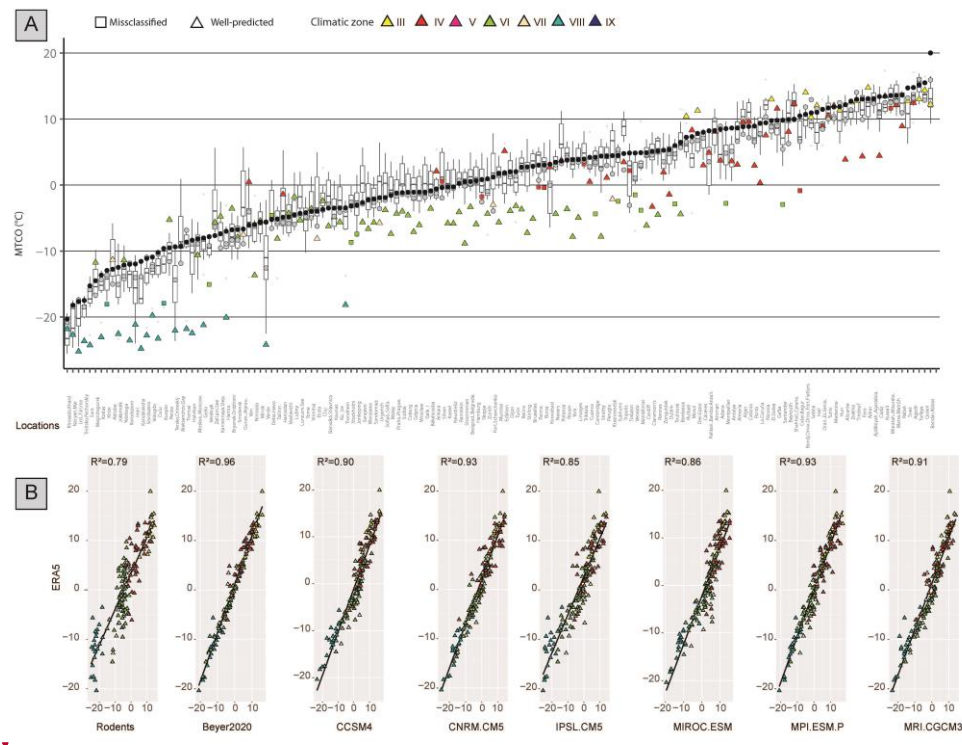


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The averaged MTCO value estimated from rodent associations is 4 °C lower than ERA5, and 2.8-6.7 °C lower than the GCMs (Table 2, Fig. 4). At the site scale, rodent-based estimations are also usually colder than the ERA5 and GCMs values, in particular for sites located in climate zone VIII (Fig. 8A). The

common variance between ERA5 and rodent-based estimations is weaker ($R^2 = 0.78$) than with the GCMs ($R^2 = 0.85-0.96$). This is mainly due to large discrepancies in site located within temperate (VI) and boreal (VIII) climate zones (Fig. 8B). Spatially, southern locations are skewed toward warmer temperature inferences, without bias exceeding 5 °C. On the other hand, the Atlantic, Baltic and Arctic facades offer colder inferences (Fig. 6).

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Figure 8: A) Present-day area-averaged MTCO estimated from 157 rodent associations. Triangles represent localities whose modern climate zone was correctly classified, while squares are localities wrongly classified. Colors represent the climatic zone estimated by

535 the Bioclimatic Model (see Table 1). MTCO estimations from Beyer et al. (2020) (grey circles) and ERA5 values (black circles) are also shown. The boxplots represent MTCO estimations from six different PMIP4 GCMs. Localities were ordered according to modern MAT values from ERA5 estimations. B) Scatterplots and linear regressions between present-day MTCO from ERA5 and the estimations from rodent assemblages or from the GCMs. All of them are statistically significant ($p < 0.05$) and R^2 is shown.

To conclude, the evaluation of present-day spatial temperature patterns reveals a close relationship
540 between small mammal communities and climate. Regressions between MAT, MTWA and MTCO and ERA5 show high R^2 values, although slightly lower than the ones established by Royer et al. (2020). This is not surprising given the larger sample size used here, including localities from ecotonal areas among different climate zones. The rodent-based inferences accurately capture the “observed” (*i.e.* ERA5) spatial patterns of macroclimate, particularly in the case of MAT predictions. In the case of MTWA and MTCO,
545 if global spatial patterns of macroclimate are well captured, estimations depict intensity biases in western and northern Europe (strong warm bias and cold bias, respectively), implying overestimated annual thermal ranges. These results indicate that the Bioclimatic Analysis (Hernández Fernández, 2001; Hernández Fernández & Peláez-Campomanes, 2003, 2005; Royer et al., 2020) has strong potentialities, not only to infer past climate conditions of isolated assemblages, but also to be integrated in paleoclimatic
550 research based on interpolation at continental scale.

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3.3 Past period reconstructions

3.3.1 The Last Glacial Maximum, a fistful of rodents

The climate zones inferred from LGM rodent associations (Fig. 9A) suggest that northern France and
555 Germany experienced a boreal climate (VIII), in which tundra-steppe rodent species, such as collared

lemmings (*Dicrostonyx torquatus*), narrow-skull voles (*Stenocranius anglicus*) or different ground squirrels (*Spermophilus* sp.), were particularly abundant (e.g. Hanquet et al., 2016; Markova et al., 2019). These rodents were part of the “mammoth steppe” or “steppe-tundra”, a uniquely high productive grassland ecosystem that supported a high biomass of large herbivores (e.g. horse, steppe bison, woolly rhinoceros and mammoth). These open landscape faunal associations are sometimes associated with woodland species, such as *Clethrionomys* sp., which suggest the presence of some discontinuous forest environments (e.g. Cyrek et al., 2000; Ponomarev et al., 2013; Nadachowski & Valde-Nowak, 2015). Only the rodent assemblage from Ireland supports a periglacial climate zone (IX), with communities entirely composed of lemmings (Woodman et al., 1997; Monaghan, 2017). Much more diverse rodent communities, including lemmings, narrow-skull voles, tundra voles, snow voles, marmots, ground squirrels, garden dormouse and wood mouse, indicate that the temperate climate zone (VI) covered southern France (Marquet, 1993; Royer et al., 2016; Crégut-Bonnoure et al., 2018) and northern and coastal areas of the Iberian (e.g. Cuenca-Bescós et al., 2009; Garcia-Ibaibarriaga et al., 2019) and Italian (e.g. Berto et al., 2017; Luzi et al., 2022a) peninsulas (Fig. 9A). As noted by García-Morato et al. (2024) in the Iberian Peninsula, the rodent communities from the southernmost areas reveal only minimal changes. In central and eastern Europe, the temperate climate zone (VI) seems to be associated with the interface around 50 °N between the southern extension of the boreal climate zone (VIII), identified in the central Urals, and the arid-temperate climate zone (VII) found in its southern foothills. In the communities of the latter climate zone, dry steppe species, such as the steppe lemming (*Lagurus lagurus*) or gray hamster (*Nothocricetulus migratorius*), became dominant (Danukalova & Yakovlev, 2006; Kosintsev & Bachura, 2013; Ponomarev et al., 2015). The Mediterranean climate zone (IV) was mostly restricted to

580 southwestern Iberia as well as central and eastern Mediterranean shores, which served as a refuge for most Mediterranean species (e.g. Berto et al., 2019a; Ceregatti et al., 2023). The geographical distribution of biomes obtained from LGM rodent associations largely matches the one described by Markova et al. (2019) and Puzachenko & Markova (2023), which divided Europe in three latitudinal zonal assemblages during this time interval: periglacial tundra, periglacial tundra-forest-steppe, and periglacial forest-steppe. Puzachenko & Markova (2023) suggest that differences between the western and eastern European faunal associations of the LGM could be related to more arid environments of the eastern regions and to the 585 impact of Atlantic influences for the western. Finally, the LGM reconstructed by the rodent-based model is characterized by cold and dry climate conditions, with faunal communities constrained by the large presence of the Fenno-Scandinavian ice sheet. These faunal communities suggest the large presence of open steppic environment on a large part of northern Eurasia, as already suggested by pollen (e.g. Tarasov et al., 2000; Binney et al., 2017; Davis et al., 2022). This environment is most likely characterized by very fragmented forested cover and a scarcity of woodland refugia, which would be nonetheless associated to the occasional presence of some thermophilous species (Davis et al., 2022).

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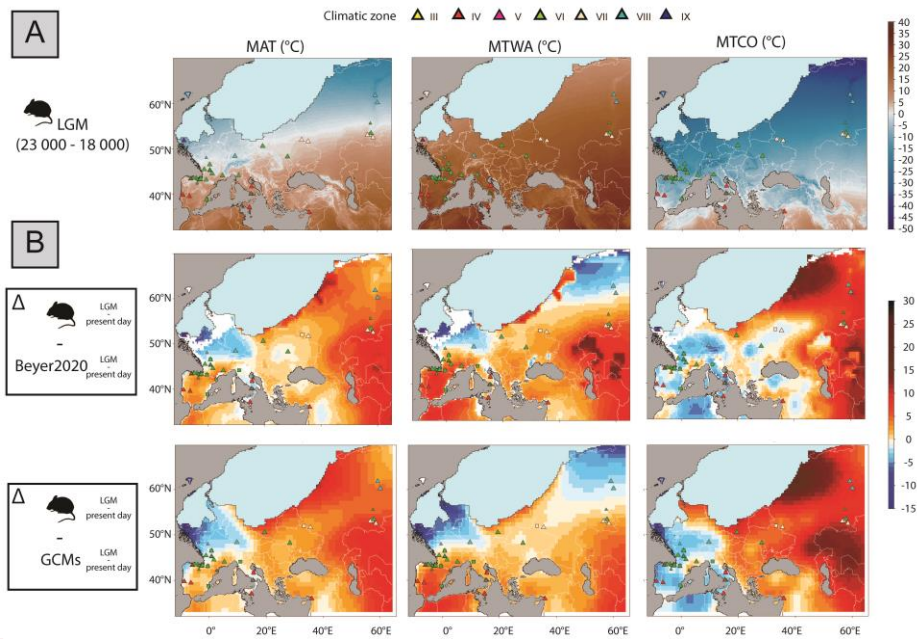


Figure 9: A) Rodent-based estimations of MAT, MTWA and MTCO for the LGM period. B) Difference between the rodent anomaly values calculated between the LGM and the present-day periods (e.g. LGM minus present-day), and those calculated for Beyer2020 and from GCMs models. Warm colors indicate that rodent-based estimations provide higher temperature changes than the PMIP4 or Beyer2020 GCM estimations, while cold colors indicate the opposite. Colored triangles represent the climatic zone estimated by the fossil rodent associations using the Bioclimatic Model for the LGM period (Table 1). These symbols show two sizes, the larger one representing the posterior probability values higher than 0.95 while the small one presents the posterior probability values smaller than 0.95.

The temperatures estimated from the LGM rodent associations show a strong latitudinal gradient (Fig. 9A), with an average MAT anomaly of -5.3 °C compared with present-day temperature (Table 2). This is consistent with Beyer2020 (-5.5 °C) and within the range of uncertainty of PMIP4 GCMs (-3 °C to -8 °C). Rodent estimations from southwestern France range from 2 to 5 °C and are relatively similar to

estimations from Beyer2020 (6 °C) and PMIP4 GCMs (3 °C to 11 °C). Rodent estimations reach around -3 °C at Brussels, while those from Beyer2020 are around 2.5 °C and PMIP4 GCMs range from -4 °C to 5 °C (Fig. B2). They are also 2-3 °C colder than other estimations based on faunal species (Puzachenko & Markova, 2023). Our rodent-based model suggests that the largest changes in MAT between LGM and present-day conditions are observed in the Russian polar latitudes and around the British-Irish ice sheet (anomalies between -5 and -10 °C), while the cooling at lower latitudes was comparatively attenuated (anomalies between 0 and -5 °C) (Fig. 10), as also observed from pollen-based climate reconstruction (e.g. Bartlein et al., 2011; Davis et al., 2022). Spatial patterns from rodent-based model exhibit thus a stronger latitudinal gradient during the LGM than today, and differ with Beyer2020 and PMIP4 GCMs (Fig. 9B & 10; Fig. B2), the latter proposing a less marked latitudinal gradient in MAT across the western Palearctic. This leads rodent-based model to propose that MAT anomalies between LGM and present day conditions were higher than PMIP4 GCMs and Beyer2020 in northwestern part of Europe (in blue in Fig. 9B) and smaller in the southwestern and eastern part of Europe (in red in Fig. 9B). Particularly notable differences in anomalies are observed in the eastern area for which Beyer2020 models suggest larger MAT changes than rodents, as in southern Ural, where rodent anomaly estimations are small; this is also probably emphasized due to the absence of rodent associations in the southeastern part of the study area for this time interval, which may produce spurious temperature inferences for lower southeastern areas (see red area in Fig. 10).

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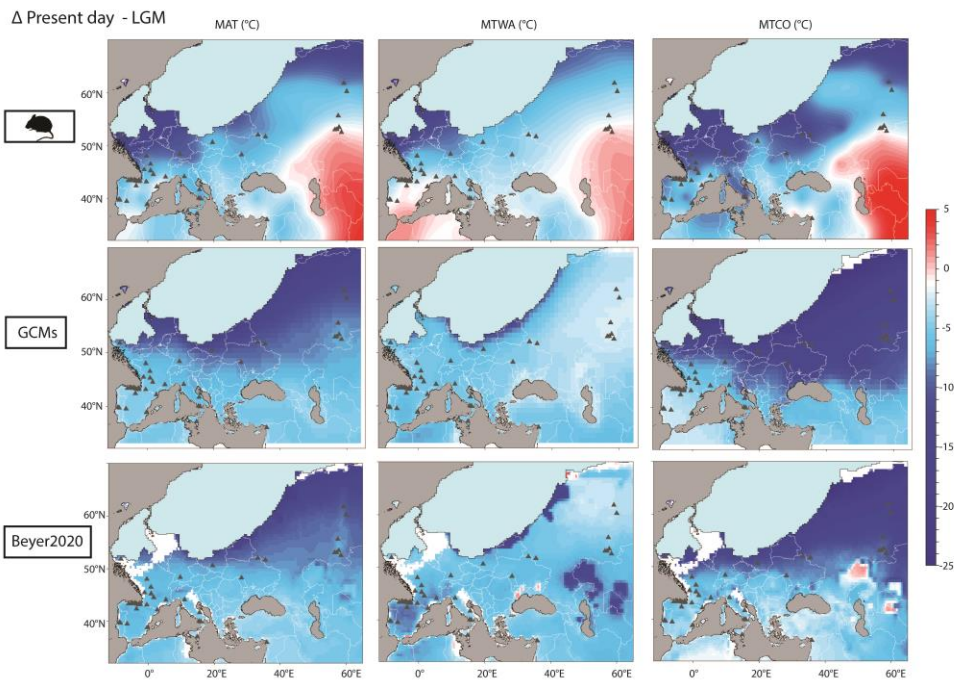
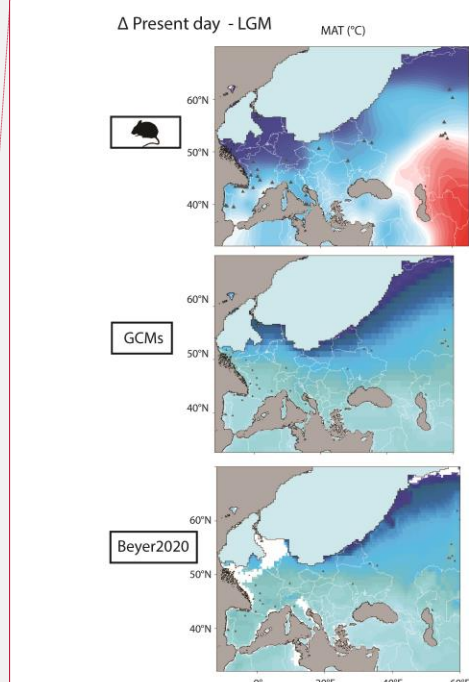


Figure 10: MAT, MTWA and MTCO anomalies calculated between present-day and LGM conditions (LGM minus present-day) for the rodent-based, PMIP4 and Beyer2020 estimations. Cold colors indicate lower temperatures during the LGM compared to present-day, while warm colors signify the opposite.



