

Advancing Last Glacial Maximum paleoclimate reconstructions in Europe using pollen data: a multi-method (mega)biomization approach

**Gabriel Fénisse^{1*}, Manuel Chevalier², Odile Peyron³, David Vincent Bekaert¹,
Pierre-Henri Blard^{1,4}**

1. Centre de Recherches Pétrographiques et Géochimiques UMR 7358, 15 Rue Notre Dame des Pauvres,
54 500 Vandoeuvre-lès Nancy, France

2. Institute of Geosciences, Sect. Meteorology, Rheinische Friedrich-Wilhelms-Universität Bonn, Auf dem
Hügel, 20, 53 121 Bonn, Germany

3. Institut des Sciences de l'Evolution-Montpellier (ISEM), University of Montpellier, UMR 5554 CNRS,
EPHE, IRD, Montpellier, France

4. Laboratoire de Glaciologie, Département de Géosciences, Environnement et Société, ULB, Brussels,
Belgium

Journal: Climate of the past (CP)

*Corresponding author.

E-mail address: gabriel.fenisse@univ-lorraine.fr (Gabriel Fénisse).

Abstract

Pollen records are among the highest-resolution spatial and temporal proxies for reconstructing past vegetation dynamics, environmental changes and climate variability. Over the past decade, a large variety of methods based on different ecological or mathematical concepts has been used to reconstruct paleoclimatic conditions from pollen assemblages. However, the accuracy of these climate reconstructions strongly depends on the choice of the modern calibration dataset, the taxonomic resolution, and/or the modelling assumptions. The lack of a univocal response still limits the application of pollen-based climate reconstructions to assess key climate changes over multiple time periods especially during the Last Glacial Maximum (LGM, ~23-19 ka BP). Here, we present a multi-method approach, including the Modern Analogue Technique (MAT), the Weighted Averaging Partial Least Squares regression (WA-PLS) and the probability density function-based Climate REconstruction SoftWare (CREST), to reconstruct European climates during the LGM. The quality and performance of our climate reconstructions show strong heterogeneity when based on large calibration datasets encompassing wide climatic and vegetation gradients, making local sampling for climate reconstructions difficult. Instead of sampling the global calibration dataset, we test the effect of the latest biomization and megabiomization methods (local calibrations based on megabiomization approaches) on climate reconstructions by introducing a new biome-based approach. Unlike previous studies, we use the weighted mean of climate variables from all megabiome scores rather than only considering the dominant (i.e., highest score) megabiome. This significantly reduces some of the statistical noise of climate reconstructions, drastically minimizing threshold and non-linear effects associated with megabiome classification changes. With these methodological advancements and our multi-method comparison, we evaluate the uncertainties (RMSEP) of the paleoclimate reconstructions for the LGM in Europe. Across climate reconstruction methods (MAT, WA-PLS and CREST methods), European LGM annual temperatures from the biomization method were on average $6.4 \pm 2.0^\circ\text{C}$ (mean SD) colder than today, consistent with megabiomization results ($6.8 \pm 2.2^\circ\text{C}$ colder). Winter temperature (mean temperature of the coldest month, MTCO) results exhibit substantial spatial variability across Europe. Local calibration techniques significantly reduce uncertainties in LGM MTCO reconstructions, but they remain highly sensitive to the choice of calibration datasets.

I. Introduction

Reconstructing past climates is essential for understanding the mechanisms driving glacial–interglacial variability and for evaluating the reliability of climate model simulations. Pollen assemblages preserved in marine, lacustrine and peat bog sediments constitute **quantitative** proxies for reconstructing past climatic conditions (e.g., *Chevalier et al., 2020*). Pollen-based paleoclimate reconstructions are available for many regions (e.g., Europe, Eurasia, Mediterranean areas) and for various time-periods as the Eemian (e.g., *Brewer et al., 2008; Sinopoli et al., 2018*), the Holocene (e.g., *Davis et al., 2003; Peyron et al., 2013; Salonen et al., 2019; Herzschuh et al., 2022a*) and other past key periods (e.g., Paleolithic, *Charton et al., 2025* and Marine Isotope Stage 3 (MIS3), *Zumaque et al., 2025*). While reconstructions of warm interglacial periods such as the Eemian and the Holocene generally show good agreement across different methods (*Sinopoli et al., 2018; Sassoon et al., 2025*), this consistency tends to break down for glacial periods (*Guiot et al., 1990; Brewer et al., 2008; Charton et al., 2025*). In particular, accurately reconstructing temperature and precipitation during the Last Glacial Maximum (LGM, **~23–19 thousand years ago**; *Hughes et al., 2013*) remains a persistent challenge as environmental gradients are strong and vegetation–climate relationships are complex (*Peyron et al., 1998; Bartlein et al., 2011; Davis et al., 2024*). Over the past decades, a wide range of approaches **has been used based on** pollen data to address the issue of glacial climate reconstructions. These include the Modern Analogue Technique (MAT, *Guiot et al., 1990*), transfer functions via the Weighted Averaging Partial Least Squares regression (WA-PLS, *Ter Braak and Juggins, 1993*), the Plant Functional Type method (PFTs, *Peyron et al., 1998*) and the Inverse Modelling approach (*Guiot et al., 2000; Wu et al., 2007*). The Inverse modelling and the algorithms developed by *Prentice et al., (2022)* and *Cleator et al., (2020)* take into account the CO₂ effect in the climate reconstructions: the algorithms explicitly account for the physiological effects of low atmospheric CO₂ concentrations (pCO₂ ≈ 180 ppm) on LGM vegetation. Despite these methodological advances, substantial discrepancies remain between the results derived from these reconstruction methods and those simulated by climate models (e.g., *Jost et al., 2005; Cleator et al., 2020*). Such inconsistencies highlight the complexity of reconstructing reliable glacial climates, particularly for regions such as Europe and the Mediterranean Basin (*Zumaque et al., 2025; Charton et al., 2025*). Improving the robustness and comparability of paleoclimate reconstructions for cold periods thus remains a key objective for the paleoclimate community.

Recent studies have emphasized that the choice of reconstruction method can significantly influence reconstructed climatic parameters (*Dugerdil et al., 2021, 2025; Robles et al., 2023; Charton et al., 2025*) as the methods and assumptions used are based on different ecological and mathematical/statistical concepts and algorithms (see *Chevalier et al., 2020* for a review). They assume that proxy–climate relationships remain constant over time and that pollen variations primarily reflect climate variations. Among all the methods available to reconstruct past climate changes from pollen data, the MAT and the WA-PLS are the most commonly used in paleoclimatology (e.g., *Davis et al., 2003, 2024; Birks and Seppä, 2004*;

Mauri et al., 2014, 2015; Liu et al., 2020; Herzsuh et al., 2022a). Most studies have applied these approaches individually, with only a few combining MAT and WA-PLS (*Sinopoli et al., 2021; Herzsuh et al., 2022a; Geng et al., 2025*). These studies demonstrated that reconstruction results can vary substantially between methods, mainly due to variations in modern pollen–climate calibration datasets, spatial coverage and the ecological tolerances assigned to plant taxa. They also highlighted the influence of fossil record quality and the reliability of the quantitative reconstruction methods themselves (e.g., *Brewer et al., 2008; Peyron et al., 2013; Chevalier et al., 2020; Dugerdil et al., 2021, 2025*).

To enhance the reliability of paleoclimatic reconstructions, a methodological framework combining several complementary approaches has been developed over the last decade (*Peyron et al., 2005, 2011; 2013, Brewer et al., 2008; Salonen et al., 2019*). This multi-method approach highlights that significant discrepancies can arise depending on the reconstruction method applied. The reliability of each method is influenced by the composition of the pollen assemblages, meaning that the most appropriate or robust approach may differ depending on the taxa present and the specific period being studied. These studies have nevertheless introduced important methodological advances, representing a significant improvement over single-method approaches, even though assessing the robustness of the results remains a complex task. The most robust method can be identified and validated by comparing its results with independent proxy evidence obtained from the same sediment core, such as chironomid assemblages or molecular biomarkers (*d'Oliveira et al., 2023; Robles et al., 2023; Martin et al., 2020*). The multi-method approach includes various methods as MAT, WA-PLS, and machine-learning techniques (e.g., Random Forest, Boosted Regression trees) (e.g., *Salonen et al., 2012, 2019; Dugerdil et al., 2021; Robles et al., 2022, 2023; d'Oliveira et al., 2023, 2025, Sassoon et al., 2025; Charton et al., 2025*). Applying this multi-method approach to the quantification of climatic conditions during glacial periods appears highly promising, yet such applications remain exceptionally scarce (e.g., *Brewer et al., 2008; Charton et al., 2025*).

Traditional statistical methods such as MAT and WA-PLS are based on fixed distance-based vegetation samples and linear relationships between pollen taxa and climate variables, respectively. These relationships may oversimplify ecological responses and fail to account for uncertainties in both modern calibration datasets and fossil assemblages. One promising avenue to better quantify climatic parameters from pollen data during the LGM is probabilistic approaches like the Probability Density Functions (PDFs) method (*Kühl et al., 2002, 2010; Trasune et al., 2024; Seirienné and Kisiellené, 2014*). Probabilistic approaches (e.g., *Kühl et al., 2002; Kühl and Litt, 2003; Gebhardt et al., 2008*) explicitly model these uncertainties and integrate the full probability distributions of taxa–climate relationships, thereby capturing the complete range of climate tolerances of the observed taxa. One version of the PDF-method named CREST (Climate REconstruction SoftWare, *Chevalier et al., 2014, Chevalier, 2022*) describes the conditional responses of taxa assemblages to climate variables, by combining generally unimodal distributions of reconstructed climate spaces from each taxon. The main innovations of CREST are (i) accounting for taxonomic uncertainties in pollen data, and (ii)

using presence-only data rather than presence/absence data. The multiplication of these PDFs yields a likelihood distribution, which represents the full range of climatic conditions in which a given assemblage can occur, derived from the statistical analysis of modern presence-only data (Chevalier, 2022).

Another promising opportunity to further enhance the reliability of climate reconstructions for glacial periods is to integrate biomization techniques within each reconstruction method following *Prentice et al., (1996)*. Applying such biome-based constraints has been tested with the MAT method and appears to be a particularly promising (*Guiot et al., 1993*) yet still underexplored approach (*Dugerdil et al., 2025*). Biomization techniques have been developed to convert modern and fossil pollen assemblages into specific vegetation types (i.e., biomes or megabiomes), thereby linking the ecological, physiological (metabolic processes) and physiognomic (vegetation structure) data with both current and past climatic and environmental conditions (*Prentice et al., 1996; Li et al., 2024, Dugerdil et al., 2025*). These techniques have been widely employed to reconstruct past regional vegetation patterns particularly since the LGM (e.g., *Peyron et al., 1998; Dallmeyer et al., 2019, biome 6000 project and references therein; Li et al., 2024*). While such approaches can arguably improve climate interpretations and facilitate comparisons across spatial and temporal scales, most studies have used them as a way to drastically restrict the ranges of paleoclimate reconstructions by relying only on the dominant biome (i.e., the biome with the highest score) (e.g., *Guiot et al., 1993; Tarasov et al., 1999, 2013; Davis et al., 2003, 2024*). However, transitional states, ecological gradients, and the variability of biome scores are often overlooked in these studies, potentially amplifying threshold effects and non-linearities in the reconstructions (*Dallmeyer et al., 2019*). A crucial step toward improving the accuracy of paleoclimate reconstructions is therefore to better use biome information to inform the modern calibration dataset underpinning the different reconstruction methods.

Across Europe, LGM pollen records generally reveal a high diversity of forests, steppes, and tundra (*Peyron et al., 1998; Davis et al., 2024*), although cold steppe environments were predominant (e.g., *Binney et al., 2017; Davis et al., 2024*), pointing towards more arid climatic conditions than today. However, because modern cold climates are underrepresented in Europe, climate reconstructions remain challenging. Although Europe exhibits an exceptional diversity of continental proxy records, the magnitude and spatial patterns of LGM cooling are still widely debated. This uncertainty largely arises because different proxies often yield divergent reconstructions of temperature change (e.g., *Davis et al., 2024*), and substantial disagreements persist between climate model simulations and proxy-based reconstructions (e.g., *Bartlein et al., 2011; Cleator et al., 2020; Kageyama et al., 2021*). Seasonality during the LGM is primarily documented by pollen data (*Davis et al., 2024*) but remains poorly constrained, despite its potentially uncertain impact on reconstructed LGM cooling signals. Quantifying European paleoclimates is also particularly important for better constraining the role of continental thermal amplification in climate dynamics (*Seltzer et al., 2021*) and for evaluating future climate changes using climate models (*Ramstein et al., 2007; Harrison et al.,*

2014) within the framework of the Paleoclimate Modelling Intercomparison Projects (PMIP; Joussaume et al., 1999; Braconnot et al., 2012). Although many climate reconstructions have been carried out for the LGM in Europe (Peyron et al., 1998; Jost et al., 2005; Wu et al., 2007, Guiot et al., 2000, Davis et al., 2024), they generally rely on a single reconstruction method and are based on different datasets, which can contribute to inconsistencies among the results.

In this study, we present a unique methodological framework that combines MAT, WA-PLS, and CREST to provide robust climate estimates for Europe during the LGM. Our goal is to significantly improve the accuracy of paleoclimate reconstructions by adapting biomization techniques - both the classical biomization (Prentice et al., 1996) and the megabiomization (Li et al., 2024) - to our pollen datasets. We use biomization as a constraint to select the most suitable modern pollen samples, thereby enhancing the calibration step within each reconstruction method. Using these approaches, we generate specific calibration datasets that are restricted to single biomes. We also use biomization scores that consider not only dominant biomes to achieve more robust climate reconstructions but also reconstructions based on all biome information to account for biomization uncertainties. We test our multi-method framework on two glacial time periods: (i) to reconstruct climate changes during the LGM using the well-known pollen record from Lake Bouchet (France), and (ii) to reconstruct spatial climate patterns across Europe and the Mediterranean region during the LGM.

II. Pollen Datasets

II.1 - Fossil pollen dataset

43 European fossil pollen samples spanning the LGM 19-23 ka (cal BP) were selected (Table 1). Locations of pollen records, data sources, archive types, identification number, taxonomic diversity and resolution of pollen data are summarized in Table 1. Most fossil pollen data used in this study have been recently compiled by Davis et al. (2024). Additional European fossil records that were not included in Davis et al. (2024) are reported in Table 1 and in Appendix 1. Aquatic and anthropic pollen taxa were excluded from the LGM fossil pollen assemblages. Pollen assemblages were extracted from databases, such as ACER 1.0 (Sanchez Goñi et al., 2017), PANGAEA Database (<https://www.pangaea.de/>), and Neotoma Paleoecology Database (<https://www.neotomadb.org/>; Williams et al., 2018). Raw pollen counts were used when available or digitized from the published diagrams (Table 1). Lakes are the most abundant archive, and peat bogs are second, followed by alluvial and colluvial sediments (Fig Appendix 1.a). One site sequence (Venice) contains only 7 taxa, while others include up to 70 taxa, with 80% of sequences having more than 10 taxa, reflecting differences in taxonomic resolution and geographical location (Fig Appendix 1.b). While CREST remains effective with a small number of taxa (~8–10; Chevalier, 2019) due to the use of continuous probability distributions, MAT and WA-PLS generally require ≥10 taxa to produce reliable climate reconstructions (Guiot et al., 1993; Peyron et al., 1998).

Shrub and non-arboreal taxa dominate the LGM pollen assemblages (from 40 to 80%), except for certain records like Azzano Decimo, Rio Diodis and Pian del Lago, Orgiano records

(northern Italy) for which we observe a prevalence of *Pinus* (>40%; **Fig appendix 1.c**). A table summarizing each taxon and vegetation types is available in **Appendix 1**. Most of the LGM samples are dominated by arid-adapted taxa (including Poaceae, *Artemisia* and Chenopodiaceae/Amaranthaceae). Steppic taxa such as Poaceae and *Artemisia* primarily dominate lower-latitude areas (<40°N), although, the high pollen productivity and wind transport of *Artemisia* taxa could somehow overestimate the abundance of steppic biomes (Xu et al., 2010).

In contrast to the study of Davis et al. (2024), marine pollen records were excluded here due to taxonomic, preservation, and chronological biases when compared to terrestrial records (Daniau et al., 2019; Xu et al., 2016). However, the “Les Echets” record was excluded because of incomplete dating information, such as uncalibrated radiocarbon years and/or dating uncertainties.

The Lake du Bouchet pollen sequence (Eastern France) serves as a reference to study potential methodological biases in reconstructing LGM climates. Its high temporal resolution, continuity, and taxonomic richness (56 pollen taxa) make it particularly valuable for assessing the impact of different reconstruction techniques.

From all pollen data, a harmonization table was extracted from *LegacyPollen 2.0* (Li et al., 2024; Herzschuh et al., 2022b) and processed to match the identification of pollen data between modern and fossil samples.

SiteName	Latitude (°N)	Longitude (°E)	Elevation (m)	TANN Modern (°C)	PANN Modern (mm)	MTCO Modern (°C)	MTWA Modern (°C)	Archive	Country	Source	Reference	Data Type	Number of data points included in the LGM
Lake Xinias (1)	39.05	22.27	500	15.0	690.6	3.0	23.6	Lake	Greece	EPD (E#976)	Bottema (1979)	Raw Count	26
Cova de les Malladetes (2)	39.06	-0.32	20	17.4	542.2	9.2	23.1	Cave	Spain	Publi.	Dupré Ollivier. (1988)	Digitised	1
Navarrés (3)	39.10	0.68	225	16.7	546.9	7.3	24.8	Peat Bog	Spain	EPD (E#469)	Carrión & Dupré- Olivier. (1996)	Raw Count	10
Megali Limni (4)	39.10	26.30	323	15.6	724.1	8.6	25.4	Lake	Greece	Publi.	Margari et al. (2009)	Digitised	5
Ioannina (5)	39.75	20.85	470	14.2	1100.1	1.1	21.5	Peat Bog	Greece	ACER	Tzedakis et al. (2004)	Raw Count	20
Lake Iznik (6)	40.43	29.53	88	13.4	713.0	3.7	23.0	Lake	Turkey	EPD (E#714)	Miebach et al. (2016)	Raw Count	7
Lago Grande di Monticchio (7)	40.94	15.60	1326	11.2	686.9	3.8	24.3	Lake	Italy	EPD (E#932)	Watts et al. (1996)	Raw Count	37
Mire Straldzha Kupena-3 (8)	40.98	24.31	1356	10.1	893.8	4.4	25.0	Lake	Bulgaria	EPD (E#209)	Tonkov et al. (2014)	Digitised	6
Lake Ohrid (9)	41.10	20.63	693	15.3	1019.1	0.3	24.9	Lake	Albania /North Macedonia	Publi.	Sadori et al. (2016)	Digitised	7
Torreçilla de Valmadrid (10)	41.45	-0.90	570	14.0	433.5	5.2	23.0	Colluvium	Spain	Publi.	Valero-Garces et al. (2004)	Digitised	1
Valle di Castiglione (11)	41.89	12.75	44	16.0	974.5	5.8	24.0	Lake	Italy	ACER	Follieri et al. (1989)	Raw Count	2
Lake Estanya (12)	42.03	0.53	670	12.6	711.5	2.8	23.4	Lake	Spain	Publi.	Vegas-Villarubia et al. (2013)	Digitised	3
Stracciaccappa (13)	42.13	12.32	220	14.5	850.2	5.8	23.3	Lake	Italy	ACER	Giardini. (2007)	Raw Count	2

Banyoles (14)	42.13	2.75	173	14.1	883.3	5.0	23.5	Lake	Spain	EPD (E#931)	Pérez-Obiol & Julia. (1994)	Raw Count	61
Lago di Monterosi (15)	42.22	12.43	237	15.0	1084.8	5.5	23.9	Lake	Italy	Publi.	Bonatti. (1970)	Raw Count	5
Lago Vico (16)	42.32	12.17	510	13.4	1086.2	4.6	22.7	Lake	Italy	Publi.	Magri & Sadori. (1999)	Digitised	15
Lagaccione (17)	42.57	11.85	355	14.1	867.9	4.8	22.7	Lake	Italy	ACER	Magri. (1999)	Raw Count	7
Freychinede (18)	42.78	1.43	1350	12.4	626.7	-1.6	20.3	Lake	France	Publi.	Jalut et al. (1992)	Digitised	2
Dziguta (19)	42.99	41.07	35	11.0	1302.7	2.9	22.2	Peat Bog	Georgia	Publi.	Arslanov et al. (2007)	Digitised	1
Lourdes (20)	43.03	-0.08	430	14.0	1619.2	0.9	17.1	Lake	France	Publi.	Reille & Andrieu. (1995)	Digitised	15
Tourbiere de l'Estarres (21)	43.09	-0.38	356	12.5	1078.9	3.4	17.3	Peat Bog	France	Publi.	Jalut et al. (1988)	Digitised	1
Pian del Lago (22)	44.32	9.49	833	12.9	1034.3	6.1	21.3	Lake	Italy	Publi.	Guido et al. (2020)	Digitised	6
Lake Bouchet (23)	44.92	3.78	1200	12.2	1051.4	-0.4	19.4	Lake	France	Publi.	De Beaulieu et al. (1990)	Digitised	25
Lago della Costa (24)	45.27	11.74	7	8.3	1001.7	2.3	23.4	Lake	Italy	Publi.	Paganelli. (1996)	Digitised	8
Orgiano (25)	45.29	11.43	19	12.8	945.6	2.2	23.5	Peat Bog	Italy	Publi.	Miola et al. (2006)	Digitised	1
Venice (26)	45.63	12.65	0	13.0	960.3	3.8	23.3	Peat Bog	Italy	ACER	Pini et al. (2009)	Digitised	4
Azzano Decimo (27)	45.88	12.72	10	13.5	1145.4	2.4	22.7	Alluvial Fan	Italy	ACER	de Beaulieu & Reille. (1984)	Raw Count	6
Rio Doidis (28)	46.12	13.19	152	13.3	1299.7	1.0	21.0	Lake	Italy	Publi.	Monegato et al. (2007)	Digitised	3

Lake Sfanta Anna (29)	46.13	25.89	946	12.4	1500.9	-5.3	19.7	Lake	Romania	Publi.	Magyari et al. (2014)	Digitised	5
Travesio (30)	46.20	12.87	220	11.5	751.1	-0.6	19.7	Lake	Italy	Publi.	Monegato et al. (2007)	Digitised	1
Billerio (31)	46.22	13.21	300	12.5	1662.2	-0.1	20.1	Lake	Italy	Publi.	Monegato et al. (2007)	Digitised	1
Orvenco (32)	46.25	13.17	380	12.5	1634.6	-2.0	18.4	Alluvial Fan	Italy	Publi.	Monegato et al. (2007)	Digitised	1
Fehér Lake (33)	46.45	20.65	86	13.4	1277.0	-0.5	22.7	Lake	Hungary	Publi.	Magyari et al. (2014)	Raw Count	10
Kokad (34)	47.40	21.93	112	11.3	624.0	-1.3	21.8	Peat Bog	Hungary	Publi.	Magyari et al. (2019)	Raw Count	2
La Grande Pile (35)	47.73	6.50	330	10.5	692.1	1.3	19.0	Peat Bog	France	Publi.	de Beaulieu & Reille. (1989) + de Beaulieu (1992) + de Beaulieu & Reille (1992)	Raw Count	18
Furamoos (36)	47.99	9.87	200	10.7	1141.5	-1.6	17.0	Lake	France	Publi.	Kern et al.. (2021)	Raw Count	17
Bergsee (37)	47.57	7.94	382	8.2	1118.5	-0.3	18.3	Lake	Germany	Publi.	Duprat-Oualid et al.. (2017)	Digitised	8
Pilsensee (38)	48.03	11.19	534	9.4	1306.8	-1.8	17.3	Lake	Germany	Publi.	Küster. (1995)	Digitised	1
Nagymohos (39)	48.33	20.44	297	9.6	1110.5	-3.0	19.8	Peat Bog	Hungary	Publi.	Magyari et al. (1999)	Raw Count	14
Eifel (40)	50.30	6.51	565	9.5	751.6	-0.1	18.4	Lake	Germany	Publi.	Sirocko et al. (2016)	Raw Count	17
La Grotte Walou (41)	50.59	5.54	252	10.9	922.2	1.9	17.3	Cave	Belgium	Publi.	Damblon. (2011)	Digitised	1
Kersdorf-Briesen (42)	52.33	14.27	44	9.2	657.2	-0.3	18.9	Lake	Germany	Publi.	Strahl. (2005)	Digitised	4
Mickunai (43)	54.72	25.53	143	6.3	650.0	-2.8	17.8	Lake	Lithuania	Publi.	Satkunas & Grigiene. (2012)	Digitised	2

Table 1. Reference table of fossil pollen data including (i) site locations and archives, (ii) modern annual and monthly climate data, and (iii) selected biomes and megabiomes derived from the European Centre for Medium-Range Weather Forecasts Reanalysis v5 (ERA5; from January 1940) for each site. These values are used to infer climate anomalies during the most climatically stable interval of the LGM (23–19 ka). Green and blue lines indicate modified and additional pollen sites, respectively, relative to Davis et al. (2024). See Fig. 2 for definitions of biome and megabiome acronyms.

II.2 - Age models

Age models previously based on CLAM v. 1.2 were updated using the Bayesian age-depth model Bacon (BACON routine in R, Blaauw et al., 2010). Radiocarbon ages were calibrated with the INTCAL20 calibration curve (Reimer et al., 2020). A linear accumulation/sedimentation rate was assumed over time to extend age models beyond the youngest and oldest available ^{14}C age ranges. In addition, ^{40}Ar age constraints were also included for the Füramoos fossil site. All ages are reported in calibrated years before 1950 (cal BP).

II.3 - Modern pollen and climate datasets

Calibrating with modern samples is advantageous because pollen data are highly resolved spatially, assumed to be largely free of preservation biases, and associated with directly measured climate variables. A modern dataset covering broad climatic gradients is required to provide a reliable calibration and ensure robust climate reconstructions (e.g., Birks, 1995; Juggins, 2013). The modern pollen training dataset used in this study has been compiled from the Eurasian Modern Pollen database v2 (EMPD2; <https://empd2.github.io>, <https://www.pangaea.de/>). It contains a total of 8,746 modern samples mostly across the Palearctic biogeographic realm, from Asia to Europe. The modern pollen dataset was harmonized (standardization of taxonomic labels) using the same table used for the fossil pollen data (i.e., LegacyPollen 2.0). Modern climate variables associated with these modern pollen samples were extracted through nearest-neighbor interpolation from ERA5 reanalysis (<https://rmets.onlinelibrary.wiley.com/doi/10.1002/qj.3803>), at a spatial resolution of 30 seconds (i.e., 1 km^2), with temporal averages spanning from 1940 to present (Hersbach et al., 2020). We used monthly averages of daily mean data to extract the mean annual and seasonal climates (i.e., the coldest and warmest climate states of the year). The modern climate conditions at fossil site locations, extracted from the modern dataset and represented by colored points in Appendix 2, generally show latitudinal dependency, with warmer and drier climates concentrated at lower latitudes.

III. Calibration methods

III.1 - Local calibration methods from (mega)biomes

III.1.1 - Modern calibration based on (mega)biomes

Modern datasets that cover extensive geographic regions (e.g., Europe) span a wide range of climatic conditions and are thus often challenging for reconstruction methods

designed to estimate pollen-climate relationships (i.e., WA-PLS and CREST). In Europe, this difficulty is compounded by the underrepresentation of modern cold climates, limiting their use for reconstructing past cold conditions. The presence of such heterogeneity can reduce the ability of these methods to accurately match fossil samples with modern analogues. Without proper pre-processing of modern analogues, the performance, reliability, and robustness of reconstruction methods are compromised, potentially leading to less precise climate estimates (Cao et al., 2022).

Biomes are large-scale ecological units characterized by dominant vegetation types and the climatic and environmental conditions that support them (e.g., Prentice et al., 1992, 1996). They capture broad vegetation patterns and climate-vegetation relationships over space and time, facilitating comparisons across regions and temporal scales. Biomization processes prepare the data by classifying the pollen assemblages into PFTs and biomes, which are then used in reconstruction methods. Guiot et al. (1993) suggested using the biomization approach of Prentice et al. (1992) to better distinguish between steppe and tundra environments, thereby improving the interpretation of fossil assemblages when good modern analogues are lacking. The scarcity of suitable modern analogues strongly depends on the temporal window considered for reconstruction, particularly during climatic periods characterized by vegetation compositions substantially different from those observed today.

In this study, biome and megabiome classification methods were applied to modern and fossil (LGM) European pollen assemblages. By processing a large European modern dataset (see **section II.3**) through the biomization procedure, we minimize the risk of lacking analogues and integrate spatial heterogeneity of the modern samples to reconstruct regional vegetation patterns. The methodology for processing pollen data to extract climatic signals is illustrated in **Fig.1**.

Figure 1. Schematic representation of the methodological approach developed in the subsection III of this study. Gray vertical boxes (on the left of this figure) illustrate methodological steps performed in this study. Reconstruction methods are developed in section IV.

III.1.2 - Biomization procedure

Biomization was originally designed to reconstruct past vegetation patterns across specific regions of the world (e.g., Europe, Africa) for key periods such as the Mid-Holocene or the LGM (Prentice et al. 1996). This approach relies on a standardized methodology that uses modern and/or fossil pollen data (Prentice and Webb, 1998; Prentice et al., 1996, 2000; Peyron et al., 1998) and generally proceeds from taxa to PFTs and then from PFTs to biomes through a square-root transformation using pollen taxon abundances (Prentice et al., 1996; Prentice and Webb, 1998). Here, the taxa list defines PFTs following the European biomization scheme from Peyron et al. (1998) and Tarasov et al. (2000). A pollen abundance threshold of 0.5% (Prentice et al., 1996) - 0.2% for *Corylus* - is subtracted from the initial pollen taxon abundances to account for pollen transport effects (Prentice et al., 1998). Counts for *Larix* and *Pinus* were multiplied by factors of 15 and 0.5, respectively, to account for their specific levels of production (i.e., underproduction and low preservation) and pollen overproduction, respectively (Bigelow et al., 2003; Binney et al., 2017).

We assigned 98 pollen taxa to 25 PFTs (Supp Mat., from Prentice et al., 1996), using the sum of the square roots of the pollen abundances corrected for thresholds. This approach allows for floristic and functional heterogeneity within key biomes. Then, biome affinity scores were calculated by considering the sum of the PFT scores belonging to each biome. Intermediate biomes (Tarasov et al., 1998) were used to distinguish warm and cold conditions from steppe and desert biomes by re-assigning PFT scores based on the dominant biome. Additionally, PFTs were combined into 16 biomes following Prentice et al. (1996) and using the standardized biome assignment procedure from Harrison et al. (2010) and Dallmeyer et al. (2019). The Taxa-PFT and PFT-biome biomization tables are available in **Supplementary materials (csv file)** with the following biomes: cold deciduous forest (CLDE), taiga (TAIG), pioneer (PION), cold mixed forest (CLMX), cool conifer forest (COCO), temperate deciduous forest (TEDE), cool/warm mixed forest (COMX/WAMX), xerophytic shrubs (XERO), tundra (TUND), cool/warm steppes (COST/WAST), cold/hot desert (CODE/HODE), anthropogenic (ANTH), and aquatic (AQU) biomes.

Biomization studies have considered three main hypotheses regarding the approach to (i) selecting the pollen-PFT assignment based on vegetation and environmental distributions from specific regions (Prentice et al., 1996, 2000), (ii) prioritizing the least PFT-rich biome when affinity values for multiple biomes are identical (Harrison et al., 2010; Dallmeyer et al., 2019) and (iii) choosing dominant biomes with the highest affinity score (absolute proportion of a particular biome) across different regions (Xu et al., 2013). Generally speaking, biomization

may help mitigate the impact of non-analogue situations (i.e., when modern samples are considered too different from the fossil ones to be used for reconstructions) by reducing taxonomic complexity and grouping taxa into climatically constrained plant functional types (Prentice et al., 1996; Birks, 1998).

III.1.3 – Megabiomization procedure

Megabiomes are broad vegetation categories that group multiple biomes into larger ecological and climatic units (Dallmeyer et al., 2019). This classification, used alongside biomes in this study, relies on a more spatially extensive and global framework, yielding results that are more directly comparable to global vegetation models. Compared to the biomization procedure, only the content of the European classifications (linking taxa to PFTs and PFTs to biomes) is modified, while the methodology for calculating affinity scores remains the same. This classification aims to (i) define a small set of biomes (i.e., called megabiomes) based on shared PFTs, and (ii) cover a broader climatic range than individual biomes.

In this study, we used the megabiome classifications from Dallmeyer et al. (2019) and Cao and Tian, (2021). The main aim of the PFTs–megabiome assignment is to track key signals of land-cover changes (e.g., wetland extent, conifer dominance) while minimizing the influence of the chosen biome classification (Prentice et al., 1998). Megabiome assignments are primarily used in some vegetation models (e.g., BIOME4, Kaplan, 2003), particularly when coupled with climate model simulations (as GCMs, Haywood et al., 2009). Affinity scores from pollen taxa were only calculated for pollen taxa percentages greater than 0.5% in order to increase signal-over-noise ratios (e.g., Chen et al., 2010), following the same scheme as that of the previously described biomization approach (see **section III.1.2**). For particular species, such as *Larix* and *Pinus*, we applied the same pollen production and transport corrections as described above for the biomization.

For Europe, 242 pollen taxa were grouped into PFTs and further assigned to 6 megabiomes (Dallmeyer et al., 2019): *temperate forest (TEFO)*, *boreal forest (BOFO)*, *warm-temperate forest (BOFO)*, *tundra and polar desert (TUND)*, *grassland and dry shrubland (STEP)*, and *desert (DESE)*. We directly used the algorithm implemented in R (Cao and Tian, 2021; R version 4.2.3, <https://www.r-project.org/>). When affinity scores were found equal, the megabiome with the fewest PFTs was selected. The correspondence of biome and megabiome tables are reported in **Appendix 3** for typical taxa in **Appendix 4**. **Table 2** summarizes pollen taxa to biome and megabiome assignment schemes used in this study.

	Taxa	PFTs	Abundance	Ref.
Biome	98	25	16	<i>Prentice et al., 1998</i>
Megabiome	242	41	7	<i>Binney et al., 2017</i> <i>Marinova et al., 2019</i> <i>Cao et al., 2019</i>

Table 2. Summary table of pollen taxa, plant functional types (PFTs), and (mega)biomes used in the biomisation frameworks, also provided in Supplementary Material 1.

III.2 - A weighted-mean approach to assess (mega)biome scores

One of the most notable issues of the (mega)biomization approaches is the sensitivity of reconstructed climates to small variations in biome scores (*Cruz-Silva et al., 2022*). The dominant biome effect (i.e., the biome with the highest affinity score) represents a significant source of uncertainty and poses major challenges for the reliability of reconstructed climate variables. This attribution of dominant (mega)biomes ignores potentially important (mega)biome contributions that are close to the maximum score and result in abrupt paleoclimate changes that merely reflect competition between (mega)biome scores rather than any significant bioclimatic shift.

To address this issue, we reconstruct fossil climate datasets for each (mega)biome using the three reconstruction methods (**section IV**, MAT, WA-PLS, and CREST), distinguishing the modern calibration dataset (**section II.3**, EMPD2) by (mega)biome (biome-specific calibration datasets). We then calculate (mega)biome scores for each fossil sample and combine them with the climate reconstructions for each (mega)biome using a (mega)biome affinity score-weighted mean of climate variables (**Fig.1**). Finally, we evaluate the impact of using the (mega)biome affinity score-weighted mean approach of all fossil (mega)biome scores rather than relying solely on the dominant biome's climate signal. **Then, our weighting procedure assumes that biome affinity scores approximate probabilities in the statistical sense. This makes our approach conceptually closer to the probabilistic framework of Cruz-Silva et al. (2022), who combine biomisation with a dissimilarity-based method to estimate biome membership likelihoods.**

IV. Methods

IV.1 - Climate reconstruction methods

We apply three distinct approaches, grounded in different ecological and modelling assumptions, to the same modern and fossil datasets, to identify and discuss the methodological biases specific to each reconstruction method.

IV.1.1 - Assemblages approach: Modern Analogue Technique (MAT)

The Modern Analogue Technique (MAT; *Overpeck et al., 1985; Guiot, 1990*) is widely used to reconstruct past climate variations over time scales ranging from the last million years to the Holocene, and has been applied in particular to glacial periods (*Guiot et al., 1993; Davis et al., 2024; Zumaque et al., 2025; Charton et al., 2025*). It measures the dissimilarity between a fossil pollen assemblage and a set of modern assemblages from the modern dataset (*Guiot et al., 1989, 1990*). Climate reconstructions are performed by estimating a dissimilarity coefficient (hereafter SQChord, for “Squared chord distance”, (*Overpeck et al., 1985*) based on the closest modern analogues, using an optimal number of analogues “k” that minimizes the RMSEP (i.e., Root Mean Squared Error of Prediction, *Juggins, 2020*). This parameter “k” is specific to each climatic variable and fossil sequence (“k” ranges from 8 to 10). Generally speaking, the MAT method appears to perform better with pollen taxa that are diverse and poorly resolved taxonomically like family (*Birks, 1995, Williams and Shuman, 2009, Viau and Gajewski, 2009*). We used the *rioja* package in R (Analysis of Quaternary Science data, version 1.0-6, R Core Team, <https://cran.r-project.org/web/packages/rioja/index.html>; *Juggins, 2020*) to perform MAT reconstructions. Climate reconstruction uncertainties were quantified using the root mean square error of prediction (RMSEP) derived from leave-one-out cross-validation.

IV.1.2 - Transfer function: Weighted Partial Least Squares method (WA-PLS)

The Weighted Averaging Partial Least Squares method (WA-PLS; *Ter Braak and Juggins, 1993*) is a transfer function based on climatic optima and tolerances of a pollen taxon defined by its spatial niches. With this method, the climatic responses of taxa are assumed to be Gaussian (*Ter Braak and Looman, 1986*). This reconstruction method assumes unimodal (Gaussian) species response. The number of components (i.e., portion of the covariance between species abundance data and environmental variables) for paleoclimate reconstructions was selected based on those that produce the lowest root mean square error (RMSEP), a high prediction linear correlation coefficient (R^2), and less biased reconstructions to minimize mean and maximum bias (*Ter Braak and Juggins, 1993*). A minimization of the number of components (npls; *Ter Braak and Juggins, 1993*) is performed to weight and integrate potential interactions between taxa, in addition to the link that connects them to the climate. The *rioja* package was also used to carry out WA-PLS reconstructions. Uncertainties for WA-PLS reconstructions were similarly assessed through RMSEP obtained via leave-one-out cross-validation.

IV.1.3 - Probability Density approach: Climate REconstruction SoftWare (CREST)

Probabilistic methods provide more accurate and flexible climate reconstructions than traditional statistical methods, with lower dependence on taxonomic resolution (*Netzel et al., 2025*). CREST describes the conditional responses of taxa assemblages to climate variables by integrating modern pollen–climate relationships (*Chevalier et al., 2014; Chevalier, 2022*). Most

often, when pollen is identified at the genus or family level, the probabilistic method combines the individual species' parametric PDFs into a single PDF representing the pollen observed in the fossil sequence. Once estimated for all taxa, the PDFs for the taxa present in a sample are multiplied together, each weighted according to its observed abundance. CREST is particularly well suited for regions where pollen data are scarce or geographically unevenly distributed (Chevalier, 2019; Chevalier et al., 2020). In detail, this method defines the conditional response of a plant species to a climate as a parametric PDF. The taxon-climate link is established by combining these PDFs, weighted by the abundance species that make up the genera and families of the observed pollen. A composite likelihood distribution is obtained by multiplying the individual PDFs, providing a complete probabilistic representation of the climatic conditions compatible with the observed assemblage - thus accounting for the full ecological range rather than only optimal conditions. This approach allows CREST to quantify uncertainty explicitly, offering a robust framework for evaluating reconstruction reliability and comparing it with other statistical methods (MAT or WA-PLS).

To date, CREST has proven particularly effective in regions with sparse or poorly sampled data where other techniques cannot readily be used (Chevalier et al., 2020) and has been widely applied to several tropical ecosystems such as savannas (e.g., Chevalier and Chase, 2015, 2016; Chevalier et al., 2021). CREST reconstructions were generated using the *CrestR* package (<https://github.com/mchevalier2/crestr>, Chevalier, 2022).

V. Results

Climate reconstruction uncertainties for WA-PLS and MAT are expressed as root mean square errors of prediction (RMSEP), calculated from leave-one-out cross-validation of the modern training dataset, by comparing observed and reconstructed climate values (Birks, 1995).

V.1 – (Mega)biome affinity score results

V.1.1 - Modern (mega)biome distribution maps

The modern distribution of biomes (from EMPD2 pollen dataset) across Eurasia shows that these are geographically homogeneous (Fig 2.1.a), with typical frequencies of biomes from 5% to 20% (Fig 2.1.b), except for cold deciduous forest (CLDE), desert (both cold (HODE) and hot HODE)) and supplementary biomes (pioneer (PION), anthropogenic (ANTH) and aquatic (AQU)), which are all minor (<1%) across Europe. Western Europe (e.g., France, Spain, Italy) exhibits the greatest biome diversity.