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Rodent-based changes in MTWA and MTCO between present-day and LGM conditions are similar to those obtained for MAT, although changes in MTCO are stronger than MTWA (Table 2, Fig. 10 & Fig. B2). On average the change in MTCO reaches almost -7 °C, while the MTWA anomalies only reach -3.4

°C (Table 2), with almost lowest LGM to present-day changes for the southern latitudes. It is in agreement
640 with Davis et al. (2022), who show that LGM climatic cooling was significantly greater in winter than in
summer using updated LGM pollen estimations in Eurasia (Peyron et al., 1998; Jost et al., 2005; Wu et
al., 2007). Our estimations are relatively close to Beyer2020 and PMIP4 GCMs (Table 2). However,
spatial patterns differ significantly between the rodent estimations and the other models. Rodent-based
estimations of MAT, MTWA and MTCO are colder in the northwest region and warmer in the eastern
645 region compared to Beyer2020 and PMIP4 GCMs (Fig. 9B).

Figure 10 summarizes temperature changes between present-day and LGM conditions across all models
and indicators. A pronounced meridional gradient is evident in all models and for all indicators, with
stronger cooling in the north than in the south. In addition to this meridional gradient, the rodent model
reveals a geographical gradient, showing LGM temperatures that are much colder in the northwest and
650 slightly warmer in the southeast compared to present-day conditions. This pattern is consistent across
MAT, MTWA, and MTCO, but does not appear in Beyer2020 or the GCMs. It is linked to the presence
of an Arctic rodent association in the northwest, possibly indicating lower heat input associated with a
weak AMOC. The lack of this zonal gradient in GCMs may be due to an overly strong AMOC, despite
improvements from PMIP3 to PMIP4 (Kageyama et al., 2020).

655 As noted by Davis et al. (2022), although the traditional view of the LGM has been defined for many
years, many questions still remain to be explored, when more precise quantification is researched. The
LGM is depicted as a very different period compared to today, with distinct climate, vegetation and
landscape, together with a different orographic context including large ice-sheets, which have fully

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impacted faunal communities. Typical cold rodent species have been recovered throughout mid- and high latitudes, and were mainly limited by natural barrier like mountains to reach southern latitudes. They form ecotone rodent communities, mixing species from polar, boreal and temperate environments, and are far from reflecting typical full periglacial communities, except for the ones located at the closest range of the ice-sheet. The quantification obtained with the rodent-based model do support the global view of a colder LGM world, but with MAT anomalies no larger than -5.5 °C compared to the present-day conditions, and underpins that changes in MTCO were stronger than in MTWA. Rodent associations produce nonetheless spatial temperature pattern different than the ones estimated from Beyer2020, suggesting notably greater temperature changes in the northwestern part of Europe, while the temperature anomalies in the southwestern and the eastern part of Europe were weaker than Beyer2020 and PMIP4 GCMs.

3.3.2 Once upon a time in the Late Glacial

Compared to the LGM picture, the Heinrich Stadial experienced sizable changes in species distribution throughout the western Palearctic (e.g. Royer, 2016; Royer et al., 2016; Markova et al., 2019). However, climate zone distribution remains globally similar between these two periods (compare Fig. 11 with Fig. 9A). Northern Europe yielded more sites with Arctic rodent associations, like in Belgium, Poland and the northern Ural Mountains (Teterina, 2009; Stewart & Parfitt, 2011; Ponomarev et al., 2012; López-García et al., 2024), forming a composite mix of boreal (VIII) and polar (IX) climatic zones. The transition between climatic zones VI and VIII appears south of 50° N in the western part of Europe and around the 55° N in the eastern part, while the central Europe remain dominated by an arid-temperate climate zone

(VII), as shown in Fig. 11. The Iberian and Italian peninsulas show both a mix of Mediterranean (IV) and temperate (VI) climate zones. With the warming of the Bølling and the Allerød, large changes occurred at species level (Kalthoff, 1998; Jeannet, 2009; Royer et al., 2016, 2021; Rofes et al., 2020; Wong et al., 2017). Changes in the climate zone distribution occur slightly with boreal climate zone (VIII) in western Europe retreating towards northern latitudes, as the ice sheet melted. The temperate climate zone (VI) slightly develops to the north up to 50°N, while the central and eastern Europe seems to present a pattern relatively similar to previous intervals with the presence of an arid-temperate climate zone (Fig. 11). Yet, to date, there is still a general lack of information on the southeastern part of the study area for this time interval making it difficult to understand how exactly the arid-temperate climate zone (VII) has changed.

The Iberian and Italian Peninsulas still deliver rodent associations of both Mediterranean (IV) and temperate (VI) climate zones, although the latter are becoming rare. There are few fossil sites to cover the Younger Dryas and most of them are in Western Europe. They do not reveal remarkable changes in climate zone distribution, despite the cooling of this event. The British Isles still experienced boreal (VIII) and polar (IX) climate zones attested by the presence of typical boreal and polar lemming (Price, 2003; Arbez et al., 2021), while a boreal climate zone sets up in the northern part of Urals (Fig. 11).

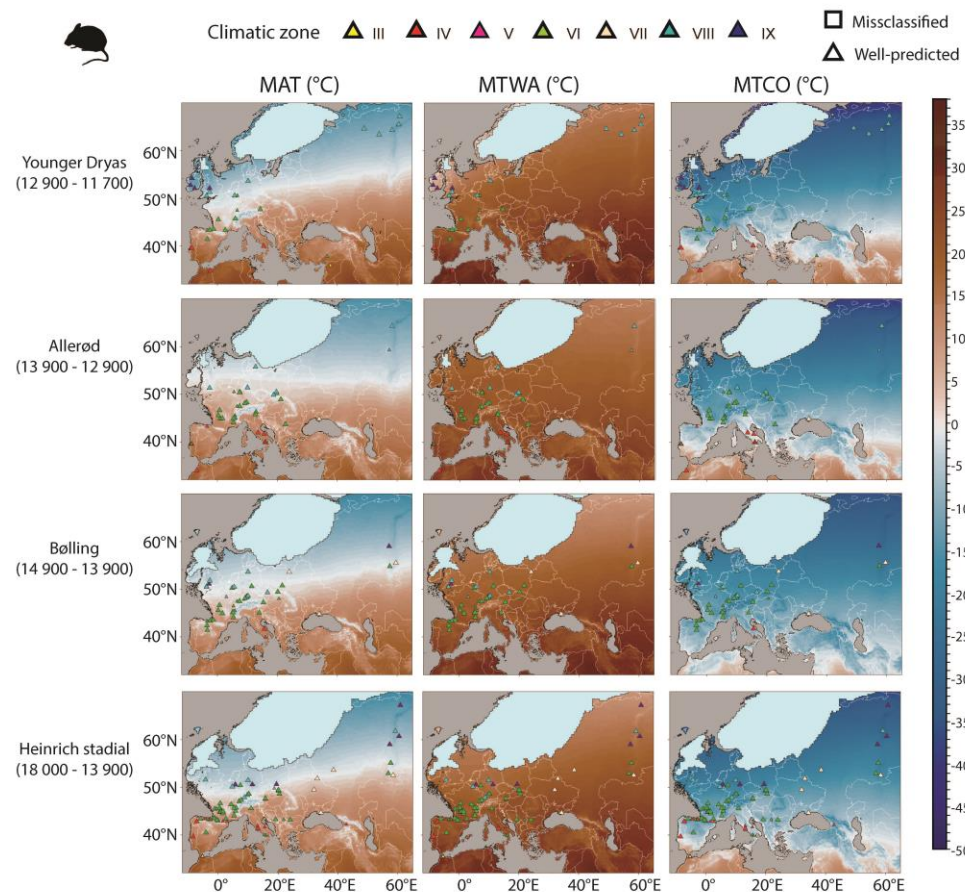
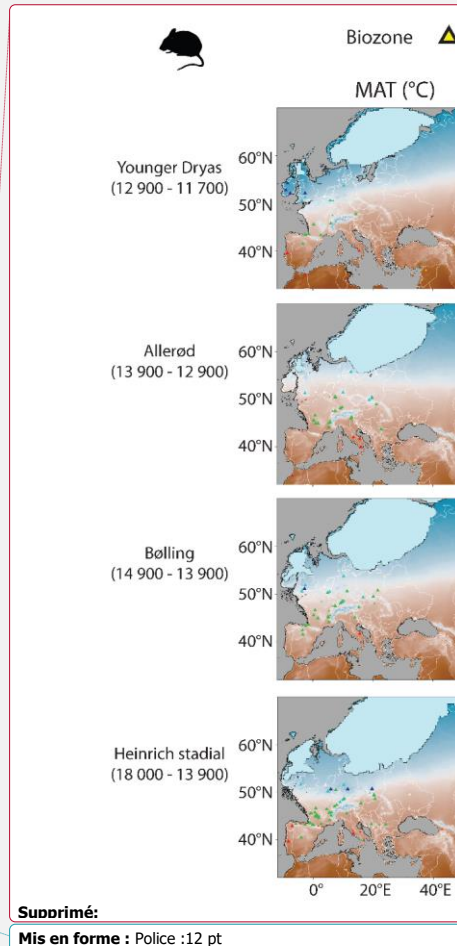


Figure 11: Rodent-based estimations in MAT, MTWA and MTCO for the Heinrich Stadial, Bolling, Allerød and Younger Dryas periods. Colored triangles represent the climatic zone estimated by the fossil rodent associations using the Bioclimatic Model (Table 1). These symbols show two sizes, the larger one representing the posterior probability values higher than 0.95 while the small one presents the posterior probability values smaller than 0.95.



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Average climate estimations obtained from rodent associations present a gradual temperature warming between LGM and present day (Table 2). MAT of different Late Glacial events remains however within
705 a relatively narrow range of values (7.6 to 8.7 °C), with MAT value at 8.1 °C since the Heinrich. MTWA values vary little (between 22.1 and 23.1 °C), while MTCO values range from -7.6 to -3.9 °C. These estimations obtained with rodent-based model are relatively close to those of Beyer2020, in particular for MAT (Table 2). For MTWA and MTCO, Beyer2020 estimations suggest larger temperature changes across the events, while rodent-based reconstructions suggest only small changes in MTWA and still
710 larger MTCO anomalies for Bølling-Allerød-Younger Dryas periods (Table 2).

These spatial temperature reconstructions of Late Glacial events differ from Beyer2020 in the same way (Fig. 12). Except the southeastern part for which no rodent association is available, the main disagreements come from a different latitudinal gradient of changes in the western part of Europe, and differences in northeastern part of Europe. For the northwestern part of Europe, the rodent-based model
715 estimates that MAT, MTWA and MTCO anomalies between Late Glacial events and present day conditions were systematically higher than Beyer2020 (in blue in Fig. 12), suggesting thus larger temperature anomalies throughout all the Late Glacial. For instance, for the Bølling and the Allerød, MAT anomalies from rodent-based model are estimated around -12.5 / -8 °C in England, compared with -5 / -3.5 °C for the Beyer2020 model. By contrast, the rodent-based model yields smaller temperature
720 anomalies for the southwestern part of Europe, as well as for the eastern part of Europe during the Heinrich Stadial and Bølling. For instance, MAT anomalies of Heinrich Stadial and Bølling in the southwestern France are estimated around -3 / -3.5 °C for the rodent, thus relatively close of the one of Beyer 2020 estimated at -4.5 / -5 °C. For the northeastern part of Europe, Beyer2020 estimated greater

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anomalies for MAT and MTCO between Late Glacial events and present day (in red in Fig. 12) than the rodents. For the region of Moscow, MAT anomalies of Beyer2020 range from -13.5 to -11 °C for the Heinrich Stadial and Bølling, while rodent-based model estimated MAT anomalies between -9 and -10 °C.

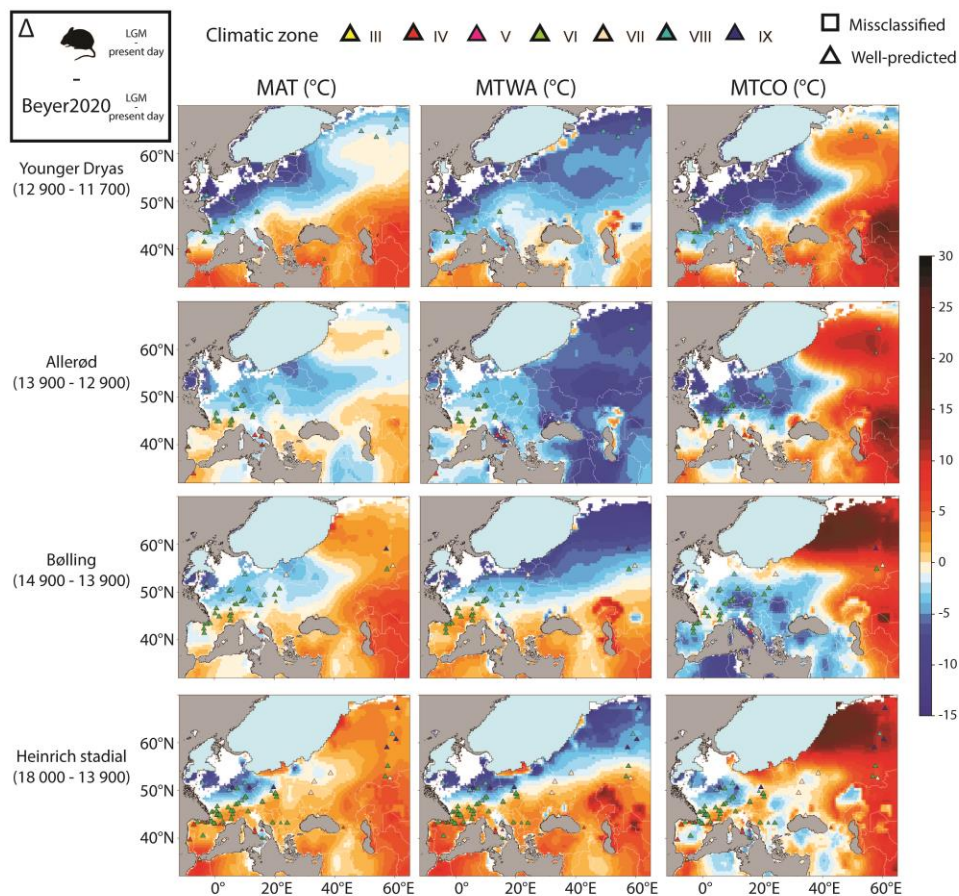
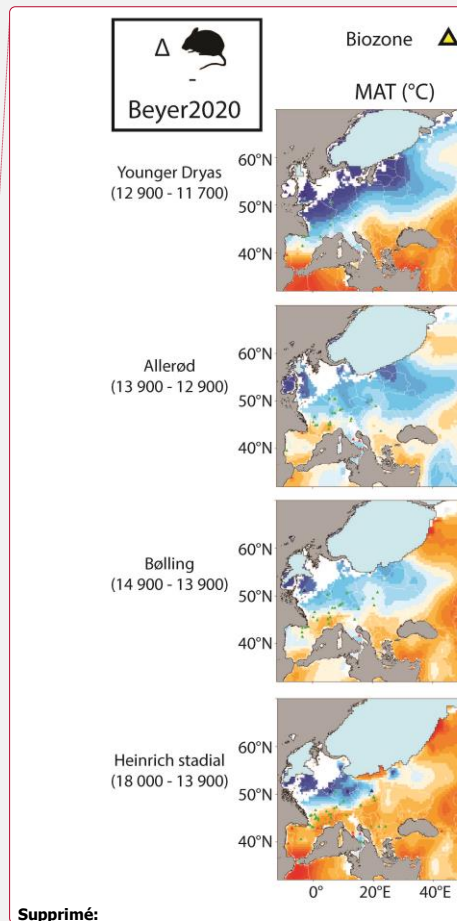


Figure 12: Difference between the rodent anomaly values calculated between the past (Heinrich Stadial, Bølling, Allerød and Younger Dryas) and the present-day periods (e.g. LGM minus present-day), and those calculated for Beyer2020 models. Warm colors indicate that rodent-based estimations provide higher temperature changes than Beyer2020 estimations, while cold colors indicate the opposite. Colored triangles represent the climatic zone estimated by the fossil rodent associations using the Bioclimatic Model for the past period (Table 1). These symbols show two sizes, the larger one representing the posterior probability values higher than 0.95 while the small one presents the posterior probability values smaller than 0.95.