While cool conifer and cold mixed forests are primarily located in Scandinavia, cool mixed forests, taiga, and xerophytic woodlands surround the Mediterranean region. The warm mixed forest biome is dominant in southern Spain, Italy, and parts of the Near and Middle East. The clustering of different biomes in close geographic regions is attributed to broad climate patterns, altitude gradients, anthropogenic impacts (e.g., deforestation, agriculture, climate change), and/or local effects (e.g., proximity to water sources). The lack

of data in **Western Siberia** results in an underrepresentation of cold modern climate conditions.

Mean annual temperatures (TANN) are spatially variable in Europe and distinguished by (mega)biomes, reflecting ecological and climatic differences across regions (**Figs 2.1.c and 2.2.c**). TANN is generally negative in tundra regions (TUND, medians $\sim -9^{\circ}\text{C}$) and significantly higher in temperate forests (TEDE), cool mixed forests (COMX), warm mixed forests (WAMX), warm steppes (WAST), xerophytic woodlands (XERO), and hot deserts (HODE) (**Fig 2.1.b**). Other biomes, such as cold deciduous forests (CLDE), taiga (TAIG), pioneer (PION), cold mixed forests (CLMX), cool mixed forests (COMX), and cold steppes (COST), exhibit intermediate climatic conditions. The overlap of COMX and TEDE biomes in geographic and climatic spaces is likely due to their physiognomic similarities (*Binney et al., 2017*). As proposed by *Prentice et al. (1998)* and *Tarasov et al. (2000)*, using the same biomization procedure as in this study, we observe a dominance of tundra and taiga in Russia, where modern conditions are among the driest in Europe.

The modern results derived from the major megabiome analysis (**Fig 2.2.a**) indicate a strong dominance of the temperate megabiome (TEDE) ($\sim 65\%$, **Fig 2.2.b**) across Europe, covering much of Western Europe and seemingly obscuring the greater diversity of biomes observed in **Fig 2.1.a**. While mountain regions exhibit a mix of CLMX, COMX, and COST biomes, the megabiomization analysis yields a predominance of TEDE, TUND and STEP (**Fig 2.1.b**). The climate space of the temperate megabiome (TEDE, **Fig 2.2.c**) is more arid (i.e., colder and drier) than the temperate biome (TEDE, **Fig 2.1.c**). Consequently, steppe megabiomes – including boreal forest (BOFO), grassland and dry shrubland (STEP), warm desert (DESE), and tundra and polar desert (TUND) - are sparse, although they share common locations with their modern biome counterparts (**Fig 2.2.c** and Table in **Appendix 3**).

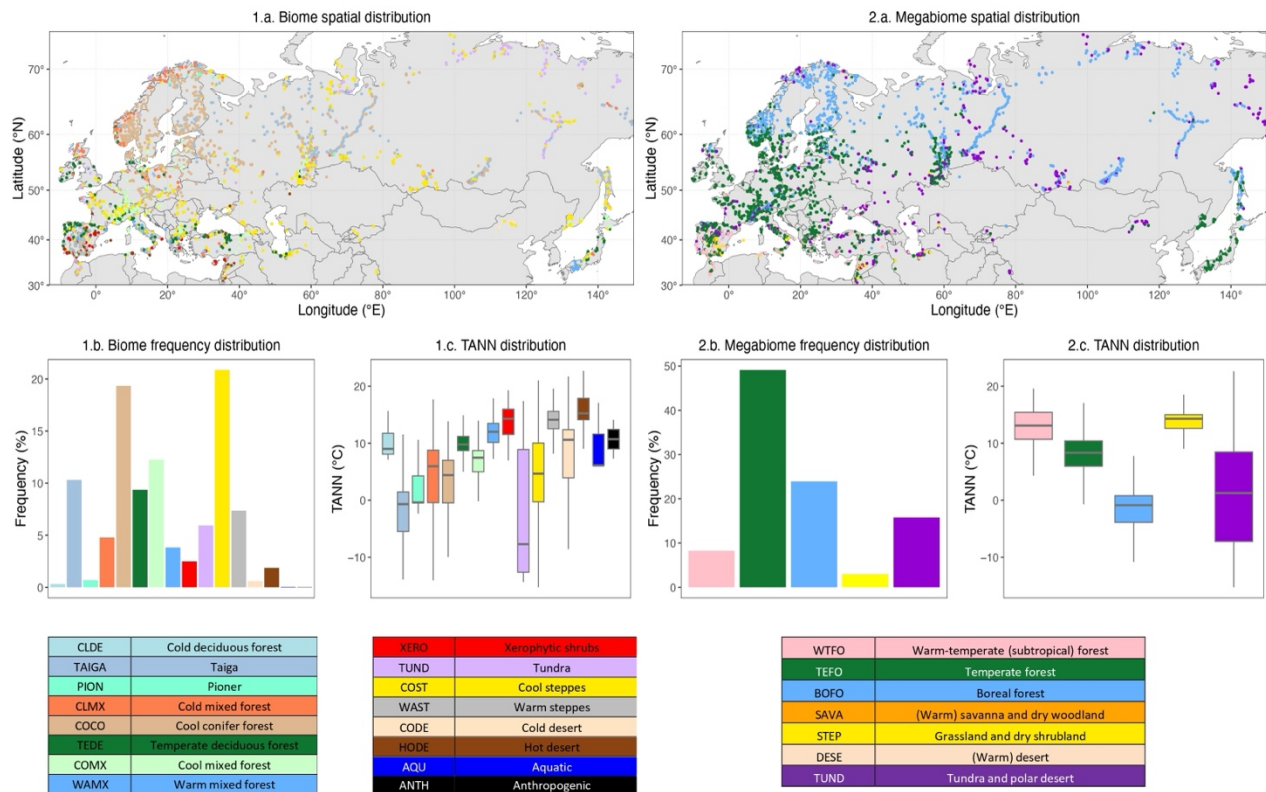


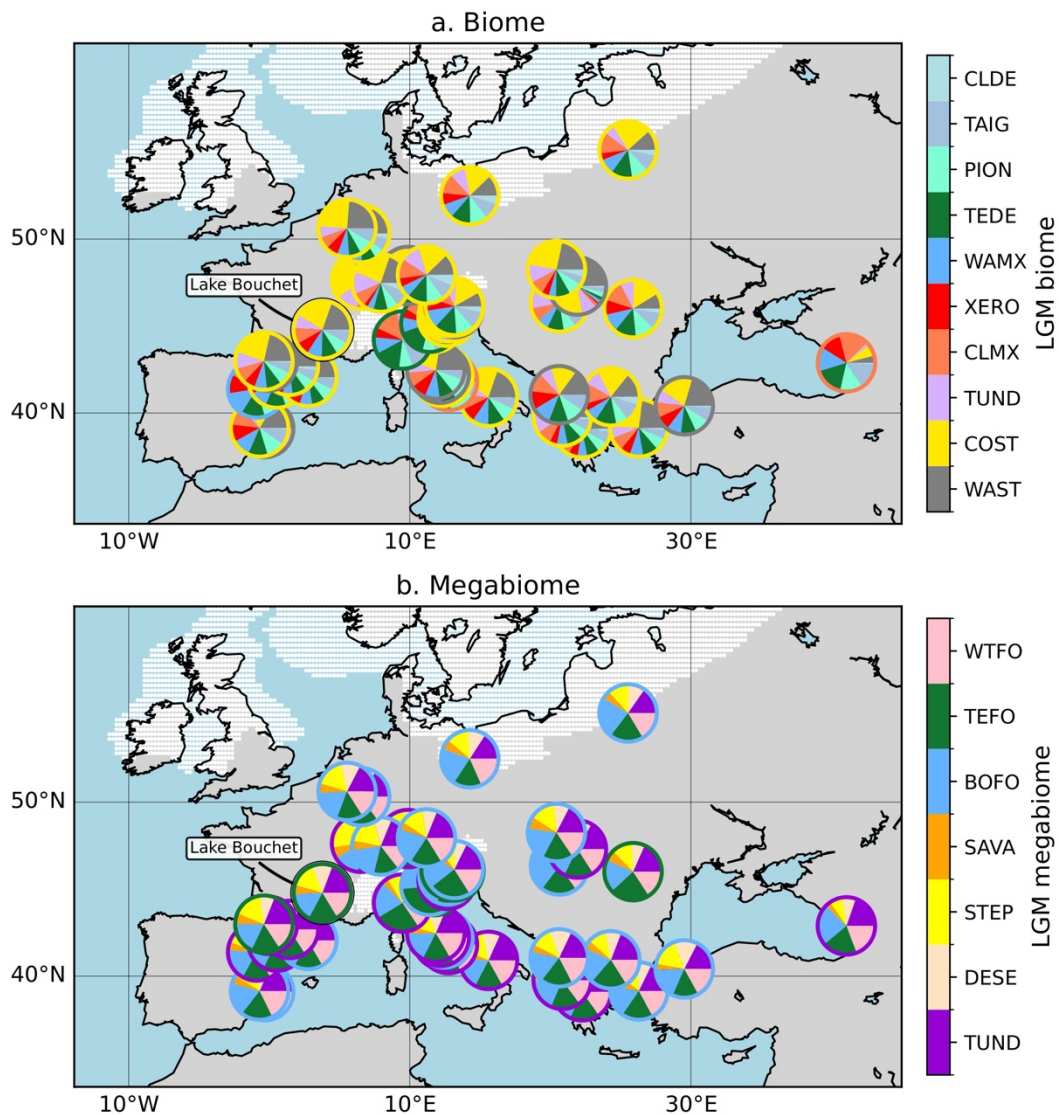
Figure 2. European biome (1) and megabiome (2) spatial and modern climate distributions, using ECMWF Reanalysis v5 (ERA5; from January 1940, <https://www.ecmwf.int/en/forecasts/dataset/ecmwf-reanalysis-v5>) and EMPD2 dataset (Eurasian Modern Pollen Database, Davis et al., 2020). The biome classification, code and output database are available in **Supplementary materials**. The megabiome schema is described and in open access in Li et al., 2024, (<https://doi.panqaea.de/10.1594/PANGAEA.965907>). TANN = Mean Annual Temperature.

V.1.2 - Fossil (mega)biomes during the LGM

LGM biome score results from the 43 selected European fossil sites reveal a clear dominance of the cool steppes, called COST (colored outlines around the pie charts from **Fig 3.a**). However, the dominant megabiome reconstructions oppose temperate (TEFO) and tundra and polar desert (TUND) megabiomes (**Fig 3.b**), with a few instances of steppic conditions around the Mediterranean region. In detail, (mega)biome scores of the LGM samples are very close to each other, indicating a strong competition and therefore only a weak dominance of any particular (mega)biome. While the mean DESE biome score remains null throughout the LGM, the combined scores of arid megabiomes (i.e., grassland and dry shrubland (STEP) + desert (DESE) + tundra and polar desert (TUND)) generally represent a proportion comparable to that of the TEDE megabiome (points with black outlines in

Appendix 5). Even when one megabiome appears dominant during the LGM, several other megabiomes also display substantial scores. These results (**Figs 3.a and 3.b**) indicate an absence of a dominant vegetation ensemble, while transitional vegetation conditions are also apparent through the co-occurrence of multiple (mega)biomes. The selection of the dominant (mega)biome is thus based on marginal differences between competing scores, which underscores the limitation of this approach when several (mega)biomes co-exist within the same climatic period. By accounting for non-dominant (mega)biomes, our (mega)biome affinity score-weighted mean method based on (mega)biome scores can better capture underlying signals and provide more nuanced climate reconstructions across Europe.

By comparing biome and megabiome dominance scores, we show that present-day steppe conditions (COST and WAST biomes) do not systematically correspond to the steppic (STEP) and tundra (TUND) megabiomes. As defined in **Appendix 3**, these results suggest that the (mega)biome classifications (based on pollen and PFTs) in the two schemes reflect distinct climatic conditions (**Fig 1**). This therefore suggests that the choice of classification could influence the reconstructed climate conditions. The search for the best analogues across different climatic spaces grouped by (mega)biome highlights the challenges of distinguishing local climatic conditions and isolating LGM vegetation analogues for climate reconstructions at the European scale.



610

611 **Figure 3.** Percentage of fossil biomes **(a)** and megabiomes **(b)** in pollen sequences during the
 612 LGM across Europe. Colored outlines around the pie charts indicate the dominant
 613 (mega)biomes. The position of the Lake Bouchet samples is outlined with a thin black circle
 614 and labeled in the figure. The white area represents the ice sheet extent (Peltier and Solheim,
 615 2004, Ehlers et al., 2011; Seguinot et al., 2018). *Geographic coordinates are displayed in*
 616 *WGS84.*

617

618 V.2 - Cross-validation of the climate reconstruction models

619

620 To assess the quality, performance and robustness of modeled climates using the three
 621 different methods, we apply a cross validation procedure from modern dominant biome
 622 datasets. Using the same calibration pipeline as for climate reconstructions, the cross-
 623 validation framework integrates (mega)biome-specific climate estimates from modern
 624 samples through a multi-biome weighting scheme, and compares the resulting values with
 observed modern climate data. By synthesizing the correlations and errors of the climatic

variables across (mega)biomes (**Table 3**), we observe that all reconstruction methods reproduce the general trends of the modern climates reasonably well, except for WA-PLS and CREST using global calibration (i.e., EMPD2 modern calibration dataset).

While MAT produces robust climatic reconstructions under the global calibration approach ($R^2 \geq 81\%$, $RMSEP \leq +3.86^\circ\text{C}$), the two other methods (WA-PLS and CREST) generally yield lower R^2 values and higher errors ($R^2 \leq 61\%$, $RMSEP \geq +4.23^\circ\text{C}$), although they show improved performance when applied within the (mega)biomisation framework. The errors from global calibrations are systematically higher than those obtained from (mega)biome calibrations. This observation suggests that calibration techniques from (mega)biomes increase the uncertainties in climate reconstructions. Error variability in the (mega)biomization procedure is larger across reconstruction methods than between the two calibration datasets (biomes). However, the quality and density of the calibration data, as well as the calibration techniques used, also influence the results and ultimately contribute to the uncertainties of the climate reconstructions.

Interestingly, the quality of the correlations of temperature reconstructions (including the three variables) are generally similar across biomes and mebiomes. WA-PLS and CREST exhibit lower or, in some cases, broadly comparable predictive performance relative to MAT, with generally reduced skill in terms of reconstruction accuracy and slightly higher associated errors depending on the climatic variable considered.

However, a clear seasonal dependency emerges: winter temperatures (MTCO) are associated with larger errors ($RMSEP \geq \pm 3.51^\circ\text{C}$ in RMSEP), particularly when using MAT and CREST. This bias suggests that these methods struggle to capture the winter climatic conditions, possibly due to limitations in the underlying calibration data or in the sensitivity of the proxies to winter conditions. In contrast, summer (MTWA) and annual mean temperatures (TANN) are more precisely reconstructed across reconstruction methods, with the small errors around the mean.

Calibration	Reconstruction method	Climate variables		
		TANN (R^2 ; RMSEP)	MTWA (R^2 ; RMSEP)	MTCO (R^2 ; RMSEP)
Global	MAT	(84%; 2.96)	(87%; 2.87)	(81%; 3.86)
	WA-PLS	(58%; 4.89)	(41%; 4.54)	(50%; 5.98)
	CREST	(52%; 4.23)	(60%; 4.68)	(61%; 5.91)
Biome	MAT	(93%; 2.41)	(88%; 2.13)	(91%; 3.61)
	WA-PLS	(85%; 2.95)	(78%; 3.06)	(84%; 3.74)
	CREST	(87%; 3.11)	(88%; 3.34)	(79%; 4.36)
Megabiome	MAT	(95%; 2.40)	(90%; 2.09)	(94%; 3.51)
	WA-PLS	(89%; 2.79)	(87%; 2.94)	(77%; 4.77)
	CREST	(82%; 3.46)	(80%; 3.01)	(84%; 4.93)

Table 3. Model performances for the reconstruction of three climate variables – TANN, MTWA and MTCO - using the Root Mean Squared Error of Prediction (RMSEP) and the squared correlation coefficient between observed and predicted values (R^2). k (optimal number) and $npls$ (optimal number of components) of modern analogues are selected to minimize prediction errors in the MAT and WA-PLS, respectively. R codes are reported in Supplementary materials.

V.3 - 40 last-year climate reconstructions from affinity score-weighted means

Mean annual temperature anomalies (i.e., $TANN_{reconstructed} - \text{Modern climate}$) over the past 40,000 years, obtained by combining the (mega)biomization and the three different reconstruction methods used in this study, are presented for the Lake Bouchet sequence in **Fig.4**. The near-zero climate anomalies observed for the present day at both sites confirm the accurate calibration of the reconstruction methods. TANN variations from both methods alternate between cold steppe (COST) and warm steppe (WAST) biomes (**Fig.3**) from 40 to 10 cal ka BP, before being mostly driven by temperate (TEDE) biomes from 10 cal ka BP until present. Using the megabiomization approach, we observe the same temperate (TEDE) dominance between 0 and 10 cal ka BP, preceded by an alternation between tundra (TUND) and steppe (STEP) megabiomes from 40 to 10 cal ka BP. As shown in **Fig.3**, the COST biome and the TUND megabiome mainly dominate at Lake Bouchet during the LGM. The dominant (mega)biome method produces larger TANN variations due to alternance between these two co-dominant arid (mega)biomes, which correspond to distinct climatic conditions (**Fig 4**).

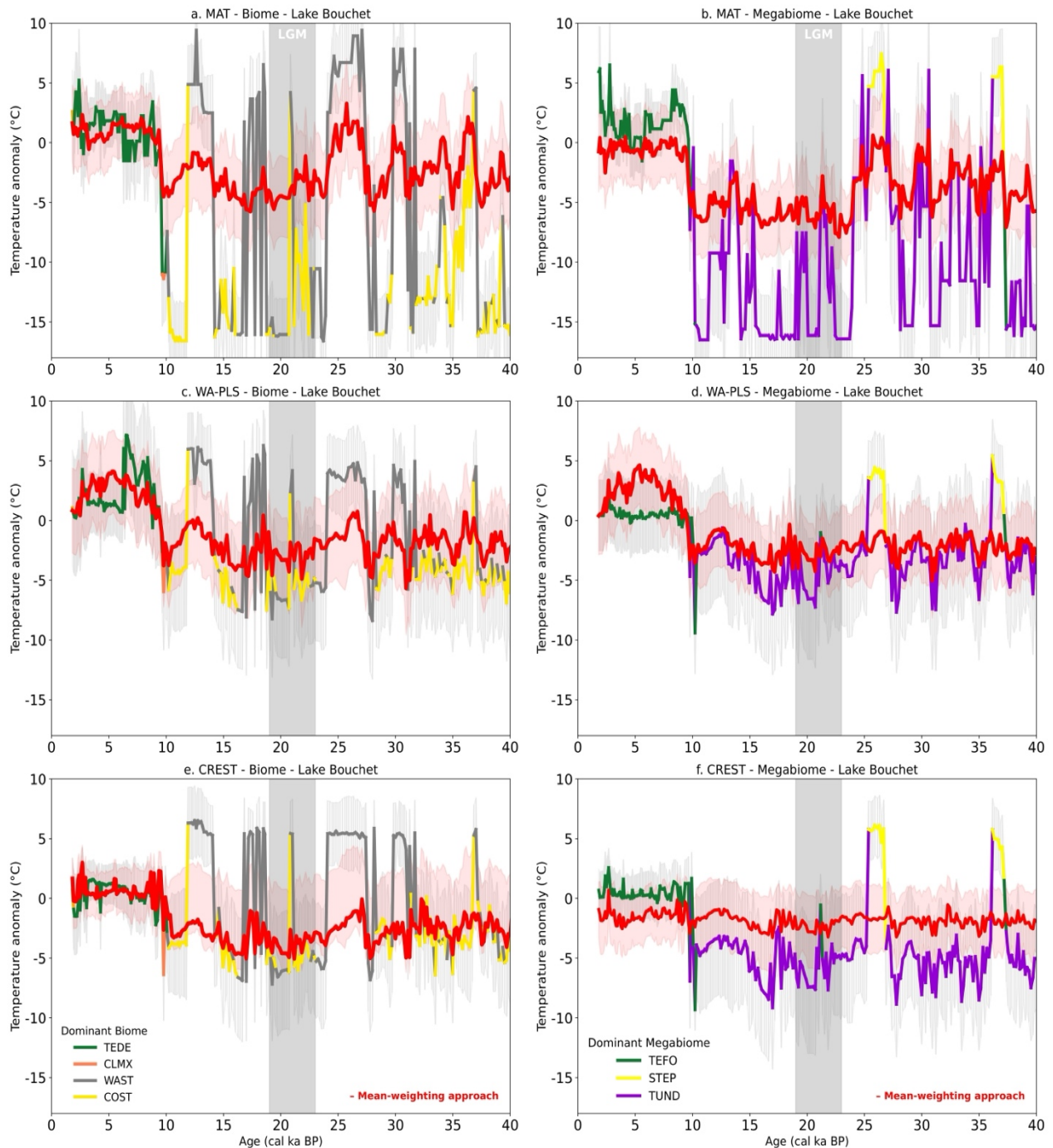
While the temporal variations in (mega)biome dominance at Lake Bouchet are comparable across reconstruction methods, the same (mega)biomes (i.e., based on identical modern and fossil sub-datasets) produce different TANN reconstructions depending on the method and calibration procedures (e.g., biomes vs. megabiomes) applied (**Fig.4**). The MAT method suggests strong instability in temperature (TANN) variations before 10 cal ka BP, as a result of alternating dominant (mega)biomes. However, TANN variations appear synchronous and of similar amplitude (from -15 to 10°C) between biome and megabiome results from MAT (**Figs 4.a and 4.b**). In contrast, TANN variations derived from the WA-PLS (**Figs 4.c and 4.d**) and CREST (**Figs 4.e and 4.f**) methods indicate more stable climatic conditions that are consistent for a given classification. Nonetheless, TANN variations from WA-PLS and CREST are generally colder with the megabiomization approach than with the biomization approach (**Figs 4.e and 4.f**). Based on temperate (mega)biomes, TANN variations obtained with WA-PLS and CREST during the deglaciation gradient (10–0 cal ka BP) show smaller extents of cooling using the biome rather than the megabiomization procedure. Annual climatic conditions reconstructed using the biome and megabiomization approaches are consistent across methods during the LGM, with temperature anomalies of $-3 \pm 4^\circ\text{C}$, $-3 \pm 3^\circ\text{C}$ and $-1 \pm 2/-4^\circ\text{C}$ obtained from the MAT, WA-PLS and CREST methods, respectively, for the biomization approach, and $-3 \pm 3^\circ\text{C}$, $-2 \pm 3^\circ\text{C}$ and $-2 \pm 1/-4^\circ\text{C}$, respectively, for the megabiomization approach.