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As a consequence, temperatures obtained from rodent-based reconstructions are far from changing uniformly across Europe between the Late Glacial events (Fig. 13). It shows larger spatial variations than Beyer2020 temperature changes. Indeed the Beyer2020 model shows more spatially uniform changes for the MAT across Europe between the Late Glacial events, with main changes located in areas close to the

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ice-sheet, while some longitudinal variations have been observed for MTWA and MTCO estimations (Fig. B3). Conversely, rodent-based model suggests greater latitudinal and longitudinal variation in changes. After the LGM, the increase of MAT rodent-based estimations during Heinrich Stadial is larger along the Atlantic seaboard than in central Europe. Southwestern France and the north of Spain experienced a warming between 1.5 to 3 °C, while temperature changes are lower than 1 °C in Belgium, Germany or Poland. The northern eastern part shows an increase of 3 °C and 6 °C for MAT and MTCO, respectively. Beyer2020 suggests a general raise of around 2 °C for MAT, with increase no larger than 1.5 °C in southwestern France and Spain, and between 1.2 and 5 °C in Belgium, Germany or Poland. During the Bølling, MAT and MTCO fall with the rodent-based model for the middle and the lower latitudes, while they rise in the northwest, as in Belgium and Germany, where a MAT increase of 2 to 3 °C is found. The Allerød presents sizable changes, with a MAT warming between 1 and 3 °C in all western Europe. The southern latitude is mainly impacted by an increase in MTCO, with for instance increase of 3.5 °C for the north of Spain and of 2 °C for southwestern France. The northern latitudes show an increase in MTWA, reaching up to 2.5 °C as in Brussels. The Younger Dryas event brings back well-marked glacial conditions before the beginning of the current interglacial, particularly along the Atlantic coast and the British Isles. The latter experienced MAT decrease exceeding 5 °C (Fig. 13), while Beyer2020

shows no sizeable changes in this areas, except in Scotland, with an MAT increase around 2.5 °C (Fig. B3).

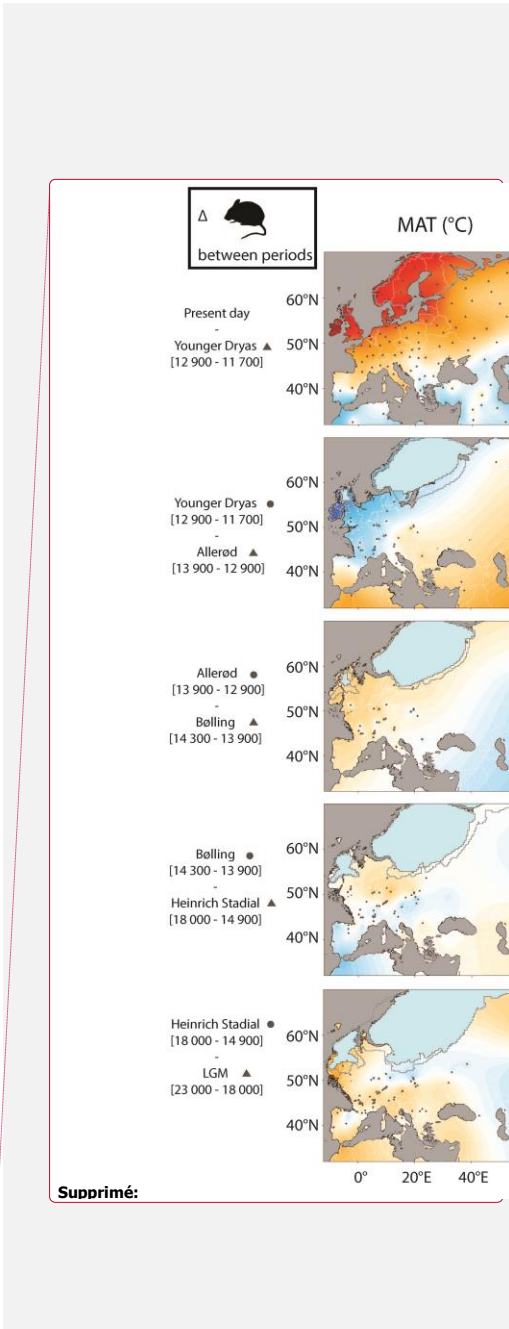
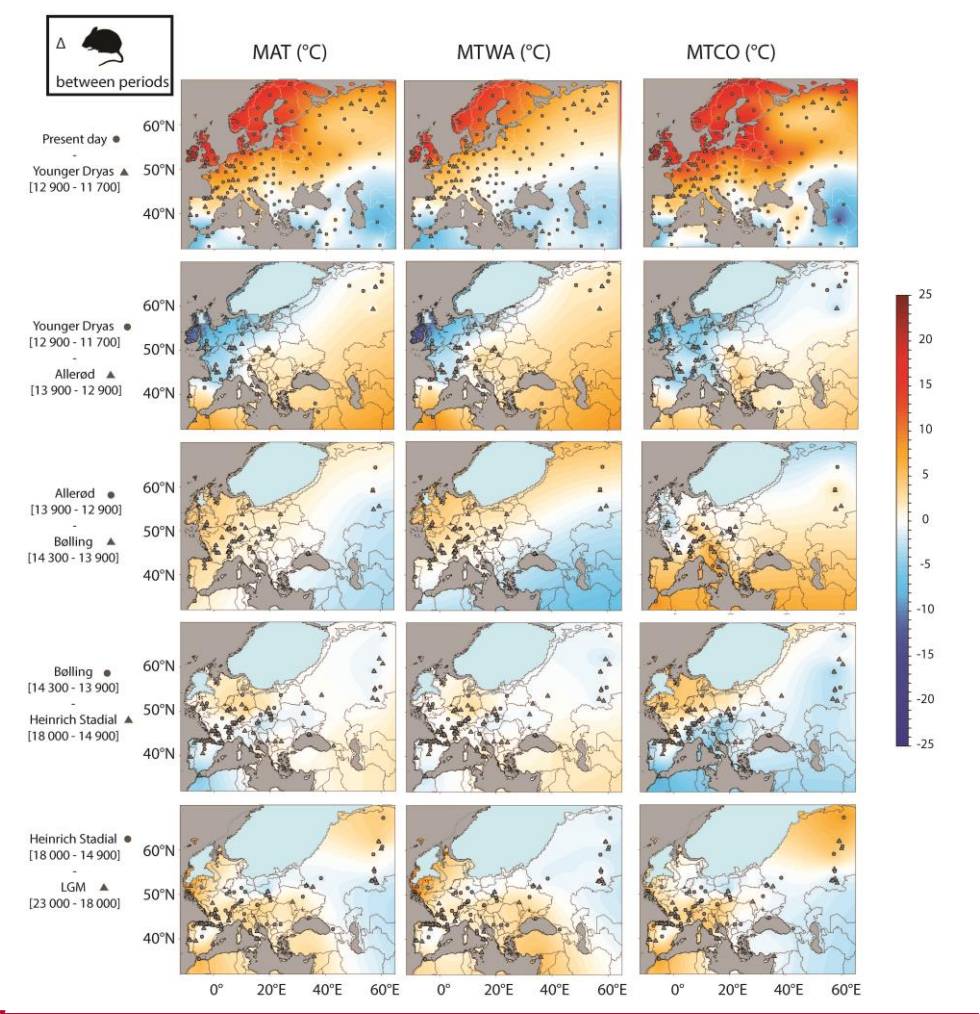


Figure 13: Differences in MAT, MTWA and MTCO between each successive time periods in rodent-based estimations. Triangles and circles represent the position of fossil localities used in each pair of time intervals. The ice sheet of the most recent period is represented in blue, while the limits of the older one appears in grey.

The Late Glacial period experienced significant climatic shifts, marked by rapid climate oscillations, which led to a dynamic re-shaping of living spaces, with the progressive retreat of ice sheets freeing up new areas in the northern regions, while rising sea levels simultaneously submerged substantial portions of coastal regions. These changes have restrained other areas, isolated some islands and induced significant changes in plant communities. All these biotic and abiotic changes have led to considerable changes in faunal associations throughout Europe, triggering range shifts, local extirpations, extinctions, population replacement, isolation in refugia or recolonization processes (e.g. Stewart et al., 2010; Brace et al., 2016; Baca et al., 2017; Puzachenko & Markova, 2019; Magyari et al., 2022). At the community scale, the changes remain slow as shown by the progressive rise of temperate climate zone (VI) throughout the Late Glacial (Fig. 11), and in the early Holocene for the northern latitude. In southwestern France, the changes in small mammal associations are gradual taking all of the Late Glacial events to switch progressively from the typical glacial community to the typical interglacial community (Royer et al., 2016), including also the presence of certain species only at certain events (Royer, 2016; Royer et al., 2018). These Late Glacial periods produce therefore rodent associations mixing typical taxa of northern environments, with new southern and eastern taxa (Royer et al., 2016), which gradually evolve in latitude in line with the events (e.g. Cordy, 1991; Wong et al., 2020; López-García et al., 2024). These faunal changes reflect temperature changes that vary both in time and space, producing spatial pattern that differs from Beyer2020. Rodent results suggest that the northwestern part of Europe experiences larger

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temperature changes, while temperature anomalies in the southwestern and the eastern part of Europe were smaller than those estimated by Beyer2020.

795 **3.3.3 How to interpret the differences between GCMs and rodent-based inferences**

As described previously, rodent-based model provides patterns similar to GCMs for both present-day and past conditions, with for instance a basic picture of LGM as a cold world with MAT anomalies around -5.5 °C in the Western Palearctic. Yet, there are notable divergences among the approaches. These divergences are generally included in the range of GCM uncertainties and hide sizable regional differences, like between northwestern and northeastern Europe (Fig. 9B & 10). Compared to GCMs, 800 rodent associations of LGM and Late Glacial periods generate colder temperature values in the western part of Europe and warmer in eastern Europe (Fig. 9B). This leads to a stronger west-east temperature gradient in the rodent-based model against both PMIP4 GCMs and Beyer2020, especially for the coldest months.

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805 The physical interpretation of these distinct temperatures observed for past period is questionable. On the one hand, working with faunal remains require to take into account few taphonomical, analytical and ecological assumptions detailed in section 3.1. The discrepancies between our rodent-based model and PMIP4 GCMs and Beyer2020 in higher latitudes (Fig. 10) could be explained by a limitation in the Bioclimatic Analysis. Therein, MAT of the coldest areas used to generate the new version of the 810 Bioclimatic Analysis reach around -15 °C (Royer et al., 2020), in areas with typical arctic species as lemmings or tundra shrews. It is then very difficult to properly extrapolate MAT values below -15 °C,

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while some GCMs estimations easily reach up to -30 °C and even colder in eastern regions, questioning how faunal species identified through the fossil record could have survived in such conditions.

On the other hand, GCMs have their own uncertainties, biases, and sensitivity to changes in the radiative forcing and boundary conditions. Each GCM uses different sets of parameterizations to approximate sub-grid processes that cannot be resolved at coarse spatial and temporal resolutions, which strongly influence climate simulations (Taylor et al., 2012; Varela et al., 2015), resulting in a large range uncertainties across GCMs. GCMs often diverge from actual paleontological data (Jost et al., 2005; Allen et al., 2008; Braconnot et al., 2012; Latombe et al., 2018). Beyer2020 model appears to propose the best estimation for modern context (Fig. 4, 5, 7 & 8), due to bias correction. Interestingly, they evaluated their method for past period at the global scale, comparing it only to mid-Holocene and LGM pollen database (Bartlein et al., 2011). The question may arise regarding the validation of this model during unstable glacial periods when relying solely on a single proxy. This has been recently criticized, because some of the pollen sequence were not necessarily properly well attributed to the LGM (Davis et al., 2022). Furthermore, LGM is a peculiar period of the last glaciation, with a specific abiotic context. No validation has been tested for the others glacial periods, which present their own abiotic particularities.

On the basis of all these assumptions, we can finally conclude that these divergences between GCMs and rodent-based estimations could result from multiple factors that need further investigations. Beyond GCM limitations, our interpolations are “a point of view” of rodent associations, which could contribute to explain the disagreements with GCMs. Species association may exist under environmental conditions that do not exist today, but did exist in the past (Jackson & Overpeck, 2000; Williams & Jackson, 2007;

Lyman, 2017). The relationships between the species and their environment are in constant evolution, and the current observations reflect only a realized niche, potentially underestimating the plasticity and adaptive capacity of species in response to new abiotic and biotic constraints.

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Rodent-based estimations tend to show a slightly different zonal temperature gradient from the GCMs, with colder values in western Europe and warmer in eastern Europe (Fig. 9, 10 & 12). This gradient may be slightly amplified by the lack of spatial data in some regions. In the present case, some errors can be explained by the absence of close fossil sites (e.g. near the Scandinavian ice sheet), or their limited number (as in British Isles). Our rodent estimations give MAT values in the eastern Europe that are warmer than those provided by GCMs for all the time intervals of the Last Glacial period. These differences could also be related to differences in faunal communities and their paleoecology. The glacial world of the LGM and Late Glacial could not be simply compared to the current interglacial biomes. The very nature of these particular environments is not comparable, due to their unique abiotic parameters like diminished the solar radiation and the CO₂ atmospheric concentrations, and biotic factors as the important presence of a thriving mammalian megafauna. This megafauna actively shaped European vegetation structure (Malhi et al., 2016; Pearce et al., 2023; González-Varo, in press), potentially driving the diversification of distinctive rodent communities.

4 Conclusion

Rodent associations are a regularly used proxy to reconstruct local past climate and environment contexts, as they are often found in archaeological and paleontological excavations and are highly sensitive to

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environment changes. Here, we focused our study on large spatial scales, over the western Palearctic, to access continental-scale paleoclimate reconstructions based on a total of 279 archaeological and paleontological levels. Although there are entire regions with few or no data, our data set encompasses a wide range of latitudinal gradients, providing distinct climatic contexts, which give us the opportunity to address the spatial background for changes in past climate conditions across the region.

The rodent-based climate reconstructions allow for exploring spatial changes between present day conditions and different time periods ranging from the Last Glacial Maximum (LGM) to the end of the Late Glacial (i.e., 23,000 to 11,700 years before present). Our main findings highlight that rodent-based reconstructions:

- are efficient for examining large spatiotemporal variations of past climate, enabling detailed investigations of temperature changes at continental scale, since they accurately capture the modern distribution of climatic zones in the Western Palearctic, as well as (ERA5) spatial patterns of macroclimate, notably for MAT;
- exhibit a stronger latitudinal gradient during the LGM than today, with an average MAT anomaly of -5.3 °C relative to present-day conditions and more pronounced changes in MTCO than in MTWA;
- suggest a gradual warming on average from the LGM to the Late Glacial. Nonetheless, the spatial pattern of temperature change between these two periods was highly heterogeneous across Europe, with a faster

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increase of temperature in the northwestern parts of the continent than in the southwestern and eastern regions:

- produce spatial temperature patterns that are more different than those derived from GCMs, although these divergences are generally included in the range of GCM uncertainties, which points out the relevance of using paleoclimatic approaches based on multiple proxies.

Future work in under-sampled regions such as the Balkans, North Africa or the Middle East, is expected to enhance the robustness of our conclusions. This could allow for the integration of rodent-based inferences as input or comparison data for GCMs, and to new comprehensive analyses including other additional proxies. A similar approach including other taxa such as Eulipotyphla or large mammals could also be developed to explore, in particular, other climatic variables such as precipitation or aridity. These initiatives should further improve our knowledge of past climate changes.

Acknowledgements

This research was partially financed by PID2022-138275NB-I00 projects (Ministry of Science and Innovation, Spain), S.G. was funded by the Ministry of Universities and the Next Generation European Union programme through a Margarita Salas Grant from Universidad Complutense de Madrid (CT31/21). I.M. was funded by the Alexander von Humboldt Foundation through a Humboldt Postdoctoral Fellowship.

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Supprimé: Rodent associations are a regularly used proxy to reconstruct local past climate and environment contexts, because they are often found in archaeological and paleontological excavations and are highly sensitive to environment changes. Here, we focused our study on large spatial scales, over the western Palearctic, to access continental-scale paleoclimate reconstructions and to explore spatial changes between different time periods from Last Glacial Maximum (LGM) to the end of the Late Glacial, from 23,000 to 11,700 years before present. A total of 279 archaeological and paleontological levels were used to generate past climatic interpolation maps from the LGM, Heinrich Stadial, Bølling, Allerød and Younger Dryas in the western Palearctic. Although, there are entire regions with few or no data, our data set encompasses a wide range of latitudinal gradients, providing distinct climatic contexts, which give us the opportunity to address the spatial background for changes in past climate conditions across the region.¶
Our results demonstrate that rodent associations have high potential for a detailed assessment of spatial and temporal variations of past climate conditions, offering opportunities to explore regional temperature changes at continental scale. Future work in under-sampled regions such as the Balkans, North Africa or the Middle East, is expected to enhance the resolution of our conclusions. This could allow for the integration of rodent-based inferences as input or comparison data for GCMs, and to new comprehensive analyses including other additional proxies. These initiatives should further improve our knowledge of past climate changes. ¶

925 **Data and code availability**

All the analyses of the paper were performed using the R software (R core team, 2023).

The Bioclimatic [Analysis](#) is freely available through the PalBER R scripts (available at <https://github.com/AurelienRoyer/PalBER>). All the R scripts generated for all calculations, as well as the modified functions, and data are available at [https://github.com/AurelienRoyer/Climate-spatial-](https://github.com/AurelienRoyer/Climate-spatial-Interpolations-LGM-LG)

930 [Interpolations-LGM-LG](https://github.com/AurelienRoyer/Climate-spatial-Interpolations-LGM-LG), DOI: 10.5281/zenodo.14905209, in order to be fully reproducible.

Supplement

<https://github.com/AurelienRoyer/PalBER>

<https://github.com/AurelienRoyer/Climate-spatial-Interpolations-LGM-LG>,

935 DOI: 10.5281/zenodo.14905209

Author contributions

A.R. designed the study. B.L., I.M. and M.H.F. provided the data on the modern rodent assemblages and Climatic Restriction Index of rodent species. J.C. and B.P. provided GCMs and ERA5 data. A.R. provided
940 rodent fossil data. A.R., R.L. and J.C. developed the methodology. A.R. wrote R scripts. A.R., J.C., R.L., S.B., B.L., I.M., B.P., S.M. M.H.F. participated in analyzing and writing, provided edits and comments on subsequent drafts.

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945 **Competing interests**

The contact author has declared that none of the authors has any competing interests.

Financial support

This research was partially financed by PID2022-138275NB-I00 projects (Ministry of Science and
950 Innovation, Spain), S.G. was funded by the Ministry of Universities and the Next Generation European
Union programme through a Margarita Salas Grant from Universidad Complutense de Madrid (CT31/21).
I.M. was funded by the Alexander von Humboldt Foundation through a Humboldt Postdoctoral
Fellowship. A.R was financed by the Biogéosciences laboratory resources.

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References

Aguilar, J.P., Pélissié, T., Sigé, B., and Michaux, J.: Occurrence of the stripe field mouse lineage
(*Apodemus agrarius* Pallas 1771; Rodentia; Mammalia) in the Late Pleistocene of southwestern
France. C. R. – Palevol., 7(4), 217-225, <https://doi.org/10.1016/j.crpv.2008.02.004>, 2008.
960 Albouy, B., Paquin, S., Riel-Salvatore, J., Kageyama, M., Vrac, M., and Burke, A.: Evaluating the impact
of climate change and millennial variability on the last Neanderthal populations in Europe

(Marine Isotope Stage 3). Quat. Sci. Rev., 338, 108812, <https://doi.org/10.1016/j.quascirev.2024.108812>, 2024.

Allen, R., Siebert, M.J., and Payne, A.J.: Reconstructing glacier-based climates of LGM Europe and Russia? Part 3: Comparison with GCM and pollen-based climate reconstructions. Clim. Past 4, 265-280, <https://doi.org/10.5194/cp-4-265-2008>, 2008.

Allen, J.R., Hickler, T., Singarayer, J. S., Sykes, M. T., Valdes, P. J., and Huntley, B.: Last glacial vegetation of northern Eurasia. Quat. Sci. Rev., 29(19-20), 2604-2618, <https://doi.org/10.1016/j.quascirev.2010.05.031>, 2010.

970 Álvarez-Vena, A., Álvarez-Lao, D. J., Laplana, C., Quesada, J. M., Rojo, J., Garcia-Sanchez, E., and Menendez, M.: Environmental context for the Late Pleistocene (MIS 3) transition from Neanderthals to early Modern Humans: analysis of small mammals from La Güelga Cave, Asturias, northern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol., 562, 110096, <https://doi.org/10.1016/j.palaeo.2020.110096>, 2021.

975 Arbez, L., Royer, A., Schreve, D., Laffont, R., David, S., and Montuire, S.: The missing *Myopus*: plugging the gaps in Late Pleistocene small mammal identification in western Europe with geometric morphometrics. J. Quat. Sci., 36, 224-238. <https://doi.org/10.1002/jqs.3269>, 2021.

Arbez, L., Tereza, H., Royer, A., Sophie, M., and Ivan, H.: The wood lemming and the development of taiga in Late Pleistocene Central Europe. Quat. Sci. Rev., 303, 107974. <https://doi.org/10.1016/j.quascirev.2023.107974>, 2023.

980 Argus, D.F., Peltier, W.R., Drummond, R., and Moore, A.W.: The Antarctica component of postglacial rebound model ICE-6G_C (VM5a) based upon GPS positioning, exposure age dating of ice thicknesses, and relative sea level histories. Geophys. J. Int., 198, 537-563, <https://doi.org/10.1093/gji/ggu140>, 2014.

- 985 Avery, D.M.: Late pleistocene coastal environment of the Southern Cape province of South Africa:
Micromammals from Klasies river Mouth. *J. Archaeol. Sci.*, 14(4), 405-421,
[https://doi.org/10.1016/0305-4403\(87\)90028-8](https://doi.org/10.1016/0305-4403(87)90028-8), 1987.
- Baca, M., Nadachowski, A., Lipecki, G., Mackiewicz, P., Marciszak, A., Popović, D., Socha, P. Stefaniak,
K., and Wojtal, P.: Impact of climatic changes in the Late Pleistocene on migrations and
990 extinctions of mammals in Europe: four case studies. *Geol. Q.*, 61, 2, 291-304,
<http://dx.doi.org/10.7306/gq.1319>, 2017.
- Baca, M., Popović, D., Agadzhanian, A.K., Baca, K., Conard, N.J., Fewlass, H., Filek, T., Golubiński,
M., Horáček, I., Knul, M.V., Krajcarz, M., Krokhalova, M., Lebreton, L., Lemanik, A., Maul,
L.C., Nagel, D., Noiret, P., Primault, J., Rekovets, L., Rhodes, S., Royer, A., Serdyuk, N.V.,
995 Soressi, M., Stewart, J., Strukova, T., Talamo, S., Wilczyński, J., and Nadachowski, A.: Ancient
DNA of narrow-headed vole reveal common features of the Late Pleistocene population
dynamics in cold-adapted small mammals. *Proc. R. Soc. B*, 290(1993), 20222238,
<https://doi.org/10.1098/rspb.2022.2238>, 2023a.
- Baca, M., Popović, D., Lemanik, A., Bañuls-Cardona, S., Conard, N.J., Cuenca-Bescós, G., Desclaux, E.,
1000 Fewlass, H., Garcia, J.T., Hadravova, T., Heckel, G., Horáček, I., Knul, M. V., Lebreton, L.,
López-García, J.M., Luzzi, E., Marković, Z., Mauch Lenardić, J., Murelaga, X., Petculescu, A.,
Popov, V., Putalova, T., Rhodes, S.E., Ridush, B., Royer, A., Stewart, J.R., Stojak, J., Talamo,
S., Wang, X., Wójcik, J.M., and Nadachowski, A.: Ancient DNA reveals interstadials as a driver
of common vole population dynamics during the last glacial period. *J. Biogeogr.*, 50, 183-196,
1005 <https://doi.org/10.1111/jbi.14521>, 2023b.
- Bartlein, P.J., Harrison, S.P., Brewer, S., Connor, S., Davis, B.A.S., Gajewski, K., Guiot, J., Harrison-
Prentice, T.I., Henderson, A., Peyron, O., Scholze, M., Seppä, H., Shuman, B., Sugita, S.,
Thompson, R.S., Viau, A.E., Williams, J., and Wu, H.: Pollen-based continental climate
reconstructions at 6 and 21 ka: a global synthesis. *Clim. Dyn.*, 37(3), 775-802,
1010 <https://doi.org/10.1007/s00382-010-0904-1>, 2011.

- Benjamin, J., Rovere, A., Fontana, A., Furlani, S., Vacchi, M., Inglis, R.H., Galili, E., Antonioli, F., Sivan, D., Miko, S., Mourtzas, N., Felja, I., Meredith-Williams, M., Goodman-Tchernov, B., Kolaiti, E., Anzidei, M., and Gehrels, R.: Late Quaternary sea-level changes and early human societies in the central and eastern Mediterranean Basin: An interdisciplinary review. *Quat. Int.*, 449, 29-57, <https://doi.org/10.1016/j.quaint.2017.06.025>, 2017.
- 1015 Berto, C., Boscato, P., Boschin, F., Luzi, E., and Ronchitelli, A.: Paleoenvironmental and paleoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy). *Quat. Sci. Rev.*, 168, 30-41, <https://doi.org/10.1016/j.quascirev.2017.05.004>, 2017.
- 1020 Berto, C., López-García, J.M., and Luzi, E.: Changes in the Late Pleistocene small-mammal distribution in the Italian Peninsula. *Quat. Sci. Rev.*, 225, 106019, <https://doi.org/10.1016/j.quascirev.2019.106019>, 2019a.
- 1025 Berto, C., Santaniello, F., and Grimaldi, S.: Palaeoenvironment and palaeoclimate in the western Liguria region (northwestern Italy) during the Last Glacial. The small mammal sequence of Riparo Mochi (Balzi Rossi, Ventimiglia). *C. R. – Palevol.*, 18(1), 13-23, <https://doi.org/10.1016/j.crpv.2018.04.007>, 2019b.
- Beyer, R. M., Krapp, M., and Manica, A.: High-resolution terrestrial climate, bioclimate and vegetation for the last 120,000 years. *Sci. Data*, 7(1), 236, <https://doi.org/10.1038/s41597-020-0552-1>, 2020.
- 1030 Binney, H., Edwards, M., Macias-Fauria, M., Lozhkin, A., Anderson, P., Kaplan, J.O., Andreev, A., Bezrukova, E., Blyakharchuk, T., Jankovska, V., Khazina, I., Krivonogov, S., Kremenetski, K., Nield, K., Novenko, E., Ryabogina, N., Solovieva, N., Willis, K., and Zernitskaya, V.: Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. *Quat. Sci. Rev.*, 157, 80-97, <https://doi.org/10.1016/j.quascirev.2016.11.022>, 2017.

- 1035 Björck, S., Walker, M., Cwynar, L., Johnsen, S., Knudsen, K.L., Lowe, J., and Wohlfarth, B.: An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. *J. Quat. Sci.*, 13/4, 283-292, [https://doi.org/10.1002/\(SICI\)1099-1417\(199807/08\)13:4<283::AID-JQS386>3.0.CO;2-A](https://doi.org/10.1002/(SICI)1099-1417(199807/08)13:4<283::AID-JQS386>3.0.CO;2-A), 1998.
- 1040 Brace, S., Ruddy, M., Miller, R., Schreve, D. C., Stewart, J.R., and Barnes, I.: The colonization history of British water vole (*Arvicola amphibius* (Linnaeus, 1758)): origins and development of the Celtic fringe. *Proc. R. Soc. B: Biol. Sci.*, 283(1829), 20160130, <https://doi.org/10.1098/rspb.2016.0130>, 2016.
- Braconnot, P., Harrison, S. P., Kageyama, M., Bartlein, P. J., Masson-Delmotte, V., Abe-Ouchi, A., Otto-Bliesner, B., and Zhao, Y.: Evaluation of climate models using palaeoclimatic data. *Nat. Clim. Change*, 2(6), 417-424, <https://doi.org/10.1038/nclimate1456>, 2012.
- 1045 Burke, A., Peros, M. C., Wren, C. D., Pausata, F. S., Riel-Salvatore, J., Moine, O., de Vernal, A., Kageyama, M., and Boisard, S.: The archaeology of climate change: The case for cultural diversity. *PNAS*, 118(30), e2108537118, <https://doi.org/10.1073/pnas.2108537118>, 2021.
- 1050 Calandra, I., Labonne, G., Mathieu, O., Henttonen, H., Lévêque, J., Milloux, M-J, Renvoisé, É, Montuire, S, and Navarro, N.: Isotopic partitioning by small mammals in the subnivium. *Ecol. Evol.*, 5, 4132-4140. <https://doi.org/10.1002/ece3.1653>, 2015.
- Carré, M., Braconnot, P., Elliot, M., D'agostino, R., Schurer, A., Shi, X., Marti, O., Lohmann, G., Jungclauss, J., Cheddadi, R., Abdelkader di Carlo, I., Cardich, J., Ochoa, D., Salas Gismondi, R., Pérez, A., Romero, P.E., Turcq, B., Corrège, T., and Harrison, S.P.: High-resolution marine data and transient simulations support orbital forcing of ENSO amplitude since the mid-Holocene. *Quat. Sci. Rev.*, 268, 107125, <https://doi.org/10.1016/j.quascirev.2021.107125>, 2021.
- 1055 Ceregatti, L., Berto, C., Fewlass, H., Baca, M., Luzi, E., Brancaleoni, G., Pereswiet-Soltan, A., and Peresani, M.: Integration of direct radiocarbon dating, genetic studies and taxonomy of small

Code de champ modifié

mammals to investigate the chronology of past climatic oscillations: The Last Glacial Maximum sequence of Grotta della Ferrovia (Fabriano, Italy). *Quat. Sci. Rev.*, 309, 108095, <https://doi.org/10.1016/j.quascirev.2023.108095>, 2023.