Due to the strong climatic instability predicted by MAT based on both biome and megabiomization procedures, the (mega)biome affinity score-weighted mean approach

appears to have the greatest impact on MAT-derived reconstructions (**Figs 4.a and 4.b**). All TANN variations derived from the biome affinity score-weighted mean approach show climatic changes that are synchronous with the results from the dominant (mega)biomization approach, but with lower amplitudes. TANN variations from both the dominant and biome affinity score-weighted mean approaches exhibit LGM coolings, with amplitudes ranging from 2 to 8°C.

Most of the observed fluctuations in the modelled dominant vegetation (and therefore in the reconstructed climates) at Lake Bouchet thus arguably arise from a methodological limitation related to non-linear threshold effects, (mega)biome score competitions, and a high sensitivity of the estimation of dominant biomes to minor changes in vegetation assemblages. TANN reconstructed from biome affinity score-weighted means are less sensitive to this threshold effect as these transitions become gradual when including all the biome scores. The combination of these (mega)biome-specific climate reconstructions allows for more reliable and less noisy reconstructions, still capturing major climatic signals. This approach thus enhances the accuracy and robustness of pollen-based paleoclimate reconstructions by

711 explicitly accounting for the uncertainties of (mega)biomization algorithms, representing a
 712 significant methodological advancement.



713

714 **Figure 4.** TANN anomaly (LGM – Modern climate, LGM cooling) reconstructed over time at
 715 Lake Bouchet using three different reconstruction methods for (mega)biomization procedures.
 716 Bold curves show TANN reconstructed and their climatic errors (1σ) from the dominant
 717 (mega)biome (colored according to the dominant biome). Bold red curves report the weighted
 718 mean TANN reconstructed from (mega)biome scores. Confidence in mean-weighting is

indicated by red areas. The grey area indicates the LGM time interval. The modern climate reference is $T_{ANN} = 8.3^{\circ}\text{C}$. All climate data were processed using the current biomization assignment scheme in CREST (**Fig.2**).

V.4 – Multi-method temperature reconstructions using the (mega)biome affinity score-weighted mean approach during the LGM

V.4.1 – Annual temperature anomalies

LGM climate anomalies based on the (mega)biome affinity score-weighting approach and the three reconstruction methods are shown in **Fig.5** and summarized in **Appendix 7**. For the three different reconstruction methods, results at each core site are presented as anomalies compared to the modern climate estimated from ERA5-reanalysis (*Hersbach et al., 2020; Table 2*). From both vegetation classification methods, the LGM cooling across all fossil sites ranges from 1°C to 12°C , in line with LGM conditions significantly different from today. The mean European LGM cooling using the three reconstruction methods (MAT, WA-PLS, and CREST) yield $6.5 \pm 2.3^{\circ}\text{C}$, $7.1 \pm 2.0^{\circ}\text{C}$, and $5.8 \pm 2.4^{\circ}\text{C}$ (mean SD, 1σ) from the biomization method (**Figs 5.a, 5.c and 5.d**) and $7.0 \pm 2.2^{\circ}\text{C}$, $7.0 \pm 2.0^{\circ}\text{C}$ and $6.5 \pm 2.0^{\circ}\text{C}$ from the megabiome method (**Figs 5.b, 5.d and 5.f**), respectively. The largest LGM coolings are observed in mountain ranges, such as the Alps and the Pyrenees ($\sim 10^{\circ}\text{C}$), with an agreement across all methods (standard deviation of $\sim 1^{\circ}\text{C}$, **Appendix 8**). The Lake Bouchet (France), Kersdorf-Briesen (Germany) and Mickunai (Lithuania) fossil sites show the largest disagreement ($\sim 2^{\circ}\text{C}$ standard deviation across the three methods). We could not detect any spatial gradient, or any influence of the proximity of the Fennoscandian ice-sheet from these two sets of reconstructions (i.e., biomization and megabiome techniques, **Fig.5**).

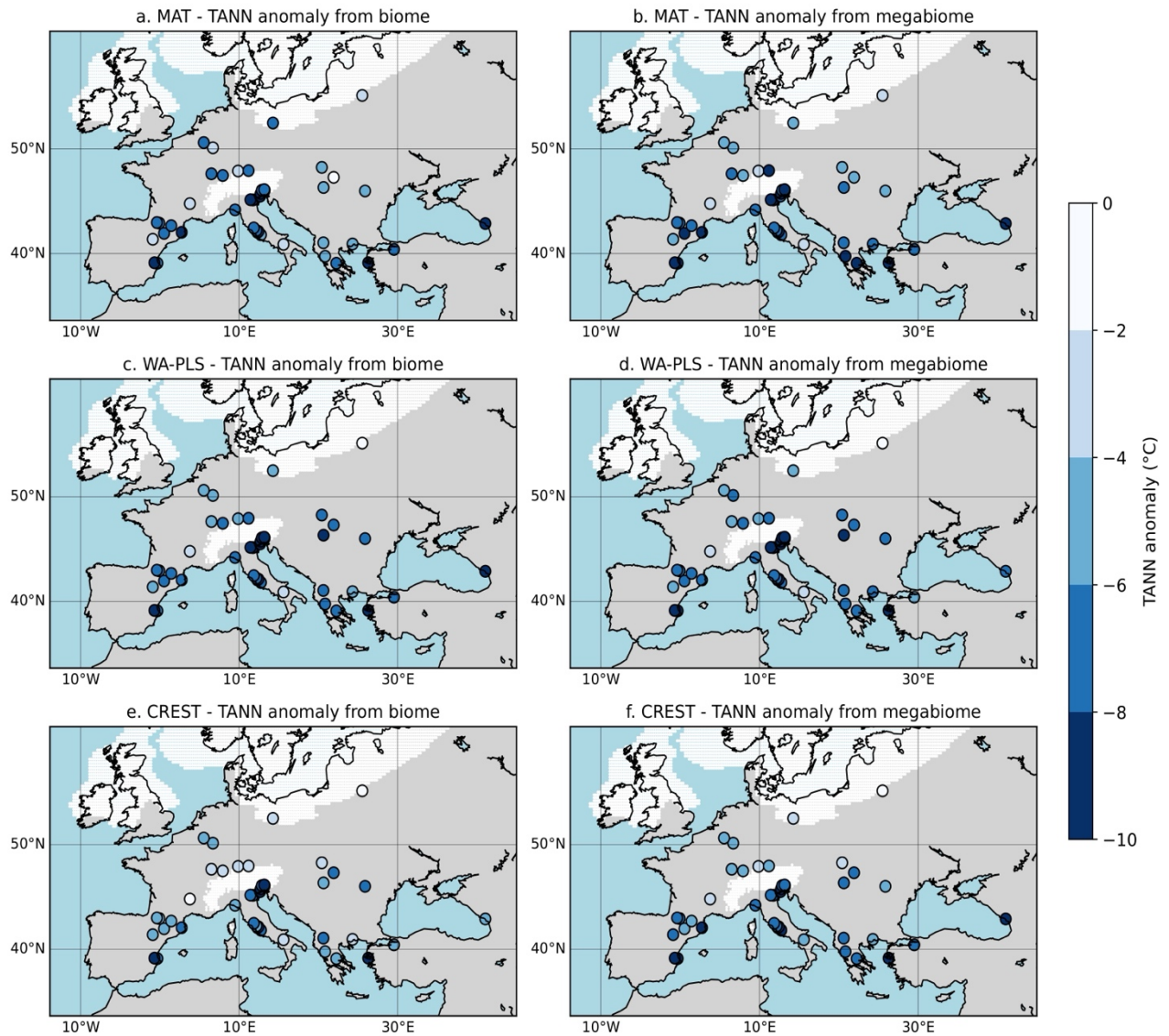


Figure 5. Annual temperature anomaly results (LGM – Modern climate) using the biomization (first line; a, b and c) and megabiomization (second line; d, e and f) processes from three different methods (MAT, WA-PLS and CREST). Modern climates and LGM climate results are reported in **Appendix 7**. The white area represents the ice sheet extent (Peltier and Solheim, 2004, Ehlers et al., 2011; Seguinot et al., 2018). *Geographic coordinates are displayed in WGS84.*

V.4.2 – Seasonal temperature anomalies

The first row of Fig.6 (Figs 6.a-c) presents reconstructed LGM summer temperature (MTWA) anomalies based on the biomization procedure, with values of $-3.7 \pm 2.3^{\circ}\text{C}$, $-3.7 \pm 2.2^{\circ}\text{C}$, and $-3.5 \pm 2.4^{\circ}\text{C}$ (mean SD) for MAT, WA-PLS, and CREST, respectively. The three reconstruction methods yield the most negative MTWA anomalies in southeastern Europe ($\sim -5^{\circ}\text{C}$), whereas values are more homogeneous and closer to zero in northern and western Europe. MTWA anomalies derived from the megabiomization procedure (Figs 7.a-c) are

–5.0 ± 2.2°C, –5.3 ± 2.2°C, and –5.1 ± 2.4°C for the same reconstruction methods, respectively, yielding similar spatial patterns in MTWA anomalies (**Fig.7**) that from the biome assignments (**Fig.6**). The winter temperature (MTCO, second row of **Figs 6 and 7**) anomalies are –7.7 ± 4.0°C, –8.5 ± 2.9°C, and –6.2 ± 3.5°C from biomization procedure and –7.0 ± 4.0°C, –7.1 ± 3.1°C, and –6.1 ± 4.0°C from megabiomization procedure, for MAT, WA-PLS, and CREST, respectively.

Seasonality anomalies (i.e., seasonal amplitudes) can be calculated from the difference between MTWA and MTCO anomalies at each site, derived from biomization and megabiomization procedures, as shown in the third row of **Figs 6 and 7** (panels g-i). **Negative LGM–modern seasonal anomalies indicate that seasonality during the LGM was weaker than under present-day conditions, while positive values indicate a stronger seasonal contrast relative to the modern climate.** Results from the biomization procedure (**Fig 6.g-i**) show seasonality anomaly patterns that are broadly consistent with those obtained from the megabiomization approach (**Fig 7.g-i**). Across Europe, the reconstructed gradients indicate a reduction in LGM seasonality from western to eastern Europe relative to present-day conditions. In contrast, several sites located in southeastern Europe (e.g., Lake Xinias, Megali Limni and Dziguta) exhibit marked increases in seasonality since the LGM, reaching values of approximately 8°C, comparable to those reconstructed for the extreme western part of Europe.

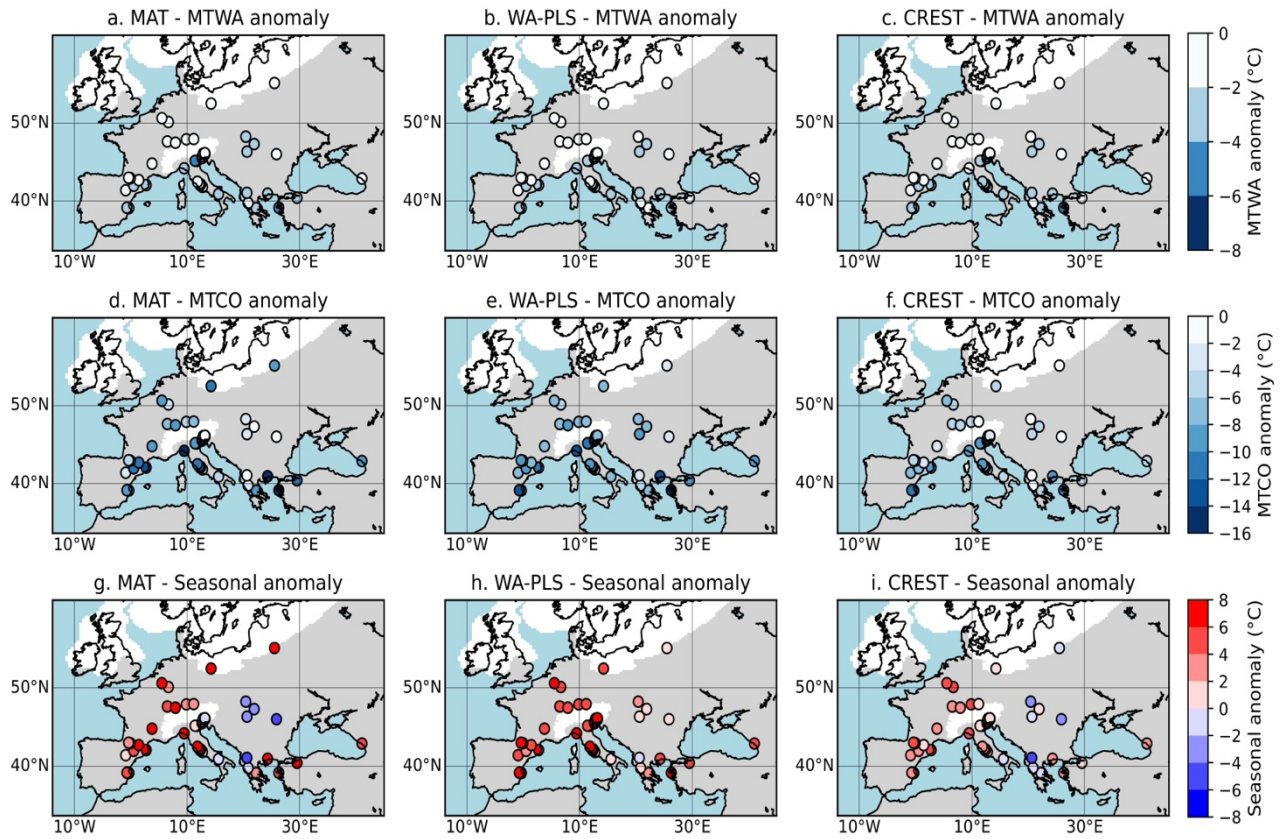


Figure 6. Monthly (MTWA and MTCO, in **a-c** and **d-f**, respectively) temperature anomaly (LGM – Modern climate) results, using the biomization process for the three different pollen-based climate reconstruction methods. From MTWA and MTCO results, seasonal anomalies are reported on **Figs g-i**. Modern climates and LGM climate results are reported in **Appendix 7**. The white area represents the ice sheet extent (Peltier and Solheim, 2004, Ehlers et al., 2011; Seguinot et al., 2018). **Geographic coordinates are displayed in WGS84.**

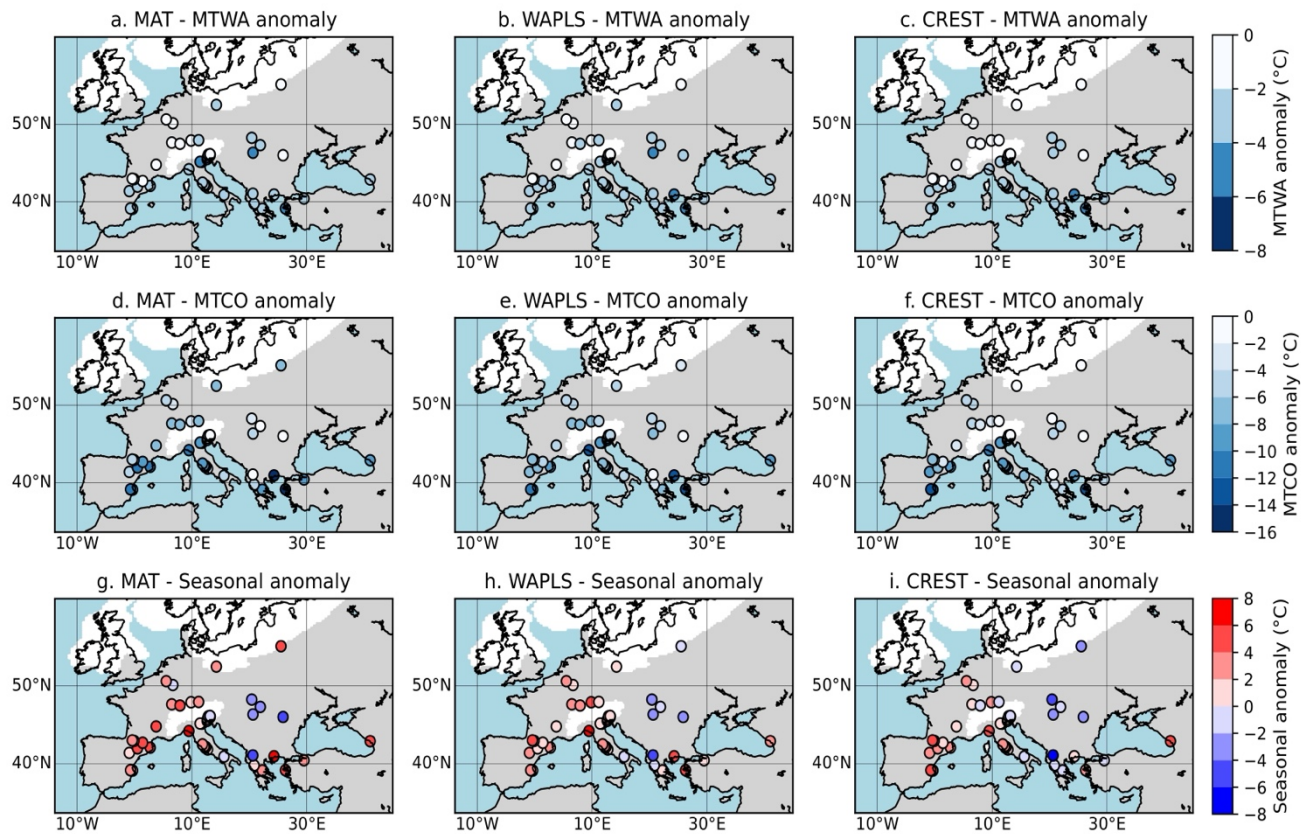


Figure 7. Monthly (MTWA and MTCO, in **a-c** and **d-f**, respectively) temperature anomaly (LGM – Modern climate) results, using the megabiomization process for the three different pollen-based climate reconstruction methods. From MTWA and MTCO results, seasonal anomalies are reported on **Figs g-i**. Modern climates and LGM climate results are reported in **Appendix 7**. The white area represents the ice sheet extent (Peltier and Solheim, 2004, Ehlers et al., 2011; Seguinot et al., 2018). *Geographic coordinates are displayed in WGS84.*

V.4.3 - Inter-model means from annual and seasonal temperature anomalies

Because TANN, MTWA, and MTCO display spatially homogeneous patterns across Europe, and because the three reconstruction methods yield comparable spatial averages, we averaged the outputs (mean $\pm$ SD; **Fig.8**) from the three methods for both the biomization (**Figs 8.a and 9.c**) and megabiomization (**Figs 8.b and 8.d**) procedures in order to reconstruct mean spatial climate conditions during the LGM. **Compared to annual and summer temperatures, MTCO results show greater dispersion across European sites despite higher internal errors (Appendix 6), consistent with the validation uncertainties discussed in Section V.2. Seasonal uncertainties are then derived as the quadratic sum of summer and winter temperature errors. Mean errors for these two climatic variables are reported in Appendix 8, also accounting for external uncertainties derived from inter-site dispersion.**

Across Europe, LGM cooling averaged $6.4 \pm 2.0^{\circ}\text{C}$ and $6.8 \pm 3.4^{\circ}\text{C}$ (**Appendix 7**) based on biome and megabiome assignments, respectively (**Fig 8.a-b**). These results are generally

consistent across reconstruction methods, with inter-method standard deviations below $+2^{\circ}\text{C}$ (**Appendix 8**). Inter-model mean MTWA anomalies are similar for both reconstruction methods and for biome versus megabiome assignments, with mean multi-method values of $-3.6 \pm 2.2^{\circ}\text{C}$ and $-5.1 \pm 2.2^{\circ}\text{C}$, respectively. Inter-model mean MTCO anomalies are $-7.4 \pm 3.3^{\circ}\text{C}$ for the biomization approach (**Fig 7.d–f**) and $-6.7 \pm 3.4^{\circ}\text{C}$ for the megabiomization approach (**Fig 7.d–f**). Mean seasonal anomalies across methods are $3.8 \pm 2.8^{\circ}\text{C}$ and $1.6 \pm 2.7^{\circ}\text{C}$ for biome and megabiome assignments, respectively (**Fig 8.c–d**). Seasonal anomalies are relatively consistent across methods using the biomization approach, with inter-method standard deviations of $\sim 2^{\circ}\text{C}$ (**Appendix 8**).

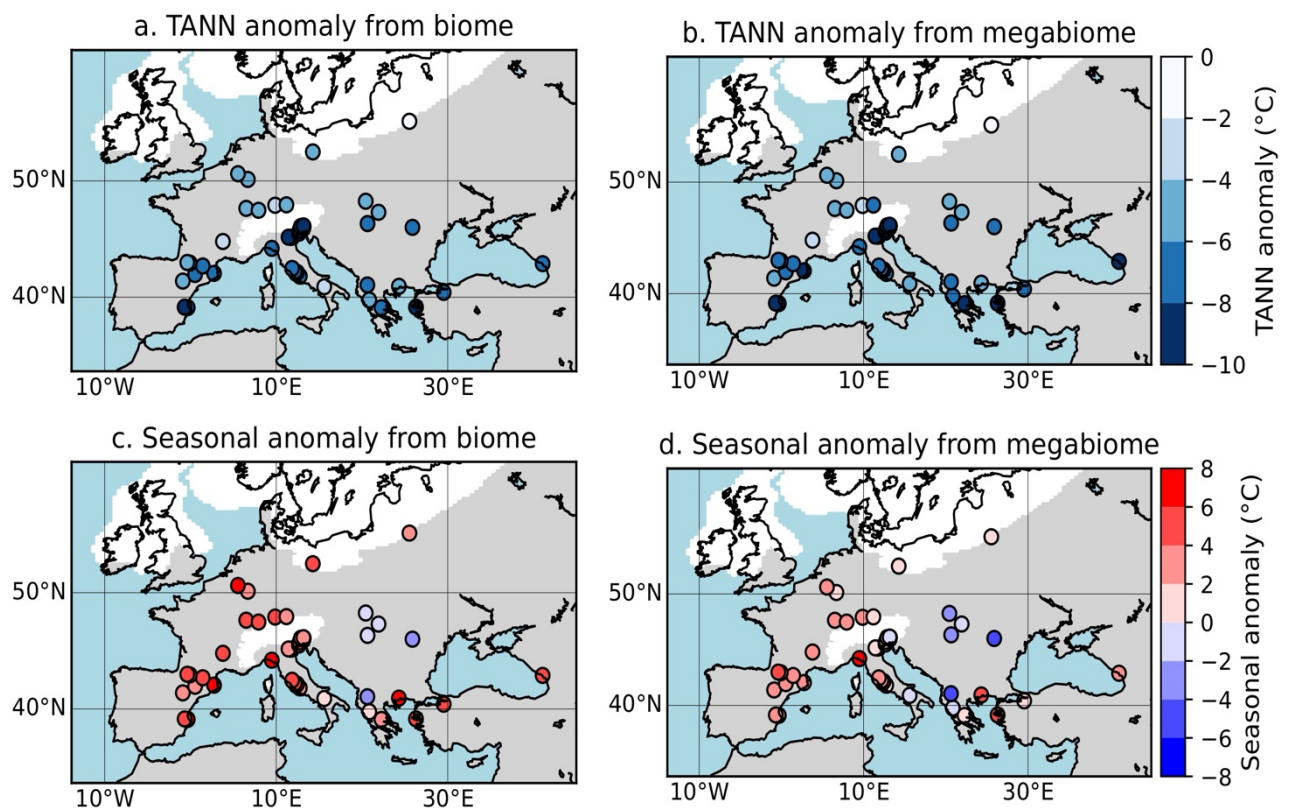


Figure 8. Mean annual temperature (**a and c**) and seasonal index (**b and d**) anomaly results (LGM – Modern climate) using averages of biomization and megabiomization results from three different pollen-based climate reconstruction methods. Seasonal anomalies = MTWA - MTCO anomalies. Standard deviation maps of climate anomalies are reported in **Appendix 8**. The white area represents the ice sheet extent (Peltier and Solheim, 2004, Ehlers et al., 2011; Seguinot et al., 2018). *Geographic coordinates are displayed in WGS84.*

V.5 – Methodological implications on paleoclimate reconstructions

V.5.1 - Local and global calibration effects on climate reconstructions

To isolate and quantify the impact of local calibration (i.e., (mega)biomization procedures) on global climate reconstructions during the LGM across Europe, **Fig 9.a** shows TANN anomalies calculated as the difference between climates obtained using the (mega)biome mean-weighting approaches and those derived from global calibration (i.e., by sampling the entire calibration EMPD2 pollen dataset).

As the MAT method is inherently based on dissimilarity coefficients (*Guiot et al., 1989*), it is theoretically able to directly identify the dominant analogues with no requirement for (mega)biome calibration using all modern pollen spectra. As a result, one expects only a minimal (if any) effect of (mega)biomization on TANN reconstructions from the MAT method (**Fig 9.a**). Here, only a few fossil sites show a warming effect ($\sim +5^{\circ}\text{C}$) of reconstructed TANN using local calibrations based on (mega)biomes (Venice, Billerio and Feher) rather than the global calibration. Then, **the MAT method may therefore be suitable for large-scale spatial studies using global datasets to reconstruct annual temperatures across Europe, although its performance statistics should be interpreted with caution given its sensitivity to spatial autocorrelation and the potential for over-optimistic skill estimates.** While the effects of local versus global calibration TANN anomalies for MAT may depend on the time period considered and the reconstructed climate variables (*Xu et al., 2010*), the magnitude of these effects remain generally close to zero. However, the WA-PLS method produces generally inconsistent results between local and global calibration results, with a mean TANN anomaly of $\sim -5^{\circ}\text{C}$, indicating colder TANN using local rather than global calibrations. Two significantly negative anomalies ($\sim -10^{\circ}\text{C}$), were also identified using the WA-PLS method (Lake Iznik, Kersdorf-Briesen). Similarly, the CREST method appears more sensitive to calibration, as evidenced by predominantly negative TANN anomalies (from $\sim -2^{\circ}\text{C}$ to $\sim -12^{\circ}\text{C}$, with a mean of -6.5°C , **Fig 9.a**). This underscores the importance of a robust (mega)biomization scheme – climatic and environmental gradients of the study area – when applying CREST in Europe during the LGM to ensure that reconstructed TANN remains sufficiently cold and consistent with other statistical methods (see **Figs 6 and 8**). The importance of modern regional calibrations for quantitative climate reconstructions has also been noticed in previous studies (e.g., *Trasune et al., 2024*).

As shown in **Fig. 9b**, applying the (mega)biomization procedure to MAT substantially increases reconstructed MTWA by approximately 3°C . In contrast, applying the same procedure to WA-PLS and CREST results in lower reconstructed summer temperatures, with MTWA decreasing by about 3°C . In **Fig 9.c**, the differences in MTCO anomaly results between local and global calibrations are however more variable than MTWA results, across fossil sites. MAT and CREST methods exhibit a strong dependence on the calibration dataset for winter temperature reconstructions, which could be attributed to the spatial variability of MTCO anomalies in the modern calibration dataset. In detail, the MAT method generally produces larger MTCO anomalies with local calibration than with global calibration ($+4.0^{\circ}\text{C}$ on average), whereas the WA-PLS and CREST methods tend to yield similarly lower MTCO anomalies

(−4.5°C on average). Then, these findings highlight an opposite effect of the (mega)biomization procedure from the MAT versus WA-PLS and CREST methods in reconstructing the MTWA and MTCO variables. Overall, these results highlight the dependence of climate reconstructions on the chosen method, calibration, and climatic variables. The sites most strongly affected by the (mega)biomization approach are predominantly located in Italy and along the Mediterranean coast (from Lago della Costa to Orvenco, **Fig 9.a-c**), where reconstructions of all three climatic variables show the largest deviations.

For TANN and MTWA reconstructions, MAT appears to be the most suitable reconstruction method, for identifying dominant analogues within a global calibration dataset to infer past climate conditions. However, MTCO outputs are sensitive to the modern subsamples defined by biome and megabiome classifications (**Fig.9**), from MAT and CREST methods.

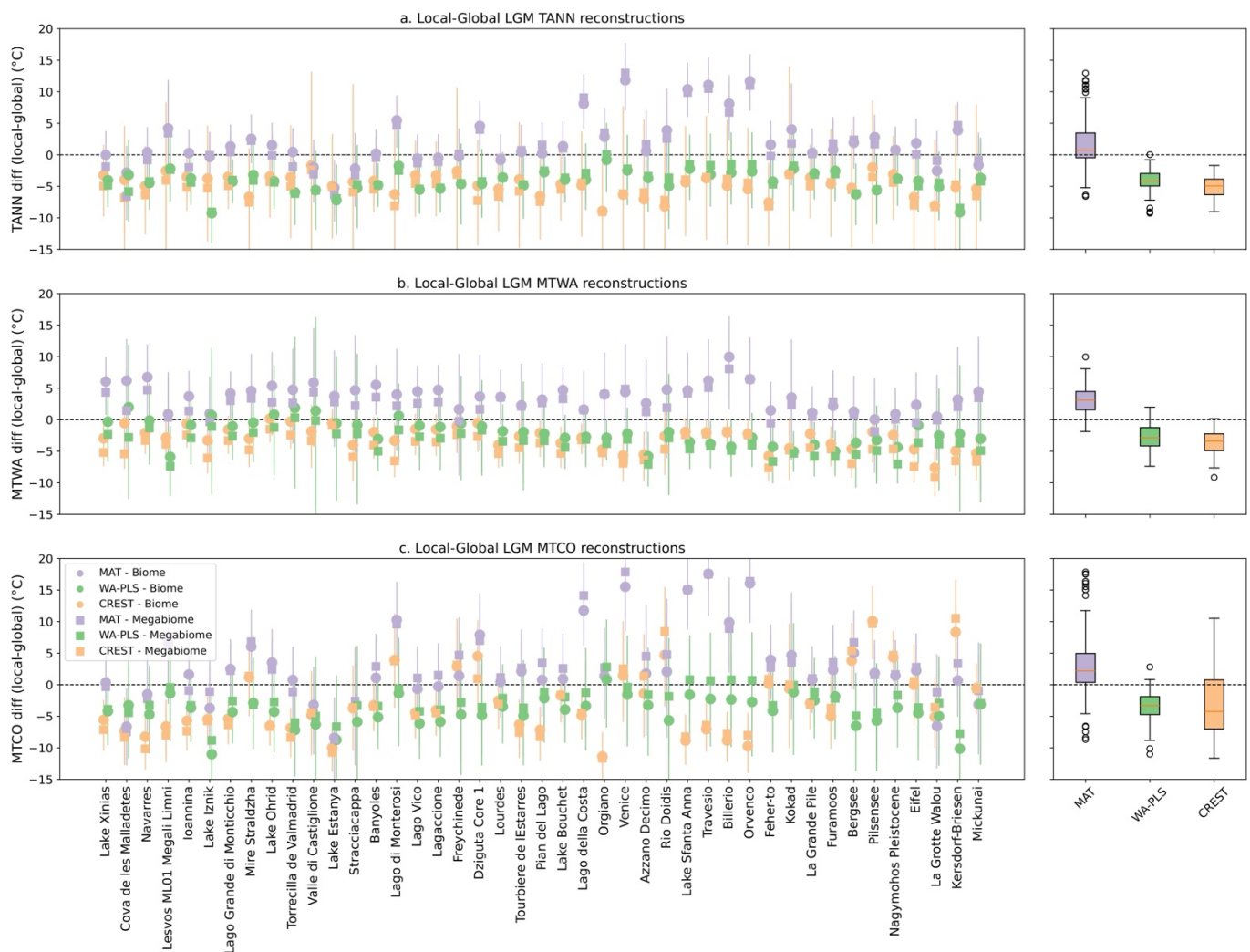


Figure 9. Mean LGM annual temperature (a), MTWA (b) and MTCO (c) anomalies for each fossil site, calculated as the difference between (mega)biomized and not-(mega)biomized

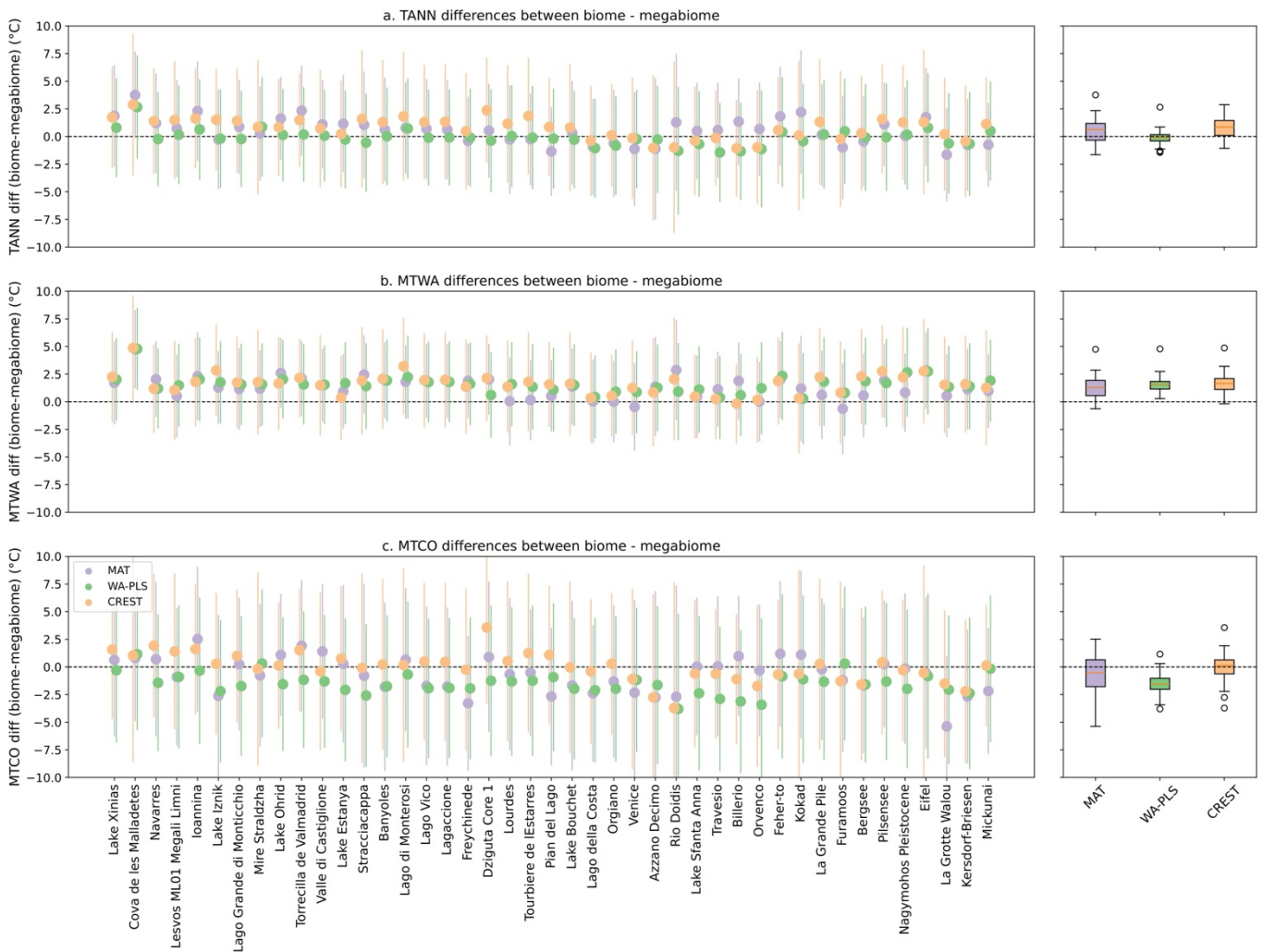
*(global calibration) climate variables for the three methods of pollen-based climate reconstruction. The biomization and megabiomization results are shown using circle and square symbols, respectively. Site names are arranged (left to right) in ascending order of latitude. Results are reported in **Appendix 7**. Errors are 1σ . The boxplots on the right represent the distributions of the mean local–global differences for each climate variable across reconstruction methods (in color).*

V.5.2 - Biomization vs. Megabiomization effects on climate reconstructions

Across reconstruction methods, TANN, MTWA and MTCO results derived from the biomization process are consistent with the megabiomization outputs (i.e., anomalies defined as the difference between the two treatments - are close to 0, **Figs 10.a and 10.b**). This result highlights the minimal impact of distinguishing between cold and hot arid conditions into steppe and desert biomes (not the case for megabiomes) on reconstructed LGM climates across Europe from three different methods.

Due to the large MTCO reconstruction errors based on the three methods (**Appendix 7**), quadratic errors between the biomization and megabiomization approaches are greater for MTCO than for TANN and MTWA (**Fig. 10a–c**). Nevertheless, MTCO anomalies reconstructed using MAT display only limited spatial variability across sites. Interquartile ranges are approximately twice as large as those obtained for MAT-based MTWA and TANN anomalies when comparing the biomization and megabiomization procedures (**Fig. 10c**).

947



948

949 **Figure 10.** Mean LGM annual temperature (a), MTWA (b) and MTCO (c) anomalies for each
 950 fossil site, calculated as the difference between biomized and megabiomized climate
 951 variables for the three methods of pollen-based climate reconstruction. Site names are
 952 arranged in ascending order of latitude. Results are reported in **Appendix 7**. Errors are 1σ .
 953 The boxplots on the right represent the distributions of the mean biome-megabiome
 954 differences for each climate variable across reconstruction methods (in color).

955

956 VI. Discussion

957 VI.1 - Comparing vegetation distributions from the (mega)biome assignments

958 The pollen-based modern biome distribution (Fig.2) closely resembles European
 959 results obtained using the same biomization method as *Prentice et al. (1998)*. In particular,
 960 the diversity of biomes in Spain (TEDE, COMX, XERO, and WAST), as well as the geographic
 961 extent of temperate forests and xerophytic vegetation, aligns well with previous findings
 962 (*Hengl et al., 2018*). However, our results indicate a broader modern extent of cold forest
 963 (CLMX) across the Scandinavian countries, relative to *Prentice et al. (1998)*.

In 2017, *Binney et al.* proposed a BIOME 6000 approach, building upon *Prentice and Webb III (1998)*, to identify dominant biomes using the biomization procedure of *Bigelow et al. (2003)*, super-PFT contributions, and BIOME 4 model biomes (*Kaplan et al., 2003*). Their biome distributions similarly reveal patterns for the TEDE, TAIGA, and TUND biomes, although with a stronger TUND dominance in Northern Europe compared to our results. Meanwhile, during the LGM, *Kaplan et al. (2016)* show that forest-cover reconstructions from vegetation models constrained by climate simulations suggest greater forest cover - and consequently less extensive steppe conditions - than pollen-based reconstructions indicate.

Furthermore, the “Regional Estimates of Vegetation Abundance from Large Sites” (REVEALS) land-cover model, described by *Kern et al. (2024)*, compiles European pollen datasets to reconstruct plant-specific parameters over time, including high-frequency events. A comparison between outputs from this vegetation model and LGM megabiome results indicates an overrepresentation of modeled arboreal vegetation (**Fig. 2**), at the expense of grasses and herbs. This discrepancy may reflect an aridification bias in climate reconstructions based on the megabiomization approach.