Code de champ modifié

Chaline, J.: Les rongeurs du pléistocène moyen et supérieur de France : (systématique, biostratigraphie, paléoclimatologie). Éditions du Centre national de la recherche scientifique, 403p., ISBN: 2222014883, 1972

Chaline, J., and Brochet, G.: Les Rongeurs: leurs significations paléoécologiques et paléoclimatiques in La Baume de Gigny (Jura). *Gallia Préhistoire*, suppl. 27, 97-109, www.persee.fr/doc/galip_0072-0100_1989_sup_27_1_2563, 1989.

Comas-Bru, L., Harrison, S. P., Werner, M., Rehfeld, K., Scroxton, N., Veiga-Pires, C., and SISAL Working Group Members: Evaluating model outputs using integrated global speleothem records of climate change since the last glacial. *Clim. Past*, 15(4), 1557-1579, <https://doi.org/10.5194/cp-15-1557-2019>, 2019.

Cordy, J.M.: Palaeoecology of the Late Glacial and early Postglacial of Belgium and neighbouring areas, in: *The Late Glacial in Northwest Europe: Human adaptation and environmental change at the end of the Pleistocene*, edited by: Barto, N., Roberts, A.J., and Roe, D.A., Council for British Archaeology, 40–47, 1991.

Courtiol, A., and Rousset, F.: Modelling isoscapes using mixed models. *bioRxiv*, 207662. <http://dx.doi.org/10.1101/207662>, 23 october 2017.

Courtiol, A., Rousset, F., Rohwäder, M.S., Soto, D.X., Lehnert, L.S., Voigt, C.C., Hobson, K.A., Wassenaar, L.I., and Kramer-Schadt, S.: Isoscape computation and inference of spatial origins with mixed models using the R package IsoriX, in: *Tracking animal migration with stable isotopes*, Academic Press, 207-236, <https://doi.org/10.1016/B978-0-12-814723-8.00009-X>, 2019.

- Crégut-Bonnoure, E., Boulbes, N., Desclaux, E., and Marciszak, A.: New insights into the LGM and LG
1085 in Southern France (Vaucluse): the mustelids, micromammals and horses from Coulet des
Roches. *Quat.*, 1(3), 19, <https://doi.org/10.3390/quat1030019>, 2018.
- Cuenca-Bescós, G., Straus, L.G., Morales, M.R.G., and Pimienta, J.C.G.: The reconstruction of past
environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave
(Cantabria, Spain). *J. Archaeol. Sci.*, 36(4), 947-955, <https://doi.org/10.1016/j.jas.2008.09.025>,
1090 2009.
- Cuenca-Bescós, G., Rofes, J., López-García, J. M., Blain, H. A., Roger, J., Galindo-Pellicena, M. A.,
Bennázar-Serra, M. L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., and
Carbonell, E.: Biochronology of Spanish Quaternary small vertebrate faunas. *Quat. Int.*, 212(2),
109-119, <https://doi.org/10.1016/j.quaint.2009.06.007>, 2010.
- 1095 Cyrek, K., Nadachowski, A., Madeyska, T., Bochenski, Z., Tomek, T., Wojtal, P., Miekina, B., Lipecki,
G., Garapich, A., Rzebik-Kowalska, B., Stworzewicz, E., Wolsan, M., Godawa, J., Kosciów, R.,
Fostowicz-Frelik, L., and Szyndlar, Z.: Excavation in the Deszczowa Cave (Kroczyckie Rocks,
Czestochowa Upland, Central Poland). *Folia Quaternaria*, 71, 5-84, 2000.
- Daams, R., and van der Meulen, A.J.: Paleoenvironmental and paleoclimatic interpretation of
1100 micromammal faunal successions in the Upper Oligocene and Miocene of North Central Spain.
Paleobiol. Cont., 14, 241-257, 1984.
- Daams, R., Freudenthal, M., and van der Meulen, A.J.: Ecostratigraphy of micromammal faunas from the
Neogene of Spain. *Scr. Geol., Special Issue*, 1, 287-302, 1988.
- Danukalova, G., and Yakovlev, A.: A review of biostratigraphical investigations of palaeolithic localities
1105 in the Southern Urals region. *Quat. Int.*, 149(1), 37-43,
<https://doi.org/10.1016/j.quaint.2005.11.016>, 2006.

- Davis, B.A.S., Fasel, M., Kaplan, J. O., Russo, E., and Burke, A.: The climate and vegetation of Europe, North Africa and the Middle East during the Last Glacial Maximum (21,000 years BP) based on pollen data. *Clim. Past Discuss.*, 2022, 1-66, <https://doi.org/10.5194/cp-20-1939-2024>, 2022.
- 1110 Dee, D.P., Uppala, S.M., Simmons, A.J., Berrisford, P., Poli, P., Kobayashi, S., Andrae, U., Balmaseda, M.A., Balsamo, G., Bauer, P., Bechtold, P., Beljaars, A.C.M., van de Berg, L., Bidlot, J., Bormann, N. , Delsol, C., Dragani, R., Fuentes, M., Geer, A.J., Haimberger, L., Healy, S.B., Hersbach, H., Hólm, E.V., Isaksen, L., Kållberg, P., Köhler, M., Matricardi, M., McNally, A.P., Monge-Sanz, B.M., Morcrette, J.-J., Park, B.-K., Peubey, C., de Rosnay, P. , Tavolato, C., 1115 Thépaut, J.-N., and Vitart, F.: The ERA-Interim reanalysis: Configuration and performance of the data assimilation system. *Q. J. Roy.*, 137(656), 553-597, <https://doi.org/10.1002/qj.828>, 2011.
- Discamps, E., Thomas, M., Dancette, C., Gravina, B., Plutniak, S., Royer, A., Angelin, A., Bachellerie, F., Beauval, C., Bordes, J.-G., Deschamps, M., Ducasse, S., Langlais, M., Laroulandie, V., 1120 Mallye, J.-B., Michel, A., Perrin, T., and Rendu, W. : Breaking free from field layers: the interest of Post-Excavation Stratigraphies (PES) for producing reliable archaeological interpretations and increasing chronological resolution. *J. Paleolit. Archaeol.*, 6(1), 29, <https://doi.org/10.1007/s41982-023-00155-x>, 2023.
- Domínguez-García, Á.C., Laplana, C., Sevilla, P., Álvarez-Vena, A., and Collado Giraldo, H.: Small 1125 mammals of the Holocene sequence of Postes Cave (SW Spain): biogeographic and palaeoenvironmental implications for southwestern Iberia. *Hist. Biol.*, 35(4), 483-497, <https://doi.org/10.1080/08912963.2022.2045981>, 2023.
- Domínguez-García, Á.C., López-García, J.M., Núñez-Lahuerta, C., Galán, J., and Cuenca-Bescós, G.: 1130 Palaeoclimatic analysis of Quaternary terrestrial small mammal assemblages from the Sierra de Atapuerca (Burgos, Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 112532, <https://doi.org/10.1016/j.palaeo.2024.112532>, 2024.

- Dufresne, J.L., Foujols, M.A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H., Benshila, R., Bony, S., Braconnot, P., Brockmann, P., Cadule, P., Cheruy, F., Codron, F., Cozic, A., Cugnet, D., de Noblet, N., Duvel, J.-P., Ethé, C., Fairhead, L., Fichet, T., Flavoni, S., Friedlingstein, P., Grandpeux, J.-Y., Guez, L., Guilyardi, E., Hauglustaine, D., Hourdin, F., Idelkadi, A., Ghattas, J., Joussaume, S., Kageyama, M., Krinner, G., Labetoulle, S., Lahellec, A., Lefebvre, M.-P., Lefevre, F., Levy, C., Li, Z.X., Lloyd, J., Lott, F., Madec, G., Mancip, M., Marchand, M., Masson, S., Meurdesoif, Y., Mignot, J., Musat, I., Parouty, S., Polcher, J., Rio, C., Schulz, M., Swingedouw, D., Szopa, S., Talandier, C., Terray, P., Viovy, N., and Vuichard, N.: Climate change projections using the IPSL-CM5 Earth System Model: from CMIP3 to CMIP5. *Clim. Dyn.*, 40, 2123-2165, <https://doi.org/10.1007/s00382-012-1636-1>, 2013.
- Emile-Geay, J., Cobb, K. M., Carré, M., Braconnot, P., Leloup, J., Zhou, Y., Harrison, S.P., Corrège, T., McGregor, H.V., Collins, M., Discoll, R., Elliot, M., Schneifer, B., and Tudhope, A.: Links between tropical Pacific seasonal, interannual and orbital variability during the Holocene. *Nat. Geosc.*, 9(2), 168-173, <https://doi.org/10.1038/ngeo2608>, 2016.
- Erbajeva, M., and Alexeeva, N.: Chapter 21. Late Cenozoic Mammal Faunas of the Baikalian Region: Composition, Biochronology, Dispersal, and Correlation with Central Asia, in: *Fossil mammals of Asia: Neogene biostratigraphy and chronology*, Columbia University Press, 495-507, <https://doi.org/10.7312/wang15012-021>, 2013.
- Escudé, É., Renvoisé, É., Lhomme, V., and Montuire, S.: Why all vole molars (Arvicolinae, Rodentia) are informative to be considered as proxy for Quaternary paleoenvironmental reconstructions. *J. Archaeol. Sci.*, 40(1), 11-23, <https://doi.org/10.1016/j.jas.2012.03.003>, 2013.
- Eskelinen, O.: Diet of the wood lemming *Myopus schisticolor*. *Ann. Zool. Fenn.*, 39, 49-57, <http://www.jstor.org/stable/23735802>, 2002.

- 1160 Fagoaga, A., Blain, H.A., Marquina-Blasco, R., Laplana, C., Sillero, N., Hernández, C.M., Mallol, C.,
Galván, B., and Ruiz-Sánchez, F.J.: Improving the accuracy of small vertebrate-based
palaeoclimatic reconstructions derived from the Mutual Ecogeographic Range. A case study
using geographic information systems and UDA-ODA discrimination methodology. *Quat. Sci.*
Rev., 223, 105969, <https://doi.org/10.1016/j.quascirev.2019.105969>, 2019.
- FAUNMAP Working Group: Spatial response of mammals to Late Quaternary environmental
fluctuations. *Science*, 272, 1601-1606, <https://doi.org/10.1126/science.272.5268.1601>, 1996.
- 1165 Fernández-García, M., López-García, J.M., and Lorenzo, C. (2016). Palaeoecological implications of
rodents as proxies for the Late Pleistocene–Holocene environmental and climatic changes in
northeastern Iberia. *C. R. – Palevol*, 15(6), 707-719, <https://doi.org/10.1016/j.crpv.2015.08.005>,
2016.
- 1170 Fernández-García, M., López-García, J. M., Royer, A., Lécuyer, C., Allué, E., Burjachs, F., Chacón,
G.M., Saladié, P., Vallverdú, J., and Carbonell, E.: Combined palaeoecological methods using
small-mammal assemblages to decipher environmental context of a long-term Neanderthal
settlement in northeastern Iberia. *Quat. Sci. Rev.*, 228, 106072,
<https://doi.org/10.1016/j.quascirev.2019.106072>, 2020.
- 1175 Flynn, L.J., Morgan, M.E., Barry, J.C., Raza, S.M., Cheema, I.U., and Pilbeam, D.: Siwalik rodent
assemblages for NOW: Biostratigraphic resolution in the Neogene of South Asia, in: *Evolution
of Cenozoic Land Mammal Faunas and Ecosystems: 25 Years of the NOW Database of Fossil
Mammals*, Cham: Springer International Publishing, 43-58, [https://dx.doi.org/10.1007/978-3-
031-17491-9_4](https://dx.doi.org/10.1007/978-3-031-17491-9_4), 2023
- 1180 Furió, M., Casanovas-Vilar, I., and Van Den Hoek Ostende, L.W.: Predictable structure of Miocene
insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeogr.*
Palaeoclimatol. Palaeoecol., 304(3-4), 219-229, <https://doi.org/10.1016/j.palaeo.2010.01.039>,
2011.

- García-Alix, A., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., and Martín, J.M.: Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 265, 214–225, <https://doi.org/10.1016/j.palaeo.2008.04.005>, 2008.
- 1185 García-Ibaibarriaga, N., Suárez-Bilbao, A., Iriarte-Chiapusso, M.J., Arrizabalaga, A., and Murelaga, X.: Palaeoenvironmental dynamics in the Cantabrian Region during Greenland stadial 2 approached through pollen and micromammal records: State of the art. *Quat. Int.*, 506, 14–24, <https://doi.org/10.1016/j.quaint.2018.12.004>, 2019.
- 1190 García-Morato, S., Domínguez-García, Á. C., Sevilla, P., Laplana, C., and Fernández-Jalvo, Y. : The last 20,000 years of climate change in the Iberian Peninsula characterized by the small-mammal assemblages. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 655, 112545, <https://doi.org/10.1016/j.palaeo.2024.112545>, 2024.
- 1195 Gent, P.R., Danabasoglu, G., Donner, L.J., Holland, M.M., Hunke, E.C., Jayne, S.R, Lawrence, D.M., Neale, R.B., Rasch, P.J., Vertenstein, M., Worley, P.H., Yang, Z.-L., and Zhang, M.: The community climate system model version 4. *J. Clim.*, 24(19), 4973–4991, <https://doi.org/10.1175/2011JCLI4083.1>, 2011
- 1200 Giorgetta, M. A., Jungclaus, J., Reick, C. H., Legutke, S., Bader, J., Böttinger, M., Brovkin, V., Crueger, T., Esch, M., Fieg, K., Glushak, K., Gayler, V., Haak, H., Hollweg, H.-D., Ilyina, T., Kinne, S., Kornblueh, L., Matei, D., Mauritsen, T., Mikolajewicz, U., Mueller, W., Notz, D., Pithan, F., Raddatz, T., Rast, S., Redler, R., Roeckner, E., Schmidt, H., Schnur, R., Segschneider, J., Six, K.D., Stockhause, M., Timmreck, C., Wegner, J., Widmann, H., Wieners, K.-H., Claussen, M., Marotzke, J., and Stevens, B.: Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5. *JAMES*, 5(3), 572–597, <https://doi.org/10.1002/jame.20038>, 2013.