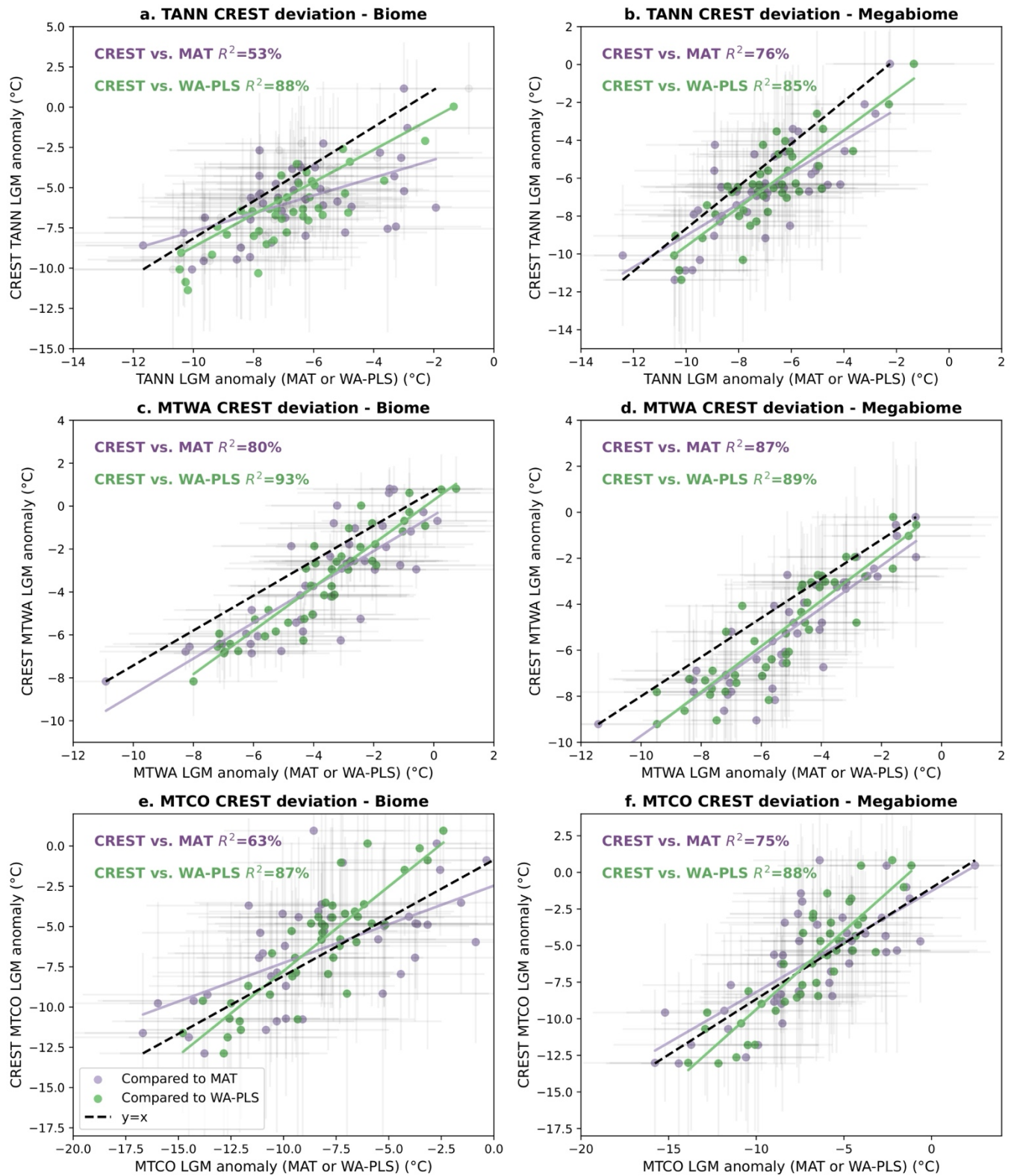
Global megabiome reconstructions in this study closely match modeled vegetation distributions from *Li et al. (2025)* and align with previous European results using the same biomization procedure (*Bigelow et al., 2003*), demonstrating good reproducibility across Europe. *Dallmeyer et al. (2019)* reported global spatiotemporal megabiome patterns from an ensemble of Earth System Model (ESM) simulations that are generally consistent with our modern megabiome reconstructions. Nevertheless, differences in the distribution of reconstructed and simulated modern megabiomes persist, largely reflecting the limited taxonomic resolution (taxa families to species) of the taxa–megabiome classification table employed in the megabiomization procedure. Biases in pollen-based megabiome reconstructions could arise from differential pollen production, dispersal, and preservation among taxa, which can lead to overrepresentation of open vegetation in regions dominated by high-producing taxa such as *Artemisia*. Moreover, some mismatches between reconstructed and observed modern megabiomes likely result from anthropogenic impact of pollen assemblages, which is not explicitly represented in the megabiomization scheme due to the absence of anthropogenic PFTs and the limited taxonomic resolution of many pollen taxa.

Then, the modern (mega)biome distribution is geographically coherent, seemingly realistic and compatible with previous studies, thus confirming the robustness of our biome outputs for European climate reconstructions.

VI.2 - Comparing climate reconstructions

As shown in **Figs 6 and 9**, the climate reconstruction methods (MAT, WA-PLS, and CREST) using (mega)biomization procedures globally yield similar results. To quantify the agreement between LGM climate reconstructions obtained from the different methods, **Figs. 11a–f** report the linear regression coefficients (R^2) between CREST results and those derived from the two traditional statistical approaches, MAT and WA-PLS. Correlation strengths are broadly similar between the biomization and megabiomization approaches (**Figs. 11a–f**). **Across all climatic variables, CREST reconstructions systematically show stronger agreement with WA-PLS than with MAT ($88\% \leq R^2 \leq 93\%$ and $53\% \leq R^2 \leq 87\%$ for “CREST vs. WA-PLS” and “CREST vs. MAT”, respectively). In contrast, correlations between CREST and MAT are generally weaker, although MTWA reconstructions display relatively comparable levels of agreement between the two comparisons ($80\% \leq R^2 \leq 93\%$, **Fig. 11c and 11.d**).**

A key advantage of this multi-method approach is that it isolates the intrinsic properties, behaviors, and weaknesses of each method. While MAT is highly dependent on the quality of analogues (*Chevalier et al., 2020*), **it is generally less sensitive to reduced taxonomic resolution than approaches relying on individual taxon–climate relationships (WA-PLS) or climatic niche estimates (CREST), because it relies on the overall similarity among assemblages rather than on the climatic response of individual taxa** (*Chevalier et al., 2020*). WA-PLS is also sensitive to the choice of modern dataset (**Fig.9**, e.g., situations with low analogue availability, *Birks and Seppä, 2005*), and it relies on unimodal vegetation-climate response (*Ter Braak and Juggins, 1993*). CREST method is less effective for taxa with low taxonomic resolution, accounts for multimodal vegetation responses to climate (*Chevalier et al., 2014*). Thus, despite using the same modern and fossil datasets, these methods yield distinct but complementary LGM climate reconstructions that can be combined together to provide robust estimates for the reconstructed climate variables.



1030
 1031
 1032
 1033
 1034
 1035

Figure 11. Linear relationship between TANN (**a and b**), MTWA (**c and d**) and MTCO (**e and f**) anomaly results (LGM – Modern climate) from the three pollen-based climate reconstruction methods, using biomization and megabiomization procedures. All R^2 values reported in this study are statistically significant, with p values < 0.01 . These plots show relationships between CREST results and those from statistical methods (MAT in blue and WA-PLS in green) from the 43 fossil sites. Errors are 1σ .

VI.3 – Pollen-based reconstruction comparisons from literature

VI.3.1 - Local calibration effects from MAT-based climate reconstructions: comparison with Davis et al. (2024)

To study the reliability of our LGM climate reconstructions with results published in literature, we compare our biomized and megabiomized multi-method results for three different climate variables with those of Davis et al. 2024. Davis et al. 2024 also used the calibration dataset (EMPD2 dataset) and some input fossil records, common with our study. Comparison maps (differences) between the two studies are presented in **Appendix 9** and summarized as boxplots in **Fig.12**. We use error metrics to compare the results of the two studies and assess the effect of methodological differences on climate reconstructions. Unlike R^2 , which is insensitive to systematic biases, error metrics (RMSE) express deviations in the original units ($^{\circ}\text{C}$), making them more suitable for comparison.

The TANN and MTWA errors (RMSE) between our multi-method reconstructions and those of Davis et al. (2024) are comparable to the individual reconstruction errors ($2\text{--}3^{\circ}\text{C}$; **Figs. 12a–b**), indicating relatively good agreement between the studies regardless of the calibration ((mega)biomization) and reconstruction methods. In contrast, MTCO anomalies show larger discrepancies between the two studies ($4\text{--}6^{\circ}\text{C}$; **Fig. 12c**). MTCO results exhibit poorer agreement between the two studies, with RMSE values approximately twice as high as those for TANN and MTWA (**Fig. 12c**), for both megabiomization and biomization approaches. Overall, across these three methods, the results of Davis et al. (2024) agree more closely with our TANN and MTWA reconstructions than with our MTCO results, with RMSE differences ranging from 0.5 to 2°C . **Appendix 9** further shows that annual climatic conditions reconstructed for sites located in northern Europe are systematically warmer in our study than in Davis et al. (2024), with differences ranging from $+5^{\circ}\text{C}$ to $+10^{\circ}\text{C}$. Interestingly, our approach leads to substantially higher MTCO anomalies in Northern Europe ($\sim +3^{\circ}\text{C}$) and lower MTCO anomalies in Southern Europe ($\sim -3^{\circ}\text{C}$).

These results align with those reported in **section V.4**, highlighting the predominant influence of the (mega)biome-type assignment scheme (**Figs 9.c and 10.b**) and reconstruction methods on MTCO anomalies, likely due to the high spatial variability of modern data within the calibration dataset. MTCO reconstructions show the strongest inter-study inconsistencies and are particularly sensitive to methodological choices. The difference in modern calibration samples used in Davis et al. 2024 and in the (mega)biome definitions of our study may explain the observed differences in reconstructed temperature, particularly the large MTCO

discrepancies. These discrepancies demonstrate the strong methodological dependence of palaeoclimate reconstructions and the importance of systematic cross-validation frameworks.

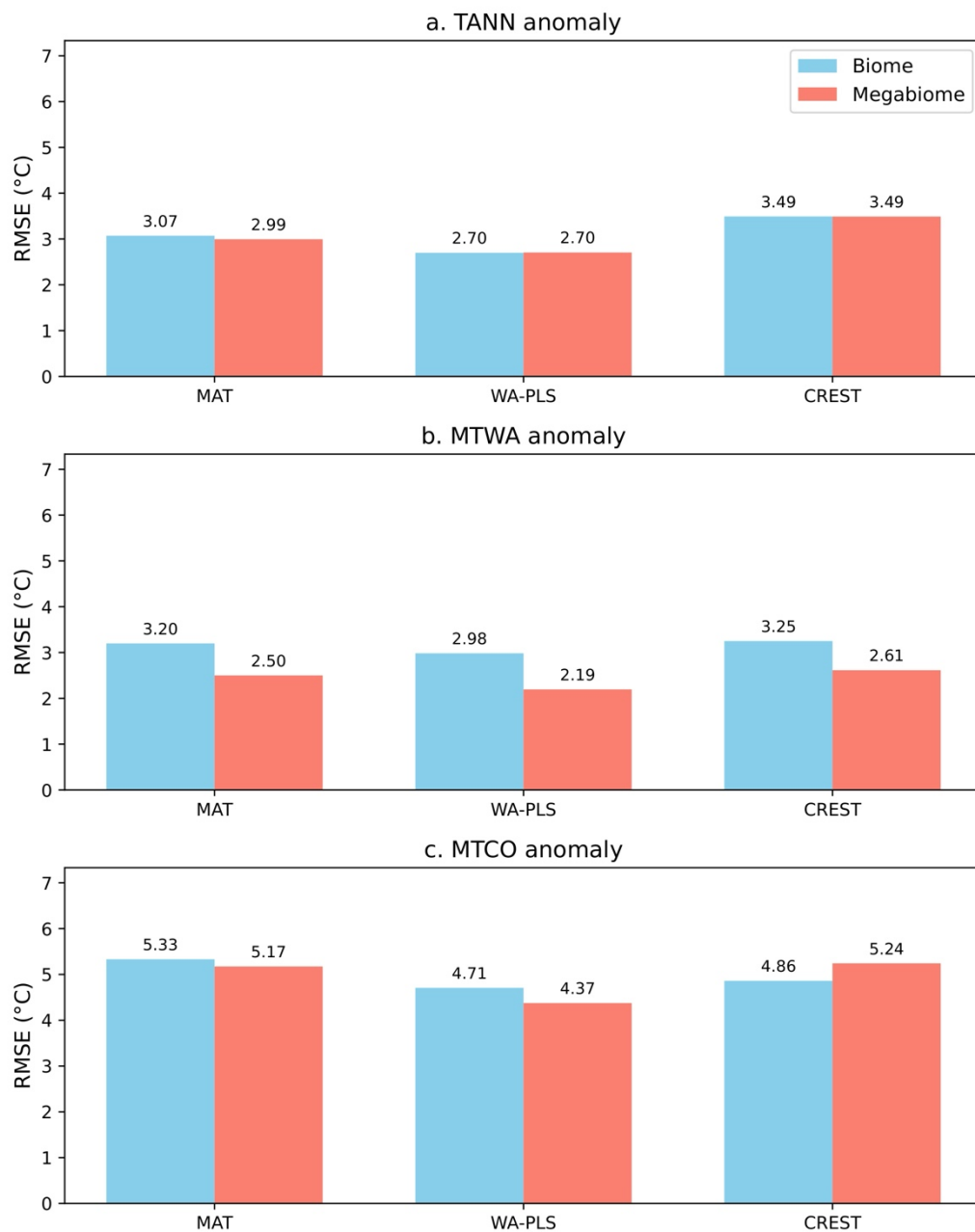


Figure 12. RMSE of mean annual (a) and monthly anomalies (b and c) (LGM – Modern climate) between our three reconstruction methods (MAT, WA-PLS, CREST) and results from Davis et al. (2024). Bars represent RMSE for Biome (blue) and Megabiome (orange), with RMSE values reported above each bar to indicate the reconstruction error relative to Davis et al. (2024).

VI.3.2 - Systematic climate discrepancies between pollen data and models

The extent of LGM cooling inferred in this study ranges from -1°C to -12°C relative to present (Fig.5) and appears to fall within the range simulated by climate models (e.g., Kageyama et al., 2021). We also provide new constraints on LGM temperature seasonality

indicating an amplification near the Atlantic coasts and a relative reduction inland, compared to present day. This continental pattern of LGM seasonality is in strong agreement with the mean model from PMIP synthesis by *Izumi et al. (2013)*, which shows a gradient from positive anomalies in Spain (+10°C) to negative anomalies (−4°C) in Eastern Europe.

However, comparing pollen-based climate reconstructions with climate model outputs is complex due to both the heterogeneous spatial coverage of the data, the variability of reconstruction methods and the dispersion among climate models (e.g., *Bartlein et al., 2011; Kageyama et al., 2021*). Moreover, proxies record extreme and local climates, while climate models tend to provide spatially-averaged climate conditions. Ongoing improvements in the spatial resolution of regional climate models make comparisons with local proxies increasingly appropriate, although significant data–model discrepancies remain (*Kageyama et al., 2021*). Similarly, expanding the availability of pollen data in Europe would further improve the robustness of such comparisons.

VII. Conclusion

This study presents the first comprehensive comparison of pollen-based climate reconstruction methods applied to the LGM in Europe, using a local calibration framework integrating both biomization and megabiomization techniques. The approach is applied to a compilation of fossil sites spanning the LGM and compared against a comprehensive modern calibration dataset (EMPD2). We propose a new conservative method for weighting reconstructed climate variables from (mega)biome affinity scores, which corrects for threshold effects in (mega)biome shifts and incorporates their continuous variations over time. We isolate and quantify the effects of calibration, biome score application methods, and reconstruction techniques on the inferred paleoclimates, and synthesize them in the form of inter-model means and deviations.

In Europe, the TANN anomalies (mean SD) obtained with biomization are $-6.5 \pm 2.3^\circ\text{C}$ (MAT), $-7.1 \pm 2.0^\circ\text{C}$ (WA-PLS), and $-5.8 \pm 2.4^\circ\text{C}$ (CREST), whereas those derived from megabiomization are $-7.0 \pm 2.2^\circ\text{C}$ (MAT), $-7.0 \pm 2.0^\circ\text{C}$ (WA-PLS), and $-6.5 \pm 2.0^\circ\text{C}$ (CREST). Due to these consistent results, we propose LGM climate anomalies (from climate modern) based on a mean model integrating the three reconstruction methods: $-6.4 \pm 2.0^\circ\text{C}$ in TANN anomalies, $-3.6 \pm 2.2^\circ\text{C}$ in MTWA anomalies, and $-7.4 \pm 3.3^\circ\text{C}$ MTCO anomalies from biomization procedure, and $-6.8 \pm 2.1^\circ\text{C}$ in TANN anomalies, $-5.1 \pm 2.2^\circ\text{C}$ in MTWA anomalies, and $-6.7 \pm 3.3^\circ\text{C}$ MTCO anomalies from megabiomization procedure across Europe.

The dependence of reconstruction method outputs on (mega)biome calibrations vary depending on both the climate variables and the fossil pollen assemblages (i.e., the sites). Local calibration is necessary for WA-PLS and CREST-based reconstructions due to the underrepresentation of cold climates in Europe. These results show that, using the biome and megabiome calibrations, the CREST (probabilistic) method shows LGM climate results generally consistent with those of **common** statistical approaches (MAT and WA-PLS), although the consistency of CREST and WA-PLS reconstructions is slightly better than with

MAT. Winter temperature (MTCO) results exhibit higher sensitivity to reconstruction methods and (mega)biomization approaches than TANN and MTWA results. Based on MTCO reconstructions, the WA-PLS and CREST method shows an opposite response to local calibration compared with MAT, amplifying seasonal anomalies relative to global calibration (+4.5°C for CREST and -4°C for MAT on average) while reducing European LGM seasonality by the biomization procedure, but less strongly (-2.5°C for CREST and +2°C for MAT on average).

Scientific contributions - Authorship contribution statement

Conceptualization: Fénisse G., Chevalier M., Peyron O., Bekaert D.V., Blard P.-H

Methodology: Fénisse G., Chevalier M., Peyron O., Bekaert D.V., Blard P.-H

Data curation: Fénisse G.

Formal analysis: Fénisse G., Chevalier M., Peyron O., Bekaert D.V., Blard P.-H

Visualization: Fénisse G.

Writing – original draft: Fénisse G.

Writing – review: Fénisse G., Chevalier M., Peyron O., Bekaert D.V., Blard P.-H

Acknowledgements

This study is financially supported by the ANR (ANR-22-CPJ2-0005-24/39 584 01, awarded to D.V. Bekaert). Manuel Chevalier was supported by the German Federal Ministry of Education and Research (BMBF) as a Research for Sustainability initiative (FONA; <https://www.fona.de/en/>) through the PalMod Phase II and Phase III projects (grant no. 01LP1926D and 01LP2308B).

Appendix

Our results including (i) compilation maps from fossil and modern pollen data; (ii) observed vs. Predicted relationship; (iii) monthly climate reconstructions since the LGM and (iv) standard deviation of four climate variables are available here.

List of Appendix

1. Site location, type of archives (a) and pollen description using taxonomic diversity parameters (b) and AP/NAP percentages (c) in 43 pollen LGM records.
2. Relationship between biome and megabiome
3. Pollen taxa observed from the fossil pollen cores
4. Percentage of arid megabiomes (STEP+DESE+TUND) at the LGM in 43 pollen sequences. Red contour points referred to the TEDE dominant megabiomes. SAVA scores are negligible.
5. Cross validation procedures between observed and predicted modern climate variables of the pollen datasets (EMPD2 dataset).
6. Standard deviation of annual temperature (a), precipitation (b), MTWA (c) and MTCO (d) anomaly results (LGM – Modern climate) using averages of biomization results from 3 different methods.
7. Mean annual and monthly map anomalies reconstructed using three methods based on biomization and megabiomization, compared with *Davis et al. (2024)*.