- 1205 González-Varo, J.P.: Avian seed dispersal out of the forests: A view through the lens of Pleistocene landscapes. *J. Ecol.*, <https://doi.org/10.1111/1365-2745.14457>, in press.
- Graham, R.W.: Quaternary Mammal Communities: Relevance of the Individualistic Response and Non-Analogue Faunas. *Pal. Soc. Papers*, 11, 141-158, <https://doi.org/10.1017/S1089332600001297>, 2005.
- 1210 Hanquet, C., Desclaux, E., and Hinguant, S.: Les rongeurs des niveaux solutréens de la grotte Rochefort (Saint-Pierre-sur-Erve, Mayenne, France): un référentiel inédit pour le dernier maximum glaciaire du nord-ouest de la France. *Quaternaire*, 27(4), 341-352, <https://doi.org/10.4000/quaternaire.7735>, 2016.
- Harzhauser, M., Daxner-Höck, G., Erbajeva, M. A., López-Guerrero, P., Maridet, O., Oliver, A., Piller, W.E., Göhlich, U., and Ziegler, R.: Oligocene and early Miocene mammal biostratigraphy of the Valley of Lakes in Mongolia. *Paleobiodivers. Paleoenviron.*, 97, 219-231, <https://doi.org/10.1007/s12549-016-0264-x>, 2017.
- 1215 Haywood, A.M., Chandler, M.A., Valdes, P.J., Salzmann, U., Lunt, D.J., and Dowsett, H.J.: Comparison of mid-Pliocene climate predictions produced by the HadAM3 and GCMAM3 General Circulation Models. *Glob. Planet. Change*, 66(3-4), 208-224, <https://doi.org/10.1016/j.gloplacha.2008.12.014>, 2009.
- 1220 Henrot, A.J., Utescher, T., Erdei, B., Dury, M., Hamon, N., Ramstein, G., Krapp, M., Herold, N., Goldner, A., E. Favre, E., Munhoven, G., and François, L.: Middle Miocene climate and vegetation models and their validation with proxy data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 467, 95-119, <https://doi.org/10.1016/j.palaeo.2016.05.026>, 2017.
- 1225 Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., De Chiara, G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes M., Geer, A., Haimberger, L.,

- 1230 Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keely, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., de Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., and Thépaut, J.N.: The ERA5 global reanalysis. *Q. J. Roy.*, 146(730), 1999-2049, <https://doi.org/10.1002/qj.3803>, 2020.
- Hernández Fernández, M.: Bioclimatic discriminant capacity of terrestrial mammal faunas. *Glob. Ecol. Biogeogr.*, 10 (2), 189-204, <https://doi.org/10.1046/j.1466-822x.2001.00218.x>, 2001.
- 1235 Hernández Fernández, M.: Rodent paleofaunas as indicators of climatic change in Europe during the last 125,000 years. *Quat. Res.*, 65(02), 308-323, <https://doi.org/10.1016/j.yqres.2005.08.022>, 2006.
- Hernández Fernández, M., and Peláez-Campomanes, P.: The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations. *Glob. Ecol. Biogeogr.*, 12 (6), 507-517, <https://doi.org/10.1046/j.1466-822X.2003.00057.x>, 2003.
- 1240 Hernández Fernández, M., and Peláez-Campomanes, P.: Quantitative palaeoclimatic inference based on terrestrial mammal faunas. *Glob. Ecol. Biogeogr.*, 39-56, <https://doi.org/10.1111/j.1466-822X.2004.00125.x>, 2005.
- Hernández Fernández, M., Álvarez Sierra, M.Á., and Peláez-Campomanes, P.: Bioclimatic analysis of rodent palaeofaunas reveals severe climatic changes in Southwestern Europe during the Plio-Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 251(3-4), 500-526, <https://doi.org/10.1016/j.palaeo.2007.04.015>, 2007.
- 1245 Hijmans, R.J., Bivand, R., Forner, K., Ooms, J., Pebesma, E., and Sumner, M.D.: Package ‘terra’. *Maintainer: Vienna, Austria*, <https://rspatial.org/>, <https://rspatial.github.io/terra/>, 2022.
- Hinton, M.A.: *Monograph of the voles and lemmings*. British Museum (Natural History), London, 1926.
- 1250 Hinz, M., Schmid, C., Knitter, D., Tietze, C.: oxcAAR: Interface to 'OxCal' Radiocarbon Calibration, <http://dx.doi.org/10.7892/boris.127058>, 2018.

Code de champ modifié

Hokr, Z.: A method of the quantitative determination of the climate in the Quaternary period by means of mammal associations. Sbornik of the geological Survey of Czechslovakia, 18, 209-219, 1951.

IUCN: The IUCN Red List of Threatened Species. Version 3, May 2017. <https://www.iucnredlist.org>.
1255 Accessed on [23 June 2021], 2021.

Izvarin, E., Ulitko, A., Panina, S., Zazovskaya, E., and Nekrasov, A.: Voronin Grotto (Middle Urals, Russia): Analysis of vertebrate assemblage with taphonomic remarks and reconstruction of the Late Bronze Age and Early Iron Age human environment in the east end of Europe based on small mammals. Quat. Int., 632, 178-191, <https://doi.org/10.1016/j.quaint.2022.02.031>, 2022.

1260 Jackson, S.T., and Overpeck, J.T.: Responses of plant populations and communities to environmental changes of the Late Quaternary. Paleobiology, 26, 194-220, <https://doi.org/10.1017/S009483730002693>, 2000.

Jeannet, M.: L'environnement tardiglaciaire préalpin: essai de restitution basée sur le potentiel climatique et écologique des microvertébrés. Revue archéologique de l'Est, 58, 5-56, 2009.

1265 Jeannet, M.: L'écologie quantifiée. Essai de description de l'environnement continental à l'aide des microvertébrés. Préhistoires méditerranéennes, (1). <https://doi.org/10.4000/pm.492>, 2010

Jeannet, M.: Vergisson II (Saône-et-Loire, France): microfaune et environnement de l'Homme de Néandertal. Quaternaire, 29(3), 233-242, <https://doi.org/10.4000/quaternaire.10270>, 2018.

1270 Jovanović, M., Bogićević, K., Nenadić, D., Agustí, J., Sánchez-Bandera, C., López-García, J.M., and Blain, H.A.: New paleoecological perspectives on Late Pleistocene Neanderthals in northern Balkans: the rodent assemblages from Smolučka cave (Serbia). Archaeol. Anthropol. Sci., 14(9), 169, <https://doi.org/10.1007/s12520-022-01624-0>, 2022.

Code de champ modifié

Code de champ modifié

- Johannsen, F., Ermida, S., Martins, J.P., Trigo, I.F., Nogueira, M., and Dutra, E.: Cold bias of ERA5 summertime daily maximum land surface temperature over Iberian Peninsula. *Remote Sens.*, 11(21), 2570, <https://doi.org/10.3390/rs11212570>, 2019.
- Jost, A., Lunt, D., Kageyama, M., Abe-Ouchi, A., Peyron, O., Valdez, P.J., and Ramstein, G.: High-resolution simulations of the last glacial maximum climate over Europe: a solution to discrepancies with continental palaeoclimatic reconstructions? *Clim. Dyn.*, 24, 577-590, <https://doi.org/10.1007/s00382-005-0009-4>, 2005.
- Kageyama, M., Peyron, O., Pinot, S., Tarasov, P., Guiot, J., Joussaume, S., and Ramstein, G.: The Last Glacial Maximum climate over Europe and western Siberia: a PMIP comparison between models and data. *Clim. Dyn.*, 17, 23-43, <https://doi.org/10.1007/s003820000095>, 2001.
- Kageyama, M., Sime, L. C., Sicard, M., Guarino, M. V., de Vernal, A., almierca-Vallet, I., Abe-Ouchi, A., Bitz, C., Braconnot, P., Brady, E.C., Cao, J., Chamberlain, M.A., Feltham, D., Guo, C., LeGrande, A.N., Lohmann, G., Meissner, K.J., Menviel, L., Morozova, P., Nisancioglu, K.H., Otto-Bliesner, B.L., Oishi, R., Ramos Buarque, S., Salas y Melia, D., Sherriff-Tadano, S., Stroeve, J., Shi, X., Sun, B., Tomas, R.A., Volodin, E., Yeung, N.K.H., Zhang, Q., Zhang, Z., Zheng, W., and Ziehn, T.: A multi-model CMIP6 study of Arctic sea ice at 127 ka: Sea ice data compilation and model differences. *Clim. Past Discuss.*, 2020, 1-33, <https://doi.org/10.5194/cp-17-37-2021>, 2020.
- Kageyama, M., Harrison, S. P., Kapsch, M.-L., Lofverstrom, M., Lora, J. M., Mikolajewicz, U., Sherriff-Tadano, S., Vadsaria, T., Abe-Ouchi, A., Bouttes, N., Chandan, D., Gregoire, L. J., Ivanovic, R. F., Izumi, K., LeGrande, A. N., Lhardy, F., Lohmann, G., Morozova, P. A., Ohgaito, R., Paul, A., Peltier, W. R., Poulsen, C. J., Quiquet, A., Roche, D. M., Shi, X., Tierney, J. E., Valdes, P. J., Volodin, E., and Zhu, J.: The PMIP4 Last Glacial Maximum experiments: preliminary results and comparison with the PMIP3 simulations. *Clim. Past.*, 17, 1065-1089, <https://doi.org/10.5194/cp-17-1065-2021>, 2021.

- Kageyama, M., and Paillard, D.: Modeling and Paleoclimatology. *Paleoclimatol.*, 319-342, https://doi.org/10.1007/978-3-030-24982-3_25, 2021.
- 1300 Kalthoff, D.C.: The small mammals from the Kettig site (Rhineland-Palatinate, Germany) within the framework of the Alleröd-age mammalian fauna of central and southern Germany. *Palaontol. Z.*, 72, 407-424, <https://doi.org/10.1007/BF02988369>, 1998.
- Kosintsev, P.A., and Bachura, O.P.: Late Pleistocene and Holocene mammal fauna of the Southern Urals. *Quat. Int.*, 284, 161-170, <https://doi.org/10.1016/j.quaint.2012.06.022>, 2013.
- 1305 Lambeck, K., Rouby, H., Purcell, A., Sun, Y., and Sambridge, M.: Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. *PNAS*, 111(43), 15296-15303, <https://doi.org/10.1073/pnas.1411762111>, 2014.
- Laplana, C., Muñoz Jiménez, A., Pueyo Morer, E.L., and Sevilla, P.: Los micromamíferos y la interpretación ambiental de los yacimientos de la Cuenca de Villarroja, in: Villarroja: yacimiento clave de la paleontología riojana, edited by Alberdi, M.T., Azanza, B., Cervantes, E., Instituto de Estudios Riojanos, Logroño, 281-296, ISBN 978-84-9960-093-2, 2016.
- 1310
- Latombe, G., Burke, A., Vrac, M., Levvasseur, G., Dumas, C., Kageyama, M., and Ramstein, G.: Comparison of spatial downscaling methods of general circulation model results to study climate variability during the Last Glacial Maximum. *Geosci. Model Dev.*, 11, 2563-2579, <https://doi.org/10.5194/gmd-11-2563-2018>, 2018.
- 1315
- Lebreton, L., and López-García, J.M.: Stage or Sub-Stage: The Contribution of Small Mammals to the Characterization of Middle Pleistocene Local Climate Variation. *Quat.*, 6(4), 54, <https://doi.org/10.3390/quat6040054>, 2023.
- Legendre, S., Montuire, S., Maridet, O., and Escarguel, G.: Rodents and climate: a new model for estimating past temperatures. *Earth Planet. Sci. Lett.*, 235(1-2), 408-420, <https://doi.org/10.1016/j.epsl.2005.04.018>, 2005.
- 1320

- 1325 Lemanik, A., Baca, M., Wertz, K., Socha, P., Popović, D., Tomek, T., Lipeccki, G., Kraszewska, A., Miękina, B., Żeromska, A., Pereswiet-Soltan, A., Szyndlar, Z., Cieśla, M., Valde-Nowak, P., Mackiewicz, P., and Nadachowski, A.: The impact of major warming at 14.7 ka on environmental changes and activity of Final Palaeolithic hunters at a local scale (Orawa-Nowy Targ Basin, Western Carpathians, Poland. *Archaeol. Anthropol. Sci.*, 12(3), 66, <https://doi.org/10.1007/s12520-020-01020-6>, 2020.
- Lenardić, J.M.: First record of *Dicrostonyx* (Rodentia, Mammalia) in the late Pleistocene? Holocene sediments of Croatia. *Geol. Croat.*, 66(3), 183-189, <https://doi.org/10.4154/GC.2013.15>, 2013.
- 1330 Lenardić, J.M., Sršen, A.O., and Radović, S.: Quaternary fauna of the Eastern Adriatic (Croatia) with the special review on the Late Pleistocene sites. *Quat. Int.*, 494, 130-151, <https://doi.org/10.1016/j.quaint.2017.11.028>, 2018.
- Leonardi, M., Hallett, E. Y., Beyer, R., Krapp, M., and Manica, A.: pastclim 1.2: an R package to easily access and use paleoclimatic reconstructions. *Ecography*, 2023(3), e06481, <https://doi.org/10.1111/ecog.06481>, 2023.
- 1335 Linchamps, P., Stoetzel, E., Robinet, F., Hanon, R., Latouche, P., and Cornette, R.: Bioclimatic inference based on mammal community using machine learning regression models: perspectives for paleoecological studies. *Front. ecol. evol.*, 11, 1178379, <https://doi.org/10.3389/fevo.2023.1178379>, 2023.
- 1340 López-García, J.M., Blain, H.A., Cuenca-Bescós, G., Ruiz-Zapata, M.B., Dorado-Valiño, M., Gil-García, M.J., Valdeolmillos, A., Ortega, A.I., Carretero, J.M., Arsuaga, J.L., Bermúdez de Castro, J.M., and Carbonell, E.: Palaeoenvironmental and palaeoclimatic reconstruction of the Latest Pleistocene of El Portalón Site, Sierra de Atapuerca, northwestern Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 292 453-464, <https://doi.org/10.1016/j.palaeo.2010.04.006>, 2010.
- 1345 López-García, J.M., Luzi, E., and Peresani, M.: Middle to Late Pleistocene environmental and climatic reconstruction of the human occurrence at Grotta Maggiore di San Bernardino (Vicenza, Italy)

through the small-mammal assemblage. *Quat. Sci. Rev.*, 168, 42-54, <https://doi.org/10.1016/j.quascirev.2017.05.005>, 2017.

López-García, J.M., Cuenca-Bescós, G., Galindo-Pellicena, M.Á., Luzi, E., Berto, C., Lebreton, L., and Desclaux, E.: Rodents as indicators of the climatic conditions during the Middle Pleistocene in the southwestern Mediterranean region: implications for the environment in which hominins lived. *J. Hum. Evol.*, 150, 102911, <https://doi.org/10.1016/j.jhevol.2020.102911>, 2021.

López-García, J. M., Blain, H. A., Goffette, Q., Cousin, C., and Folie, A.: Environmental and climatic inferences for Marine Isotope Stage 2 of southern Belgium (Meuse valley, Namur Province) based on rodent assemblages. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 636, 111976, <https://doi.org/10.1016/j.palaeo.2023.111976>, 2024.

Lundelius, E.L.: The implications of disharmonious assemblages for Pleistocene extinctions. *J. Archaeol. Sci.*, 16(4), 407-417, [https://doi.org/10.1016/0305-4403\(89\)90015-0](https://doi.org/10.1016/0305-4403(89)90015-0), 1989.

Luzi, E., Berto, C., Calattini, M., Tessaro, C., and Galiberti, A.: Non-analogue communities in the Italian Peninsula during Late Pleistocene: The case of Grotta del Sambuco. *Quat. Int.*, 632, 132-138, <https://doi.org/10.1016/j.quaint.2022.02.007>, 2022a.

Luzi, E., Blanco-Lapaz, À., Rhodes, S.E., and Conard, N.J.: Paleoclimatic and paleoenvironmental reconstructions based on the small vertebrates from the Middle Paleolithic of Hohle Fels Cave, SW Germany. *Archaeol. Anthropol. Sci.*, 14(6), 107, <https://doi.org/10.1007/s12520-022-01568-5>, 2022b.

Lyman, R.L.: Quantitative paleozoology. Cambridge University Press, ISBN: 9780511813863, 2008.

Lyman, R.L.: Paleoenvironmental reconstruction from faunal remains: ecological basics and analytical assumptions. *J. Archaeol. Res.*, 25, 315-371, <https://doi.org/10.1007/s10814-017-9102-6>, 2017.

- 1370 Lyman, R.L.: Assumptions and protocol of the taxonomic identification of faunal remains in
zooarchaeology: A North American perspective. *J. Archaeol. Method Theory*, 26(4), 1376-1438,
<https://doi.org/10.1007/s10816-019-09414-0>, 2019.
- 1375 Magyari, E. K., Gasparik, M., Major, I., Lengyel, G., Pál, I., Virág, A., Korponai, J., Haliuc, A., Szabó,
Z., and Pazonyi, P.: Mammal extinction facilitated biome shift and human population change
during the last glacial termination in East-Central Europe. *Sci. Rep.*, 12(1), 6796,
<https://doi.org/10.1038/s41598-022-10714-x>, 2022.
- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.C., and Terborgh, J.W.: Megafauna and
ecosystem function from the Pleistocene to the Anthropocene. *PNAS*, 113(4), 838-846,
<https://doi.org/10.1073/pnas.1502540113>, 2026.
- 1380 Mansino, S., Ruiz-Sánchez, F.J., Fierro, I., and Montoya, P. : Mio-Pliocene rodent assemblages from
Alcoi Forn (Alcoy Basin, Eastern Spain). Biostratigraphical and palaeoclimatical inferences.
Hist. Biol., 28(8), 1050-1065, <https://doi.org/10.1080/08912963.2015.1102238>, 2016.
- 1385 Markova, E., Malygin, V., Montuire, S., Nadachowski, A., Quéré, J.P., and Ochman, K.: Dental variation
in sibling species *Microtus arvalis* and *M. rossiaemeridionalis* (Arvicolinae, Rodentia):
between-species comparisons and geography of morphotype dental patterns. *J. Mamm. Evol.*,
17, 121-139, <https://doi.org/10.1007/s10914-009-9128-8>, 2010.
- Markova, A.K., van Kolfschoten, T., Bohncke, S.J.P., Kosintsev, P.A., Mol, J., Puzachenko, A.Y.,
Simakova, A.N., Smirnov, N.G., Verpoorte, A., and Golovachev, I.B.: Evolution of European
ecosystems during Pleistocene–Holocene transition (24–8 kyr BP). *Institute of geography of
Russian Academy of Sciences*, 279, ISBN: 9785891187955, 2019.
- 1390 Markwick, P.J.: The palaeogeographic and palaeoclimatic significance of climate proxies for data-model
comparisons, in: *Deep-Time Perspectives on Climate Change: Marrying the Signal from
Computer Models and Biological Proxies*, edited by: Williams, M., Haywood, A.M., Gregory,

F.J., Schimdt, D.N., The Micropalaeontological Society, Special Publications. The Geological Society, London, 251-312, ISBN: 9781862392403, <https://doi.org/10.1144/TMS002.13>, 2007.

Code de champ modifié

1395 Marquet, J.-C.: Paléoenvironnement et chronologie des sites du domaine Atlantique français d'âge Pléistocène moyen et supérieur d'après l'étude des rongeurs. Les Cahiers de la Claise, Supplément 2, Tours, French, 1993.

Martin, R.A., Honey, J.G., and Peláez-Campanones, P.: The Meade Basin rodent project: a progress report. *Paludicola*, 3, 1-32, 2000.

1400 Minwer-Barakat, R., Garcia-Alix, A., Suárez, E.M., Freudenthal, M., and Viseras, C.: Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix basin, southern Spain. *Lethaia*, 45(4), 594-614, <https://doi.org/10.1111/j.1502-3931.2012.00324.x>, 2012.

Monaghan, N.T.: Irish Quaternary vertebrates. *Adv. Irish Quat. Stud.*, 255-291, 1405 https://doi.org/10.2991/978-94-6239-219-9_9, 2017.

Montuire, S., and Desclaux, E: Palaeoecological analysis of mammalian faunas and environmental evolution in the South of France during the Pleistocene. *Boreas*, 26(4), 355-365, <https://doi.org/10.1111/j.1502-3885.1997.tb00861.x>, 1997.

1410 Montuire, S., and Marcolini, F.: Palaeoenvironmental significance of the mammalian faunas of Italy since the Pliocene. *J. Quat. Sci.*, 17(1), 87-96, <https://doi.org/10.1002/jqs.625>, 2002.

Montuire, S., Michaux, J., Legendre, S., and Aguilar, J.P.: Rodents and climate. 1. A model for estimating past temperatures using arvicolids (Mammalia: Rodentia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 128(1-4), 187-206, [https://doi.org/10.1016/S0031-0182\(96\)00038-7](https://doi.org/10.1016/S0031-0182(96)00038-7), 1997.

- 1415 Nadachowski, A.: *Late Quaternary rodents of Poland with special reference to morphotype dentition analysis of voles*. Państwowe Wydawnictwo Naukowe, Warszawa - Krakow, 109 p., 1982.
- Nadachowski, A., Valde-Nowak, P.: New Late Pleistocene faunal assemblages from Podhale Basin, Western Carpathians, Poland: preliminary results. *Acta Zool. Crac.*, 58(2), 181-194, <https://doi.org/10.3409/azc.58.2.181>, 2015.
- 1420 Navarro, N., Montuire, S., Laffont, R., Steimetz, E., Onofrei, C., and Royer, A.: Identifying Past Remains of Morphologically Similar Vole Species Using Molar Shapes. *Quat.*, 1, 20. <https://doi.org/10.3390/quat1030020>, 2018.
- Pearce, E.A., Mazier, F., Normand, S., Fyfe, R., Andrieu, V., Bakels, C., Balwierz, Z., Binka, K., Boreham, S., Borisova, O.K., Brostrom, A., de Beaulieu, J.-L., Gao, C., González-Sampériz, P., 1425 Granoszewski, W., Hrynówizcka, A., Kolaczek, P., Kunes, P., Magri, D., Malkiewicz, M., Mighall, T., Milner, A.M., Möller, P., Nita, M., Noryskiewics, B., Agnieszka Pidel, I., Reille, M., Robertsson, A.-M., Salonen, J.S., Schläfli, P., Schokker, J., Scussolini, P., Seiriené, V., Strahl, J., Urban, B., Winter, H., and Svenning, J.C.: Substantial light woodland and open vegetation characterized the temperate forest biome before *Homo sapiens*. *Sci. Adv.*, 9(45), 1430 eadi9135.DOI: [10.1126/sciadv.adi9135](https://doi.org/10.1126/sciadv.adi9135), 2023.
- Pelletier, M., Royer, A., Holliday, T.W., Discamps, E., Madelaine, S., and Maureille, B.: Rabbits in the grave! Consequences of bioturbation on the Neandertal “burial” at Regourdou (Montignac-sur-Vézère, Dordogne). *J. Hum. Evol.*, 110, 1-17, <https://doi.org/10.1016/j.jhevol.2017.04.001>, 2017.
- 1435 Peltier, W.R., Argus, D.F., and Drummond, R.: Space geodesy constrains ice-age terminal deglaciation: The global ICE-6G_C (VM5a) model. *J. Geophys. Res. Solid Earth*, 120, 450-487, <https://doi.org/10.1002/2014JB011176>, 2015.

- Pérez-Crespo, V.A., Rodríguez, J., Arroyo Cabrales, J., and Alva Valdivia, L.M.: Variación ambiental durante el Pleistoceno tardío y Holoceno temprano en Guilá Naquitz (Oaxaca, México). *Rev. Bras. Paleontol.*, 16(3), 487-494, <https://doi.org/10.4072/rbp.2013.3.08>, 2013.
- Perpinan Lamigueiro, O., Hijmans R., and Courtiol, A.: rasterVis. R package version 0.51.6, <https://oscarperpinan.github.io/rastervis/>, 2023.
- Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, J.L., Bottema, S., and Andrieu, V.: Climatic reconstruction in Europe for 18,000 yr BP from pollen data. *Quat. Res.*, 49(2), 183-196, <https://doi.org/10.1006/qres.1997.1961>, 1998.
- Peyron, O., Bégeot, C., Brewer, S., Heiri, O., Magny, M., Millet, L., Ruffaldi, P., Van Campo, E., and Yu, G.: Late-Glacial climatic changes in Eastern France (Lake Lautrey) from pollen, lake-levels, and chironomids. *Quat. Res.*, 64(2), 197-211, <https://doi.org/10.1016/j.yqres.2005.01.006>, 2005.
- Pineda-Munoz, S., Wang, Y., Lyons, S.K., Tóth, A.B., and McGuire, J.L.: Mammal species occupy different climates following the expansion of human impacts. *PNAS* 118(2), e1922859118, <https://doi.org/10.1073/pnas.1922859118>, 2021.
- Piñero, P., Agustí, J., Blain, H.-A., and Laplana, C.: Paleoenvironmental reconstruction of the Early Pleistocene site of Quibas (SE Spain) using a rodent assemblage reconstruction. *C. R. - Palevol.*, 15, 659-668, <https://doi.org/10.1016/j.crpv.2015.06.009>, 2016.
- Piñero, P., López-García, J. M., Blain, H. A., Carnevale, G., Furió, M., Giuntelli, P., Luzi, E., Macaluso, L., Marramà, G., Pal, S., Pavia, G., Pavia, M., Pezzetti, C., Rocca, M., Sánchez-Bandera, C., Villa, A., and Delfino, M.: Multiproxy approach to reconstruct the climate and environment of a new late Middle Pleistocene vertebrate site in northwestern Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 634, 111935, <https://doi.org/10.1016/j.palaeo.2023.111935>, 2024.
- Ponomarev, D. V., van Kolfschoten, T., and van der Plicht, J.: Late Glacial and Holocene micromammals of northeastern Europe. *Russ. J. Theriol.*, 11(2), 121-130, 2012.

- Ponomarev, D., van Kolfschoten, T., and van der Plicht, J.: Late Glacial and Holocene small mammals of the Timan Ridge (Komi Republic, Russia). *Quat. Int.*, 284, 177-183, <https://doi.org/10.1016/j.quaint.2012.04.027>, 2013.
- 1465 Ponomarev, D., van Kolfschoten, T., van der Plicht, J., and Kosintsev, P.: Lateglacial desman discovered in Sed'yu-1 (Komi Republic, Russia), a site in the far northeast of Europe. *Quat. Int.*, 378, 88-98, <https://doi.org/10.1016/j.quaint.2014.03.001>, 2015.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., and Solomon, A.M.: Special paper: a global biome model based on plant physiology and dominance, soil properties and
1470 climate. *J. Biogeogr.*, 19, 117-134, <https://doi.org/10.2307/2845499>, 1992.
- Prentice, I. C., Harrison, S. P., Jolly, D., and Guiot, J.: The climate and biomes of Europe at 6000 yr BP: comparison of model simulations and pollen-based reconstructions. *Quat. Sci. Rev.*, 17(6-7), 659-668, [https://doi.org/10.1016/S0277-3791\(98\)00016-X](https://doi.org/10.1016/S0277-3791(98)00016-X), 1998.
- Price, C.R.: Late Pleistocene and Early Holocene Small mammals in South West Britain. *BAR British series* 347, 105 p., ISBN: 10 1841714852, 2003.
1475
- Puzachenko, A.Y., and Markova, A.K.: Evolution of mammal species composition and species richness during the Late Pleistocene-Holocene transition in Europe: A general view at the regional scale. *Quat. Int.*, 530, 88-106, <https://doi.org/10.1016/j.quaint.2018.12.025>, 2019.
- Puzachenko, A.Y., and Markova, A.K.: The Scandinavian ice sheet against the Atlantic ocean: How the
1480 Scandinavian ice sheet affected European small mammal assemblage during the Greenland stadial GS-2.1. *Quat. Sci. Rev.*, 305, 108013, <https://doi.org/10.1016/j.quascirev.2023.108013>, 2023.
- Quéré, J.P., and Le Louarn, H. : *Les rongeurs de France: Faunistique et biologie*. 3e édition revue et augmentée. Editions Quae, 311 p., ISBN-13: 978-2759210336, 2011.

Code de champ modifié

1485 R Core Team: R: A Language and Environment for Statistical Computing. R Foundation for Statistical
Computing, Vienna, Austria. <https://www.R-project.org/>, 2023.

Randall, D.A.: General circulation model development: past, present, and future. Elsevier, 416 p., ISBN:
9780080507231, 2000.

Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I.,
1490 Dahl-Jensen ,D., Johnsen S.J., Fischer, H., Gkinis, V., Guillevic M., Hoek, W.Z., Lowe, J.J.,
Pedro, J.B., Popp, T., Seierstad, I.K., Steffensen, J.P., Svensson A.M., Vallelonga P., Vinther,
B.M., Walker, M.J.C., Wheatley, J.J., and Winstруп, M.: 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. Quat. Sci. Rev., 106, 14-28,
1495 <https://doi.org/10.1016/j.quascirev.2014.09.007>, 2014.

Reimer, P.J., [Austin, W.E.N.](#), Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., [Butzin, M.](#),
[Cheng, H.](#), [Edwards, R.L.](#), [Friedrich, M.](#), Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton,
T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., [Muscheler, R.](#), [Palmer, J.G.](#),
[Pearson, C.](#), [van der Plicht, J.](#), Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney,
1500 C.S.M., [Wacker, L.](#), [Adolphi, F.](#), [Büntgen, U.](#), [Capano, M.](#), [Fahrni, S.M.](#), [Fogtmann-Schulz, A.](#),
[Friedrich, R.](#), [Köhler, P.](#), [Kudsk, S.](#), [Miyake, F.](#), [Olsen, J.](#), [Reinig, F.](#), [Sakamoto, M.](#), [Sookdeo,](#)
[A.](#), and [Talamo, S.](#) ; [The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve](#)
[\(0–55 cal kBP\)](#), [Radiocarbon](#), 62(4), 725-757. doi:10.1017/RDC.2020.41

Rey-Rodríguez, I., Gamarra, B., Arnaud, J., Golovanov, S., Kandel, A.W., Gasparyan, B., Wilkinson,
1505 K.N., Adler, D.S., and Weissbrod, L.: Climatic variability in the Armenian Highlands as the
backdrop to hominin population dynamics 50–25 ka. Palaeogeogr. Palaeoclimatol. Palaeoecol.,
112285, <https://doi.org/10.1016/j.palaeo.2024.112285>, 2024.