1232 Code and data availability

1233 All support data including (i) the exhaustive modern datasets and fossil pollen
1234 samples derived from the literature; (ii) our training code of (mega-)biome and three
1235 reconstruction methods; and (iii) our climate results are available in the online open
1236 repository ORDAR:

1237 <https://doi.org/10.24396/ORDAR-244>

1238

1239

1240

1241

1242

1243

1244

1245

1246

1247

1248

1249

1250

1251

1252

1253

1254

1255

1256

References

- Arslanov, K. A., Dolukhanov, P. M., and Gei, N. A.: Climate, Black Sea levels and human settlements in Caucasus Littoral 50,000–9000 BP, *Quatern. Int.*, 167–168, 121–127, <https://doi.org/10.1016/j.quaint.2007.02.013>, 2007.
- 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., Prentice, I.C., Scholze, M., Seppä, H., Shuman, B., Sugita, S., Thompson, R.S., Viau, A.E., Williams, J., Wu, H.: Pollen-based continental climate reconstructions at 6 and 21 ka: a global synthesis. *Clim. Dyn.* 37, 775–802. <https://doi.org/10.1007/s00382-010-0904-1>, 2011.
- Bigelow, N.H., Brubaker, L.B., Edwards, M.E., Harrison, S.P., Prentice, I.C., Anderson, P.M., Andreev, A.A., Bartlein, P.J., Christensen, T.R., Cramer, W., Kaplan, J.O., Lozhkin, A.V., Matveyeva, N.V., Murray, D.F., McGuire, A.D., Razzhivin, V.Y., Ritchie, J.C., Smith, B., Walker, D.A., Gajewski, K., Wolf, V., Holmqvist, B.H., Igarashi, Y., Kremenetskii, K., Paus, A., Pisaric, M.F.J., Volkova, V.S.: Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present. *J. Geophys. Res. Atmospheres* 108, 2002JD002558. <https://doi.org/10.1029/2002JD002558>, 2003.
- 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, J., Novenko, E., Ryabogina, N., Solovieva, N., Willis, K., 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.
- Birks, H.J.B.: Quantitative palaeoenvironmental reconstructions. *Stat Model Quat Sci Data Tech Guid., Statistical Modelling of Quaternary Science Data., Technical Guide 5*, Quaternary Research Association, Cambridge. 271 pp., 1995.
- Birks, H.J.B., Seppä, H.: Pollen-based reconstructions of late-Quaternary climate in Europe – progress, problems, and pitfalls., *Acta Palaeobotanica* 44(2): 317–334, 2004
- Blaauw, M., Wohlfarth, B., Christen, J.A., Ampel, L., Veres, D., Hughen, K.A., Preusser, F., Svensson, A.: Were last glacial climate events simultaneous between Greenland and France? A quantitative comparison using non-tuned chronologies. *J. Quat. Sci.* 25, 387–394. <https://doi.org/10.1002/jqs.1330>, 2010.
- Bonatti, E.: Pollen sequence in the lake sediments. In: Hutchinson, G. E. (ed.), *Lanula: an Account of the History and Development of the Lago di Monterosi, Latium, Italy*, *T. Am. Philos. Soc.*, 60, 26–31, <https://doi.org/10.2307/1005996>, 1970.
- Bottema, S.: Pollen analytical investigations in Thessaly (Greece), *Palaeohistoria*, 21, 19–40, 1979.
- Braconnot, P., Harrison, S.P., Kageyama, M., Bartlein, P.J., Masson-Delmotte, V., Abe-Ouchi, A., Otto-Bliesner, B., Zhao, Y.: Evaluation of climate models using palaeoclimatic data. *Nat. Clim. Change* 2, 417–424. <https://doi.org/10.1038/nclimate1456>, 2012.

- Brewer, S., Guiot, J., Sánchez-Goñi, M.F., Klotz, S.: The climate in Europe during the Eemian: a multi-method approach using pollen data. *Quat. Sci. Rev.* 27, 2303–2315. <https://doi.org/10.1016/j.quascirev.2008.08.029>, 2008.
- Cao, X., Herzschuh, U., Telford, R.J., Ni, J.: A modern pollen–climate dataset from China and Mongolia: Assessing its potential for climate reconstruction. *Rev. Palaeobot. Palynol.* 211, 87–96. <https://doi.org/10.1016/j.revpalbo.2014.08.007>, 2014.
- Cao, X., Tian, F.: Pollen-based biome reconstruction in R. Zenodo Code. <https://doi.org/10.5281/zenodo.7523423>, 2021.
- Cao, X., Tian, F., Dallmeyer, A., Herzschuh, U.: Northern Hemisphere biome changes (>30°N) since 40 cal ka BP and their driving factors inferred from model-data comparisons. *Quat. Sci. Rev.* 220, 291–309. <https://doi.org/10.1016/j.quascirev.2019.07.034>, 2019.
- Cao, X., Tian, F., Herzschuh, U., Ni, J., Xu, Q., Li, W., Zhang, Y., Luo, M., Chen, F.: Human activities have reduced plant diversity in eastern China over the last two millennia. *Glob. Change Biol.* 28, 4962–4976. <https://doi.org/10.1111/gcb.16274>, 2022.
- Carrión, J. S. and Dupré-Olivier, M.: Late Quaternary vegetational history of Navarrés, eastern Spain. A two core approach, *New Phytol.*, 134, 177–191, <https://doi.org/10.1111/j.14698137.1996.tb01157.x>, 1996.
- Charton, L., Combourieu-Nebout, N., Bertini, A., Lebreton, V., Peyron, O., Robles, M., Sassoon, D., Moncel, M.-H. : Vegetation and climate changes during the Middle to Upper Palaeolithic transition in the southwestern Mediterranean: What happened to the last Neanderthals during Heinrich stadial 4? *Quat. Sci. Rev.* 359, 109345. <https://doi.org/10.1016/j.quascirev.2025.109345>, 2025.
- Chevalier, M.: *crestr* : an R package to perform probabilistic climate reconstructions from palaeoecological datasets. *Clim. Past* 18, 821–844. <https://doi.org/10.5194/cp-18-821-2022>, 2022.
- Chevalier, M., Davis, B.A.S., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., Kühl, N., Maezumi, S.Y., Tipton, J.R., Carter, V.A., Brussel, T., Phelps, L.N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., De Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P.S., Chaput, M., Kupriyanov, D.: Pollen-based climate reconstruction techniques for late Quaternary studies. *Earth-Sci. Rev.* 210, 103384. <https://doi.org/10.1016/j.earscirev.2020.103384>, 2020.
- Chevalier, M.: Enabling possibilities to quantify past climate from fossil assemblages at a global scale. *Glob. Planet. Change* 175, 27–35. <https://doi.org/10.1016/j.gloplacha.2019.01.016>, 2019.
- Chevalier, M., Chase, B.M.: Determining the drivers of long-term aridity variability: a southern African case study. *J. Quat. Sci.* 31, 143–151. <https://doi.org/10.1002/jqs.2850>, 2016.
- Chevalier, M., Chase, B.M.: Southeast African records reveal a coherent shift from high- to low-latitude forcing mechanisms along the east African margin across last glacial–interglacial transition. *Quat. Sci. Rev.* 125, 117–130. <https://doi.org/10.1016/j.quascirev.2015.07.009>, 2015.

- Chevalier, M., Chase, B.M., Quick, L.J., Dupont, L.M., Johnson, T.C.: Temperature change in subtropical southeastern Africa during the past 790,000 yr. *Geology* 49, 71–75. <https://doi.org/10.1130/G47841.1>, 2021.
- Chevalier, M., Cheddadi, R., Chase, B.M.: CREST (Climate REconstruction SoftWare): a probability density function (PDF)-based quantitative climate reconstruction method. *Clim. Past* 10, 2081–2098. <https://doi.org/10.5194/cp-10-2081-2014>, 2014.
- Chevalier, M., Davis, B.A.S., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., Kühl, N., Maezumi, S.Y., Tipton, J.R., Carter, V.A., Brussel, T., Phelps, L.N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., De Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P.S., Chaput, M., Kupriyanov, D.: Pollen-based climate reconstruction techniques for late Quaternary studies. *Earth-Sci. Rev.* 210, 103384. <https://doi.org/10.1016/j.earscirev.2020.103384>, 2020.
- Cleator, S.F., Harrison, S.P., Nichols, N.K., Prentice, I.C., Roulstone, I.: A new multivariable benchmark for Last Glacial Maximum climate simulations. *Clim Past*, 16, 699–712, <https://doi.org/10.5194/cp-16-699-2020>, 2020
- Cruz-Silva, E., Harrison, S.P., Marinova, E., Prentice, I.C.: A new method based on surface-sample pollen data for reconstructing palaeovegetation patterns. *J. Biogeogr.* 49, 1381–1396. <https://doi.org/10.1111/jbi.14448>, 2022.
- Dallmeyer, A., Claussen, M., Brovkin, V.: Harmonising plant functional type distributions for evaluating Earth system models. *Clim. Past* 15, 335–366. <https://doi.org/10.5194/cp-15-335-2019>, 2019.
- Damblon, F. : L'enregistrement palynologique de la sequence pléistocène et holocène de la grotte Walou, in: La grotte Walou à Trooz (Belgique), edited by: Draily, C., Pirson, S., and Toussaint, M., Service public de Wallonie (Etudes et Documents, Archéologie, 21), https://www.academia.edu/23006376/Draily_C_Toussaint_M_and_Pirson_S_Dir_2011_La_grotte_Walou_%E0_Trooz_Belgique_Fouilles_de_1996_%E0_2004_Volume_2_Les_sciences_de_la_vie_et_les_datations_Monographie_Etudes_et_documents_Arch%E9ologie_21_Namur_Service_public_de_Wallonie_241_p (last access: 25 July 2024), 84–129, 2011.
- Daniau, A.-L., Desprat, S., Aleman, J.C., Bremond, L., Davis, B., Fletcher, W., Marlon, J.R., Marquer, L., Montade, V., Morales-Molino, C., Naughton, F., Rius, D., Urrego, D.H.: Terrestrial plant microfossils in palaeoenvironmental studies, pollen, microcharcoal and phytolith. Towards a comprehensive understanding of vegetation, fire and climate changes over the past one million years. *Rev. Micropaléontologie* 63, 1–35. <https://doi.org/10.1016/j.revmic.2019.02.001>, 2019.
- Davis, B.A.S., Brewer, S., Stevenson, A.C., Guiot, J.: The temperature of Europe during the Holocene reconstructed from pollen data. *Quat. Sci. Rev.* 22, 1701–1716. [https://doi.org/10.1016/S0277-3791\(03\)00173-2](https://doi.org/10.1016/S0277-3791(03)00173-2), 2003.
- Davis, B.A.S., Chevalier, M., Sommer, P., Carter, V.A., Finsinger, W., Mauri, A., Phelps, L.N., Zanon, M., Abegglen, R., Åkesson, C.M., Alba-Sánchez, F., Anderson, R.S., Antipina, T.G., Atanassova, J.R., Beer, R., Belyanina, N.I., Blyakharchuk, T.A., Borisova, O.K., Bozilova, E., Bukreeva, G., Bunting, M.J., Clò, E., Colombaroli, D., Combourieu-Nebout, N., Desprat, S., Di Rita, F., Djamali, M., Edwards, K.J.,

- 1394 Fall, P.L., Feurdean, A., Fletcher, W., Florenzano, A., Furlanetto, G., Gaceur, E.,
 1395 Galimov, A.T., Gałka, M., García-Moreiras, I., Giesecke, T., Grindean, R., Guido,
 1396 M.A., Gvozdeva, I.G., Herzsuh, U., Hjelle, K.L., Ivanov, S., Jahns, S.,
 1397 Jankovska, V., Jiménez-Moreno, G., Karpińska-Kończak, M., Kitaba, I.,
 1398 Kończak, P., Lapteva, E.G., Latafowa, M., Lebreton, V., Leroy, S., Leydet, M.,
 1399 Lopatina, D.A., López-Sáez, J.A., Lotter, A.F., Magri, D., Marinova, E., Matthias,
 1400 I., Mavridou, A., Mercuri, A.M., Mesa-Fernández, J.M., Mikishin, Y.A., Milecka,
 1401 K., Montanari, C., Morales-Molino, C., Mrotzek, A., Muñoz Sobrino, C.,
 1402 Naidina, O.D., Nakagawa, T., Nielsen, A.B., Novenko, E.Y., Panajiotidis, S.,
 1403 Panova, N.K., Papadopoulou, M., Pardoe, H.S., Pędziszewska, A., Petrenko,
 1404 T.I., Ramos-Román, M.J., Ravazzi, C., Rösch, M., Ryabogina, N., Sabariego Ruiz,
 1405 S., Salonen, J.S., Sapelko, T.V., Schofield, J.E., Seppä, H., Shumilovskikh, L.,
 1406 Stivrins, N., Stojakowits, P., Svobodova Svitavská, H., Święta-Musznicka, J.,
 1407 Tantau, I., Tinner, W., Tobolski, K., Tonkov, S., Tsakiridou, M., Valsecchi, V.,
 1408 Zanina, O.G., Zimny, M.: The Eurasian Modern Pollen Database (EMPD),
 1409 Version 2. <https://doi.org/10.5194/essd-2020-14>, 2020.
- 1410 Davis, B.A.S., Fasel, M., Kaplan, J.O., Russo, E., Burke, A.: The climate and vegetation
 1411 of Europe, northern Africa, and the Middle East during the Last Glacial
 1412 Maximum (21 000 yr BP) based on pollen data. *Clim. Past* 20, 1939–1988.
 1413 <https://doi.org/10.5194/cp-20-1939-2024>, 2024.
- 1414 De Beaulieu, J.L.: Pollen profile GPILXX, La Grande Pile, France.
 1415 <https://doi.org/10.1594/PANGAEA.739275>, 2010.
- 1416 De Beaulieu, J.-L., Reille, M.: Long Pleistocene pollen sequences from the Velay
 1417 Plateau (Massif Central, France): I. Ribains maar. *Veg. Hist. Archaeobotany* 1,
 1418 233–242. <https://doi.org/10.1007/BF00189500>, 1992.
- 1419 De Beaulieu, J.D., Reille, M.: A long Upper Pleistocene pollen record from Les Echets,
 1420 near Lyon, France. *Boreas* 13, 111–132. <https://doi.org/10.1111/j.1502-3885.1984.tb00066.x>, 1984.
- 1421 d'Oliveira, L., Dugerdil, L., Ménot, G., Evin, A., Muller, S.D., Ansanay-Alex, S., Azuara,
 1422 J., Bonnet, C., Bremond, L., Shah, M., Peyron, O.: Reconstructing 15 000 years
 1423 of southern France temperatures from coupled pollen and molecular
 1424 (branched glycerol dialkyl glycerol tetraether) markers (Canroute, Massif
 1425 Central). *Clim. Past* 19, 2127–2156. <https://doi.org/10.5194/cp-19-2127-2023>,
 1426 2023.
- 1427 Duprat-Oualid, F., Rius, D., Bégeot, C., Magny, M., Millet, L., Wulf, S., Appelt, O.:
 1428 Vegetation response to abrupt climate changes in Western Europe from 45 to
 1429 14.7k cal a BP: the Bergsee lacustrine record (Black Forest, Germany). *J. Quat.*
 1430 *Sci.* 32, 1008–1021. <https://doi.org/10.1002/jqs.2972>, 2017.
- 1431 Dugerdil, L., Ménot, G., Peyron, O., Jouffroy-Bapicot, I., Ansanay-Alex, S., Antheaume,
 1432 I., Behling, H., Boldgiv, B., Develle, A.-L., Grossi, V., Magail, J., Makou, M.,
 1433 Robles, M., Unkelbach, J., Vanni  re, B., Joannin, S.: Late Holocene Mongolian
 1434 climate and environment reconstructions from brGDGTs, NPPs and pollen
 1435 transfer functions for Lake Ayrag: Paleoclimate implications for Arid Central
 1436 Asia. *Quat. Sci. Rev.* 273, 107235.
 1437 <https://doi.org/10.1016/j.quascirev.2021.107235>, 2021.
- 1438 Dugerdil, L., Peyron, O., Violle, C., Joannin, S., Ménot, G., Denelle, P., Br  elheide, H.,
 1439 Chytr  y, M., Field, R., Hatim, M.Z., Gholizadeh, H., Dolezal, J., Pillar, V.D.,
 1440

- Shaltout, K.H., Schrodt, F., Garnier, E.: Functional Signatures of Surface Pollen and Vegetation Are Broadly Similar: Good News for Past Reconstructions of Vegetation. *J. Biogeogr.* 52, e15100. <https://doi.org/10.1111/jbi.15100>, 2025.
- Dupre Ollivier, M.: *Palinología y paleoambiente – nuevos datos españoles* referencias, Universidad de Valencia, 160 pp., ISBN 84-7795-000-8, 1988.
- Ehlers, J., Giddard, P.L., Hughes, P.D.: *Quaternary Glaciations – Extent and Chronology A Closer Look*, Elsevier, ISBN 9780444534477. ed. <https://doi.org/10.18814/epiugs/2008/v31i2/004>, 2011.
- Follieri, M., Magri, D., and Sadori, L.: Pollen stratigraphical synthesis from Valle di Castiglione (Roma), *Quaternary Int.*, 3–4, 81–84. [https://doi.org/10.1016/1040-6182\(89\)90076-1](https://doi.org/10.1016/1040-6182(89)90076-1), 1989.
- Gebhardt, C., Köhl, N., Hense, A., Litt, T.: Reconstruction of Quaternary temperature fields by dynamically consistent smoothing. *Clim. Dyn.* 30, 421–437. <https://doi.org/10.1007/s00382-007-0299-9>, 2008.
- Geng, J., Wu, H., Zhang, W., Li, Q., Yu, Y.: Evolution of global vegetation patterns since the last glacial maximum. *Quat. Int.* 729, 109780. <https://doi.org/10.1016/j.quaint.2025.109780>, 2025.
- Giardini, M.: Late Quaternary vegetation history at Stracciaccappa (Rome, central Italy), *Veg. Hist. Archaeobot.*, 16, 301–316, <https://doi.org/10.1007/s00334-006-0037-y>, 2007.
- Guiot, J., Pons, A., De Beaulieu, J.L., Reille, M.: A 140,000-year continental climate reconstruction from two European pollen records. *Nature* 338, 309–313. <https://doi.org/10.1038/338309a0>, 1989.
- Guiot, J.: Methodology of the last climatic cycle reconstruction in France from pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 80, 49–69. [https://doi.org/10.1016/0031-0182\(90\)90033-4](https://doi.org/10.1016/0031-0182(90)90033-4), 1990.
- Guiot, J., Reille, M., De Beaulieu, J.L., Pons, A.: Calibration of the climatic signal in a new pollen sequence from La Grande Pile. *Clim. Dyn.* 6, 259–264. <https://doi.org/10.1007/BF00193539>, 1992.
- Guiot, J., Harrison, S., Prentice, I.C.: Reconstructing of Holocene precipitation patterns in Europe using pollen and lake-level Data. *Quat. Res.* 40, 139–149. <https://doi.org/10.1006/qres.1993.1066>, 1993.
- Guiot, J., Torre, F., Jolly, D., Peyron, O., Boreux, J.J., Cheddadi, R.: Inverse vegetation modeling by Monte Carlo sampling to reconstruct palaeoclimates under changed precipitation seasonality and CO₂ conditions: application to glacial climate in Mediterranean region. *Ecol. Model.* 127, 119–140. [https://doi.org/10.1016/S0304-3800\(99\)00219-7](https://doi.org/10.1016/S0304-3800(99)00219-7), 2000.
- Harrison, S.P., Bartlein, P.J., Brewer, S., Prentice, I.C., Boyd, M., Hessler, I., Holmgren, K., Izumi, K., Willis, K.: Climate model benchmarking with glacial and mid-Holocene climates. *Clim. Dyn.* 43, 671–688. <https://doi.org/10.1007/s00382-013-1922-6>, 2014.
- Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K.E., Ni, J., Sutra, J.-P.: Ecophysiological and bioclimatic foundations for a global plant functional classification. *J. Veg. Sci.* 21, 300–317. <https://doi.org/10.1111/j.1654-1103.2009.01144.x>, 2010.
- Haywood, A.M., Dowsett, H.J., Valdes, P.J., Lunt, D.J., Francis, J.E., Sellwood, B.W.: Introduction. Pliocene climate, processes and problems. *Philos. Trans. R. Soc.*