Rofes, J., Cersoy, S., Zazzo, A., Royer, A., Nicod, P. Y., Laroulandie, V., Langlais, M., Pailler, Y.,
Leandri, C., Lebon, M., and Tresset, A.: Detecting stratigraphical issues using direct radiocarbon

- Supprimé: Beck, J.W.,
- Supprimé: Hafliðason, H.,
- Supprimé: HattZ, C.,
- Supprimé: Hoffmann, D.L.,
- Supprimé: Kaiser, K.F.,
- Supprimé: Niu, M.,
- Supprimé: Staff, R.A.,
- Supprimé: and van der Plicht, J.
- Supprimé: IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 Years cal BP
- Supprimé: Radiocarbon, 55, 1869-1887, https://doi.org/10.2458/azu_js_rc.55.16947, 2013.
- Mis en forme : Police :12 pt
- Mis en forme : Police :12 pt, Anglais (Royaume-Uni)

dating from small-mammal remains. *J. Quat. Sci.*, 35(4), 505-513, <https://doi.org/10.1002/jqs.3193>, 2020.

Rofes, J., García-Ibaibarriaga, N., Aguirre, M., Martínez-García, B., Ortega, L., Zuluaga, M.C., Bailon, S., Alonso-Olazabal, A., Castaños, J., and Murelaga, X.: Combining small-vertebrate, marine and stable-isotope data to reconstruct past environments. *Sci. Rep.*, 5, 14219, <https://doi.org/10.1038/srep14219>, 2015.

Rousset, F., Ferdy, J.B., Courtiol, A., and Eddelbuettel, D.: spaMM: mixed models, particularly spatial GLMMs. *R package version, 1(0)*, 2016.

Royer, A.: Intérêts de l'utilisation des décapages lors des fouilles archéologiques pour l'étude des restes de petits vertébrés. *PALEO*, 25, 277-286, <https://doi.org/10.4000/paleo.2819>, 2014.

Royer, A.: How complex is the evolution of small mammal communities during the Late Glacial in southwest France? *Quat. Int.*, 414, 23-33, <https://doi.org/10.1016/j.quaint.2015.12.065>, 2016.

Royer, A., Lécuyer, C., Montuire, S., Escarguel, G., Fourel, F., Mann, A., and Maureille, B.: Late Pleistocene (MIS 3–4) climate inferred from micromammal communities and $\delta^{18}\text{O}$ of rodents from Les Pradelles, France. *Quat. Res.*, 80(1), 113-124, <https://doi.org/10.1016/j.yqres.2013.03.007>, 2013.

Royer, A., Lécuyer, C., Montuire, S., Primault, J., Fourel, F., and Jeannet, M.: Summer air temperature, reconstructions from the last glacial stage based on rodents from the site Taillis-des-Coteaux (Vienne), Western France. *Quat. Res.*, 82(2), 420-429, <https://doi.org/10.1016/j.yqres.2014.06.006>, 2014.

Royer, A., Montuire, S., Legendre, S., Discamps, E., Jeannet, M., and Lécuyer, C.: Investigating the influence of climate changes on rodent communities at a regional-scale (MIS 1-3, Southwestern France). *PloS one*, 11(1), e0145600, <https://doi.org/10.1371/journal.pone.0145600>, 2016.

- 1545 Royer, A., Sécher, A., and Langlais, M.: A Brief Note on the Presence of the Common Hamster during
the Late Glacial Period in Southwestern France. *Quat.*, 1(1), 8,
<https://doi.org/10.3390/quat1010008>, 2018.
- Royer, A., Garcia Yelo, B.A., Laffont, R., and Hernandez Fernandez, M.: New bioclimatic models for
the Quaternary Palaeartic based on insectivore and rodent communities. *Palaeogeogr.*
1550 *Palaeoclimatol. Palaeoecol.*, 560, 110040, <https://doi.org/10.1016/j.palaeo.2020.110040>, 2020.
- Royer A., Laroulandie V. Bailon S., Boudadi-Maligne M., Costamagno S., Danger M., Mallye J.B., and
Rofes J.: Chapitre 3. Des restes de faune aux paléoenvironnements de Peyrazet, in : La Grotte-
abri de Peyrazet (Creysse, Lot, France) au Magdalénien : Originalité fonctionnelle d'un habitat
des derniers chasseurs de rennes du Quercy, edited by Langlais M., and V. Laroulandie, cnrs,
1555 *Supplément à Gallia Préhistoire* 43, 35-48, ISBN : 978-2-271-13647-3, 2021.
- Salzmann, U., Haywood, A.M., Lunt, D.J., Valdes, P.J., and Hill, D.J.: A new global biome reconstruction
and data-model comparison for the Middle Pliocene. *Glob. Ecol. Biogeogr.*, 17(3), 432-447,
<https://doi.org/10.1111/j.1466-8238.2008.00381.x>, 2008.
- Schürch, B., Wong, G. L., Luzi, E., and Conard, N.J.: Evidence for an earlier Magdalenian presence in
1560 the Lone Valley of southwest Germany. *J. Archaeol. Sci. Rep.*, 57, 104632,
<https://doi.org/10.1016/j.jasrep.2024.104632>, 2024.
- Sesé, C.: Interpretación paleoclimática de las faunas de micromamíferos del Mioceno, Plioceno y
Pleistoceno de la Cuenca de Guadix-Baza (Granada, España). *Estud. Geol.*, 47, 73-83,
<https://doi.org/10.3989/egeol.91471-2409>, 1991.
- 1565 Simard-Pelissier, S.: Étude paléontologique des micromammifères de la grotte du Régourdou. *Faculté des
Sciences de l'Université de Paris*, PHD thesis, 1966. 78 p., 1966.
- Sloan, L.C., Crowley, T.J., and Pollard, D.: Modeling of middle Pliocene climate with the NCAR
GENESIS general circulation model. *Mar. Micropaleontol.*, 27(1-4), 51-61,
[https://doi.org/10.1016/0377-8398\(95\)00063-1](https://doi.org/10.1016/0377-8398(95)00063-1), 1996.

Code de champ modifié

Code de champ modifié

- 1570 Socha, P.: Rodent palaeofaunas from Biśnik Cave (Kraków-Częstochowa Upland, Poland):
palaeoecological, palaeoclimatic and biostratigraphic reconstruction. *Quat. Int.*, 326, 64-81,
<https://doi.org/10.1016/j.quaint.2013.12.027>, 2014.
- Stewart, J.R., Lister, A.M., Barnes, I., and Dalén, L.: Refugia revisited: individualistic responses of
species in space and time. *Proc. Biol. Sci. B*, 277(1682), 661-671,
1575 <https://doi.org/10.1098/rspb.2009.1272>, 2010.
- Stewart, J.R., and Parfitt, S.A.: Late Quaternary environmental change at Walou Cave: evidence from a
preliminary analysis of the small mammals, in: *La Grotte Walou à Trooz (Belgique). Fouilles*
1996 à 2004, edited by : Draily, C., Pirson, S., and Toussaint, M. Département du Patrimoine et
l'Institut du Patrimoine Wallon, Namur, 38-59, ISBN-13, 978-2875220455, 2011.
- 1580 Stoetzel, E., Lalis, A., Nicolas, V., Aulagnier, S., Benazzou, T., Dauphin, Y., Abdeljalil El Hajraoui, M.,
El Hassani, A., Fahd, S., Fekhaou M., Geigle, E.-V., Lapointe, F.-J., Leblois, R., Ohler, A.,
Nespoulet, R., and Denys, C.: Quaternary terrestrial microvertebrates from mediterranean
northwestern Africa: State-of-the-art focused on recent multidisciplinary studies. *Quat. Sci.*
Rev., 224, 105966, <https://doi.org/10.1016/j.quascirev.2019.105966>, 2019.
- 1585 Stoetzel, E., Rodrigues, H. G., and Cornette, R.: Towards a better knowledge of the molar morphology
and ecology of extant and fossil grass rats (Muridae: Arvicanthis Lesson, 1842). *Quat. Res.*, 114,
1-16, <https://doi.org/10.1017/qua.2023.7>, 2023.
- Stoetzel, E., Lebreton, L., Pallier, C., Bruxelles, L., Bon, F., Lejay, M., Anderson, L., Martin, H., and
Jarry, M.: The small vertebrate assemblages from the Aurignacian deposits of the Mas d'Azil
1590 cave (Ariège, France): new data for the understanding of the MIS3 environmental changes in the
Pyrenees. *C. R. - Palevol.*, 2025 (1), 1-18. <https://doi.org/10.5852/cr-palevol2025v24a1>, 2025.
- Sueyoshi, T., Ohgaito, R., Yamamoto, A., Chikamoto, M. O., Hajima, T., Okajima, H., Yoshimori, M.,
Abe, M., O'ishi, R., Saito, F., Watanabe, S., Kawamiya, M., and Abe-Ouchi, A.: Set-up of the

PMIP3 paleoclimate experiments conducted using an Earth system model, MIROC-ESM. Geosci. Model Dev., 6(3), 819-836, <https://doi.org/10.5194/gmd-6-819-2013>, 2013.

Surov, A., Banaszek, A., Bogomolov, P., Feoktistova, N., and Monecke, S.: Dramatic global decrease in the range and reproduction rate of the European hamster *Cricetus cricetus*. Endanger. Species Res., 31, 119-145, <https://doi.org/10.3354/esr00749>, 2016.

Tarasov, P.E., Volkova, V.S., Webb III, T., Guiot, J., Andreev, A.A., Bezusko, L.G., Bykova, G.V., Dorofeyuk N.I., Kvavadze E.V., Osipova I.M., Panova N.K., and Sevastyanov, D.V.: Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. J. Biogeogr., 27(3), 609-620, <https://doi.org/10.1046/j.1365-2699.2000.00429.x>, 2000.

Taylor, K.E., Stouffer, R.J., and Meehl, G.A.: An overview of CMIP5 and the experiment design. BAMS, 93, 485-498, <https://doi.org/10.1175/BAMS-D-11-00094.1>, 2012.

Tchernov, E.: Rodent faunas and environmental changes in the Pleistocene of Israel. in: Rodents in desert environments, edited by: Prakash, I., Springer, Dordrecht, 331-362, ISBN: 978-94-010-1946-0, 1975.

Terray, L., Stoetzel, E., Ben Arous, E., Kageyama, M., Cornette, R., and Braconnot, P.: Refinement of the environmental and chronological context of the archeological site El Harhoura 2 (Rabat, Morocco) using paleoclimatic simulations. Clim. Past, 19(6), 1245-1263, <https://doi.org/10.5194/cp-19-1245-2023>, 2023.

Teterina, A.: Rodents of the North Urals in the Late Pleistocene and Holocene. Quat. Int., 201(1-2), 31-36, <https://doi.org/10.1016/j.quaint.2008.05.018>, 2009.

Tougard, C., Renvoisé, E., Petitjean, A., and Quéré, J.P.: New insight into the colonization processes of common voles: inferences from molecular and fossil evidence. PLoS One, 3(10), e3532, <https://doi.org/10.1371/journal.pone.0003532>, 2008

- van Dam, J.A.: Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: the use of small mammals as paleoprecipitation proxies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 238(1-4), 190-218, <https://doi.org/10.1016/j.palaeo.2006.03.025>, 2006.
- 1620 van de Weerd, A., and Daams, R.: Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications (I and II). *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Series B*, 81, 448-473, 1978.
- van den Hoek Ostende, L.: Insectivores (Lipotyphla, Mammalia) from the Ramblian of the Daroca-Calamocha area. *Coloquios de paleontología*, 281-310, 2003.
- 1625 van der Meulen, A.J., and Daams, R.: Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 93 (3-4), 227-253, [https://doi.org/10.1016/0031-0182\(92\)90099-Q](https://doi.org/10.1016/0031-0182(92)90099-Q), 1992.
- Varela, S., Lima-Ribeiro, M.S., and Terribile, L.C.: A short guide to the climatic variables of the last glacial maximum for biogeographers. *PloS one* 10(6), e0129037, <https://doi.org/10.1371/journal.pone.0129037>, 2015.
- 1630 Voldoire, A., Sanchez-Gomez, E., Salas y Mélia, D., Decharme, B., Cassou, C., Sénési, S., Valcke, S., Beau, I., Alias, A., Chevallier, M., Déqué, M., Deshayes, J., Douville, H., Fernandez, E., Madec, G., Maisonnave, E., Moine, M.-P., Planton, S., Saint-Martin, D., Szopa, S., Tyteca, S., Alkama, R., Belamari, S., Braune, A., Coquart, L., and Chauvin, F.: The CNRM-CM5. 1 global climate model: description and basic evaluation. *Clim. Dyn.*, 40, 2091-2121, <https://doi.org/10.1007/s00382-011-1259-y>, 2013.
- 1635 Walter, H.: *Vegetationszonen und Klima*. Eugen Ulmer, Stuttgart. ISBN-13: 978-3800124015, 1970.
- Williams, J.W., and Jackson, S.T.: Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.*, 5, 475-482, <https://doi.org/10.1890/070037>, 2007.

Code de champ modifié

- 1640 Wilson, D.E., Lacher, T.E., and Jr. Mittermeier, R.A.: The Mammals of the World-Vol. 7, Rodents II. Lynx Edicions, Barcelona, 1008 p., ISBN-13: 978-8416728046, 2017.
- Wilson, D.E., and Jr. Mittermeier, R.A.: The Mammals of the World-Vol. 8, Insectivores, Sloths and Colugos. Lynx Edicions, Barcelona, 709 p., ISBN-13: 978-8416728084, 2018.
- Wolff, J.O., and Sherman, P.W.: Rodent societies: an ecological and evolutionary perspective. University of Chicago Press, 610 p., ISBN-13: 978-0226905372, 2008.
- 1645 Wong, G.L., Starkovich, B.M., and Conard, N.J.: Human subsistence and environment during the Magdalenian at Langmahdhalde: evidence from a new rock shelter in the Lone Valley, southwest Germany. *Mitteilungen der Gesellschaft fuer Urgeschichte*, 26, 103-123, 2017.
- Wong, G.L., Drucker, D.G., Starkovich, B.M., and Conard, N.J.: Latest Pleistocene paleoenvironmental reconstructions from the Swabian Jura, southwestern Germany: evidence from stable isotope analysis and micromammal remains. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 540, 109527, <https://doi.org/10.1016/j.palaeo.2019.109527>, 2020.
- 1650 Woodman, P., McCarthy, M., and Monaghan, N.: The Irish quaternary fauna project. *Quat. Sci. Rev.*, 16(2), 129-159, [https://doi.org/10.1016/S0277-3791\(96\)00037-6](https://doi.org/10.1016/S0277-3791(96)00037-6), 1997.
- 1655 Wu, H., Guiot, J., Brewer, S., and Guo, Z.: Climatic changes in Eurasia and Africa at the last glacial maximum and mid-Holocene: reconstruction from pollen data using inverse vegetation modelling. *Clim. Dyn.*, 29(2-3), 211-229, <https://doi.org/10.1007/s00382-007-0231-3>, 2007.
- Yukimoto, S., Adachi, Y., Hosaka, M., Sakami, T., Yoshimura, H., Hirabara, M., Tanaka, T.Y., Shindo, E., Tsujino, H., Deushi, M., Mizuta, R., Yabu, S., Obata, A., Nakano, H., Koshiro, T., Ose, T., and Kitoh, A.: A new global climate model of the Meteorological Research Institute: MRI-CGCM3—Model description and basic performance—. *気象集誌. 第 2 輯* 90(0), 23-64, <https://doi.org/10.2151/jmsj.2012-A02>, 2012.
- 1660

Zheng, W., and Yu, Y.: Paleoclimate simulations of the mid-Holocene and Last Glacial Maximum by FGOALS. AAS, 30, 684-698, <https://doi.org/10.1007/s00376-012-2177-6>, 2013.