- Math. Phys. Eng. Sci. 367, 3–17. <https://doi.org/10.1098/rsta.2008.0205>, 2009.
- Hengl, T., Walsh, M.G., Sanderman, J., Wheeler, I., Harrison, S.P., Prentice, I.C.: Global mapping of potential natural vegetation: an assessment of machine learning algorithms for estimating land potential. *PeerJ* 6, e5457. <https://doi.org/10.7717/peerj.5457>, 2018.
- 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., Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., De Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., Thépaut, J.: The ERA5 global reanalysis. *Q. J. R. Meteorol. Soc.* 146, 1999–2049. <https://doi.org/10.1002/qj.3803>, 2020.
- Herzschuh, U., Böhmer, T., Chevalier, M., Dallmeyer, A., Li, C., Cao, X., Hébert, R., Peyron, O., Nazarova, L., Novenko, E.Y., Park, J., Rudaya, N.A., Schlütz, F., Shumilovskikh, L.S., Tarasov, P.E., Wang, Y., Wen, R., Xu, Q., Zheng, Z.: Regional pollen-based Holocene temperature and precipitation patterns depart from the Northern Hemisphere mean trends. <https://doi.org/10.5194/egusphere-2022-127>, 2022a.
- Herzschuh, U., Böhmer, T., Li, C., Chevalier, M., Hébert, R., Cao, X., Bigelow, N.H., Nazarova, L., Novenko, E.Y., Peyron, O., Rudaya, N.A., Schlütz, F., Shumilovskikh, L.S.: 1 LegacyClimate 1.0: A dataset of pollen-based climate 2 reconstructions from 2594 Northern Hemisphere sites covering the 3 last 30 ka and beyond., *Earth Syst. Sci. Data*, 15, 2235–2258, <https://doi.org/10.5194/essd-15-2235-2023>, 2022b.
- Hughes, P.D., Gibbard, P.L., Ehlers, J.: Timing of glaciation during the last glacial cycle: evaluating the concept of a global ‘Last Glacial Maximum’ (LGM). *Earth-Sci. Rev.* 125, 171–198. <https://doi.org/10.1016/j.earscirev.2013.07.003>, 2013.
- Izumi, K., Bartlein, P.J., Harrison, S.P.: Consistent large-scale temperature responses in warm and cold climates. *Geophys. Res. Lett.* 40, 1817–1823. <https://doi.org/10.1002/grl.50350>, 2013.
- Jalut, G., Marti, J. M., Fontugne, M., Delibrias, G., Vilaplana, J. M., and Julia, R.: Glacial to interglacial vegetation changes in the northern and southern Pyrénées: Deglaciation, vegetation cover and chronology, *Quaternary Sci. Rev.*, 11, 449–480, [https://doi.org/10.1016/0277-3791\(92\)90027-6](https://doi.org/10.1016/0277-3791(92)90027-6), 1992.
- Jost, A., Lunt, D., Kageyama, M., Abe-Ouchi, A., Peyron, O., Valdes, P.J., 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.
- Juggins, S.: Quantitative reconstructions in palaeolimnology: new paradigm or sick science? *Quat. Sci. Rev.* 64, 20–32. <https://doi.org/10.1016/j.quascirev.2012.12.014>, 2013.
- Joussaume, S., Taylor, K.E., Braconnot, P., Mitchell, J.F.B., Kutzbach, J.E., Harrison, S.P., Prentice, I.C., Broccoli, A.J., Abe-Ouchi, A., Bartlein, P.J., Bonfils, C., Dong, B., Guiot, J., Herterich, K., Hewitt, C.D., Jolly, D., Kim, J.W., Kislov, A., Kitoh, A.,

- 1535 Loutre, M.F., Masson, V., McAvaney, B., McFarlane, N., De Noblet, N., Peltier,
1536 W.R., Peterschmitt, J.Y., Pollard, D., Rind, D., Royer, J.F., Schlesinger, M.E.,
1537 Syktus, J., Thompson, S., Valdes, P., Vettoretti, G., Webb, R.S., Wyputta, U.:
1538 Monsoon changes for 6000 years ago: Results of 18 simulations from the
1539 Paleoclimate Modeling Intercomparison Project (PMIP). *Geophys. Res. Lett.*
1540 26, 859–862. <https://doi.org/10.1029/1999GL900126>, 1999.
- 1541 Juggins, S.: Rioja: Analysis of Quaternary Science Data. [https://doi.org/https://cran.r-](https://doi.org/https://cran.r-project.org/package=rioja)
1542 [project.org/package=rioja](http://www.staff.ncl.ac.uk/stephen.juggins/), <http://www.staff.ncl.ac.uk/stephen.juggins/>, 2020.
- 1543 Kageyama, M., Harrison, S.P., Kapsch, M.-L., Lofverstrom, M., Lora, J.M.,
1544 Mikolajewicz, U., Sherriff-Tadano, S., Vadsaria, T., Abe-Ouchi, A., Bouttes, N.,
1545 Chandan, D., Gregoire, L.J., Ivanovic, R.F., Izumi, K., LeGrande, A.N., Lhardy, F.,
1546 Lohmann, G., Morozova, P.A., Ohgaito, R., Paul, A., Peltier, W.R., Poulsen, C.J.,
1547 Quiquet, A., Roche, D.M., Shi, X., Tierney, J.E., Valdes, P.J., Volodin, E., Zhu, J.:
1548 The PMIP4 Last Glacial Maximum experiments: preliminary results and
1549 comparison with the PMIP3 simulations. *Clim. Past* 17, 1065–1089.
1550 <https://doi.org/10.5194/cp-17-1065-2021>, 2021.
- 1551 Kaplan, J.O., Pfeiffer, M., Kolen, J.C.A., Davis, B.A.S.: Large Scale Anthropogenic
1552 Reduction of Forest Cover in Last Glacial Maximum Europe. *PLOS ONE* 11,
1553 e0166726. <https://doi.org/10.1371/journal.pone.0166726>, 2016.
- 1554 Kaplan, J.O., Bigelow, N.H., Prentice, I.C., Harrison, S.P., Bartlein, P.J., Christensen,
1555 T.R., Cramer, W., Matveyeva, N.V., McGuire, A.D., Murray, D.F., Razzhivin,
1556 V.Y., Smith, B., Walker, D.A., Anderson, P.M., Andreev, A.A., Brubaker, L.B.,
1557 Edwards, M.E., Lozhkin, A.V.: Climate change and Arctic ecosystems: 2.
1558 Modeling, paleodata-model comparisons, and future projections. *J. Geophys.*
1559 *Res. Atmospheres* 108, 2002JD002559.
1560 <https://doi.org/10.1029/2002JD002559>, 2003.
- 1561 Kern, O.A., Maier, A., Vercauteren, N.: Landscape reconstructions for Europe during
1562 the late Last Glacial (60–20 ka BP): A pollen-based REVEALS approach.
1563 <https://doi.org/10.5194/essd-2024-306>, 2024.
- 1564 Kern, O.A., Koutsodendris, A., Pross, J.: Palynological data for the Late Glacial and
1565 Holocene (14.5–0 ka BP) from Füramoos, Southern Germany. *Data Brief* 39,
1566 107650. <https://doi.org/10.1016/j.dib.2021.107650>, 2021.
- 1567 Kühl, N., Gebhardt, C., Litt, T., Hense, A.: Probability Density Functions as Botanical-
1568 Climatological Transfer Functions for Climate Reconstruction. *Quat. Res.* 58,
1569 381–392. <https://doi.org/10.1006/qres.2002.2380>, 2002.
- 1570 Kühl, N., Moschen, R., Wagner, S., Brewer, S., Peyron, O.: A multiproxy record of late
1571 Holocene natural and anthropogenic environmental change from the
1572 Sphagnum peat bog Dürres Maar, Germany: implications for quantitative
1573 climate reconstructions based on pollen. *J. Quat. Sci.* 25, 675–688.
1574 <https://doi.org/10.1002/jqs.1342>, 2010.
- 1575 Kühl, N., Litt, T.: Quantitative time series reconstruction of Eemian temperature at
1576 three European sites using pollen data. *Veg. Hist. Archaeobotany* 12, 205–
1577 214. <https://doi.org/10.1007/s00334-003-0019-2>, 2003.
- 1578 Küster, H.: Postglaziale Vegetationsgeschichte Südbayerns, Geobotanische Studien
1579 zur Prähistorischen Landschaftskunde, Akademie Verlag, Berlin, ISBN 978-3-
1580 05-501592-2, 1995.

- Li, C., Dallmeyer, A., Ni, J., Chevalier, M., Willeit, M., Andreev, A.A., Cao, X., Schild, L., Heim, B., Herzschuh, U.: Global biome changes over the last 21,000 years inferred from model-data comparisons. <https://doi.org/10.5194/egusphere-2024-1862>, 2024.
- Liu, M., Prentice, I.C., Ter Braak, C.J.F., Harrison, S.P.: An improved statistical approach for reconstructing past climates from biotic assemblages. *Proc. R. Soc. Math. Phys. Eng. Sci.* 476, 20200346. <https://doi.org/10.1098/rspa.2020.0346>, 2020.
- Valero-Garcés, B. L., González-Sampériz, P., Navas, A., Machin, J., Delgado-Huertas, A., Pena-Monné, J. L., Sancho-Marcén, C., Stevenson, T., and Davis, B.: Paleohydrological fluctuations and steppe vegetation during the last glacial maximum in the central Ebro valley (NE Spain), *Quatern. Int.*, 122, 43–55, <https://doi.org/10.1016/j.quaint.2004.01.030>, 2004.
- Magyari, E. K., Pál, I., Vincze, I., Veres, D., Jakab, G., Braun, M., Szalai, Z., Szabó, Z., and Korponai, J.: Warm Younger Dryas summers and early late glacial spread of temperate deciduous trees in the Pannonian Basin during the last glacial termination (20–9 kyr cal BP), *Quat. Sci. Rev.*, 225, 105980, <https://doi.org/10.1016/j.quascirev.2019.105980>, 2019.
- Magyari, E. K., Kuneš, P., Jakab, G., Sümegi, P., Pelánková, B., Schäbitz, F., Braun, M., and Chytrý, M.: Late Pleniglacial vegetation in eastern-central Europe: Are there modern analogues in Siberia?, *Quaternary Sci. Rev.*, 95, 60–79, <https://doi.org/10.1016/j.quascirev.2014.04.020>, 2014.
- Magyari, E., Jakab, G., Rudner, E., and Sümegi, P.: Palynological and plant macrofossil data on Late Pleistocene short-term climatic oscillations in NE-Hungary, *Acta Palaeobot. Suppl.*, 2, 491–502, 1999.
- Magri, D. and Sadori, L.: Late Pleistocene and Holocene pollen stratigraphy at Lago di Vico, central Italy, *Veg. Hist. Archaeobot.*, 8, 247–260. <https://doi.org/10.1007/BF01291777>, 1979.
- Margari, V., Gibbard, P. L., Bryant, C. L., and Tzedakis, P. C.: Character of vegetational and environmental changes in southern Europe during the last glacial period; evidence from Lesvos Island, Greece, *Quaternary Sci. Rev.*, 28, 1317–1339. <https://doi.org/10.1016/j.quascirev.2009.01.008>, 2009.
- Marinova, E., Harrison, S. P., Bragg, F., Connor, S., de Laet, V., Leroy, S. A. G., Mudie, P., Atanassova, J., Bozilova, E., Caner, H., Cordova, C., Djamali, M., Filipova-Marinova, M., Gerasimenko, N., Jahns, S., Kouli, K., Kotthoff, U., Kvavadze, E., Lazarova, M., Novenko, E., Ramezani, E., Röpke, A., Shumilovskikh, L., Tanțău, I., and Tonkov, S.: Pollen-derived biomes in the Eastern Mediterranean–Black Sea–Caspian–Corridor, *J. Biogeogr.*, 45, 484–499. <https://doi.org/10.1111/jbi.13128>, 2019.
- Martin, C., Ménot, G., Thouveny, N., Peyron, O., Andrieu-Ponel, V., Montade, V., Davtian, N., Reille, M., Bard, E.: Early Holocene Thermal Maximum recorded by branched tetraethers and pollen in Western Europe (Massif Central, France). *Quat. Sci. Rev.* 228, 106109. <https://doi.org/10.1016/j.quascirev.2019.106109>, 2020.
- Mauri, A., Davis, B.A.S., Collins, P.M., Kaplan, J.O.: The climate of Europe during the Holocene: a gridded pollen-based reconstruction and its multi-proxy

- evaluation. *Quat. Sci. Rev.* 112, 109–127.
<https://doi.org/10.1016/j.quascirev.2015.01.013>, 2015.
- Mauri, A., Davis, B.A.S., Collins, P.M., Kaplan, J.O.: The influence of atmospheric circulation on the mid-Holocene climate of Europe: a data–model comparison. *Clim. Past* 10, 1925–1938. <https://doi.org/10.5194/cp-10-1925-2014>, 2014.
- Miebach, A., Niestrath, P., Roeser, P., and Litt, T.: Impacts of climate and humans on the vegetation in northwestern Turkey: palynological insights from Lake Iznik since the Last Glacial, *Clim. Past*, 12, 575–593. <https://doi.org/10.5194/cp-12575-2016>, 2016.
- Miola, A., Bondesan, A., Corain, L., Favaretto, S., Mozzi, P., Piovan, S., and Sostizzo, I.: Wetlands in the Venetian Po Plain (northeastern Italy) during the Last Glacial Maximum: Interplay between vegetation, hydrology and sedimentary environment, *Rev. Palaeobot. Palynol.*, 141, 53–81.
<https://doi.org/10.1016/j.revpalbo.2006.03.016>, 2006.
- Monegato, G., Ravazzi, C., Donegana, M., Pini, R., Calderoni, G., and Wick, L.: Evidence of a two-fold glacial advance during the last glacial maximum in the Tagliamento end moraine system (eastern Alps), *Quatern. Res.*, 68, 284–302.
<https://doi.org/10.1016/j.yqres.2007.07.002>, 2007.
- Netzel, T., Miebach, A., Litt, T., Hense, A.: New probabilistic methods for quantitative climate reconstructions applied to palynological data from Lake Kinneret. *Clim. Past* 21, 357–380. <https://doi.org/10.5194/cp-21-357-2025>, 2025.
- Ortega-Rosas, C.I., Guiot, J., Peñalba, M.C., Ortiz-Acosta, M.E.: biomisation and quantitative climate reconstruction techniques in northwestern Mexico— With an application to four Holocene pollen sequences. *Glob. Planet. Change* 61, 242–266. <https://doi.org/10.1016/j.gloplacha.2007.10.006>, 2008.
- Overpeck, J.T., Webb, T., Prentice, I.C.: Quantitative Interpretation of Fossil Pollen Spectra: Dissimilarity Coefficients and the Method of Modern Analogs. *Quat. Res.* 23, 87–108. [https://doi.org/10.1016/0033-5894\(85\)90074-2](https://doi.org/10.1016/0033-5894(85)90074-2), 1985.
- Paganelli, A.: Evolution of vegetation and climate in the Veneto-Po Plain during the Late-Glacial and Early Holocene using pollen stratigraphical data, *Alp. Mediterr. Quat.*, 9, 581–589. <https://doi.org/10.26382/>, 1996.
- Peltier, W.R., Solheim, L.P.: The climate of the Earth at Last Glacial Maximum: statistical equilibrium state and a mode of internal variability. *Quat. Sci. Rev.* 23, 335–357. <https://doi.org/10.1016/j.quascirev.2003.07.003>, 2004.
- Pérez-Obiol, R. P. and Julia, R.: Climatic change on the Iberian Peninsula recorded in a 30,000-year pollen record from Lake Banyoles, *Quaternary Res.*, 41, 91–98, 1994.
- Peyron, O., Magny, M., Goring, S., Joannin, S., De Beaulieu, J.-L., Brugiapaglia, E., Sadori, L., Garfi, G., Kouli, K., Ioakim, C., Combourieu-Nebout, N.: Contrasting patterns of climatic changes during the Holocene across the Italian Peninsula reconstructed from pollen data. *Clim. Past* 9, 1233–1252.
<https://doi.org/10.5194/cp-9-1233-2013>, 2013.
- Peyron, O., Bégeot, C., Brewer, S., Heiri, O., Magny, M., Millet, L., Ruffaldi, P., Van Campo, E., Yu, G.: Late-Glacial climatic changes in Eastern France (Lake Lautrey) from pollen, lake-levels, and chironomids. *Quat. Res.* 64, 197–211.
<https://doi.org/10.1016/j.yqres.2005.01.006>, 2005.

- Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., De Beaulieu, J.-L., Bottema, S., Andrieu, V.: Climatic Reconstruction in Europe for 18,000 YR B.P. from Pollen Data. *Quat. Res.* 49, 183–196. <https://doi.org/10.1006/qres.1997.1961>, 1998.
- Pini, R., Ravazzi, C., and Donegana, D.: Pollen stratigraphy, vegetation and climate history of the last 215 ka in the Azzano Decimo core (plain of Friuli, north-eastern Italy), *Quaternary Sci. Rev.*, 28, 1268–1290. <https://doi.org/10.1016/j.quascirev.2008.12.017>, 2009.
- Prentice, I.C., Villegas-Diaz, R., Harrison, S.P.: Accounting for atmospheric carbon dioxide variations in pollen-based reconstruction of past hydroclimates. *Glob. Planet. Change* 211, 103790. <https://doi.org/10.1016/j.gloplacha.2022.103790>, 2022.
- Prentice, I.C., Harrison, S.P., Jolly, D.: The climate and biomes of Europe at 6000 yr bp: comparison of model simulations and pollen-based reconstructions. *Quaternary Science Reviews*, 1998, 17 (6-7), pp.659-668. [https://doi.org/10.1016/S0277-3791\(98\)00016-X](https://doi.org/10.1016/S0277-3791(98)00016-X), 1998.
- Prentice, I.C., Webb Iii, T.: BIOME 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. *J. Biogeogr.* 25, 997–1005. <https://doi.org/10.1046/j.1365-2699.1998.00235.x>, 1998.
- Prentice, I.C., Guiot, J., Huntley, B., Jolly, D., Cheddadi, R.: Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. *Clim. Dyn.* 12, 185–194. <https://doi.org/10.1007/BF00211617>, 1996.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., Solomon, A.M.: Special Paper: A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate. *J. Biogeogr.* 19, 117. <https://doi.org/10.2307/2845499>, 1992.
- Ramstein, G., Kageyama, M., Guiot, J., Wu, H., Hély, C., Krinner, G., and Brewer, S.: How cold was Europe at the Last Glacial Maximum? A synthesis of the progress achieved since the first PMIP model-data comparison, *Clim. Past*, 3, 331–339. <https://doi.org/10.5194/cp-3-331-2007>, 2007.
- Reille, M. and Andrieu, V.: The late Pleistocene and Holocene in the Lourdes Basin, Western Pyrénées, France: new pollen analytical and chronological data, *Veg. Hist. Archaeobot.*, 4, 1–21. <https://doi.org/10.1007/BF00198611>, 1995.
- 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, 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., Talamo, S.: The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon* 62, 725–757. <https://doi.org/10.1017/RDC.2020.41>, 2020.
- Robles, M., Peyron, O., Ménot, G., Brugiapaglia, E., Wulf, S., Appelt, O., Blache, M., Vanni re, B., Dugerdil, L., Paura, B., Ansanay-Alex, S., Cromartie, A., Charlet, L., Gu dron, S., De Beaulieu, J.-L., Joannin, S.: Climate changes during the Late

- 1721 Glacial in southern Europe: new insights based on pollen and brGDGTs of Lake
 1722 Matese in Italy. *Clim. Past* 19, 493–515. [https://doi.org/10.5194/cp-19-493-](https://doi.org/10.5194/cp-19-493-2023)
 1723 [2023](https://doi.org/10.5194/cp-19-493-2023), 2023.
- 1724 Sadori, L., Koutsodendris, A., Panagiotopoulos, K., Masi, A., Bertini, A., Combourieu-
 1725 Nebout, N., Francke, A., Kouli, K., Joannin, S., Mercuri, A.M., Peyron, O., Torri,
 1726 P., Wagner, B., Zanchetta, G., Sinopoli, G., Donders, T.H.: Pollen-based
 1727 paleoenvironmental and paleoclimatic change at Lake Ohrid (south-eastern
 1728 Europe) during the past 500 ka. *Biogeosciences* 13, 1423–1437.
 1729 <https://doi.org/10.5194/bg-13-1423-2016>, 2016.
- 1730 Salonen, J.S., Korpela, M., Williams, J.W., Luoto, M.: Machine-learning based
 1731 reconstructions of primary and secondary climate variables from North
 1732 American and European fossil pollen data. *Sci. Rep.* 9, 15805.
 1733 <https://doi.org/10.1038/s41598-019-52293-4>, 2019.
- 1734 Sánchez Goñi, M.F., Desprat, S., Daniau, A.-L., Bassinot, F.C., Polanco-Martínez, J.M.,
 1735 Harrison, S.P., Allen, J.R.M., Anderson, R.S., Behling, H., Bonnefille, R.,
 1736 Burjachs, F., Carrión, J.S., Cheddadi, R., Clark, J.S., Combourieu-Nebout, N.,
 1737 Mustaphi, Colin.J.C., Debussk, G.H., Dupont, L.M., Finch, J.M., Fletcher, W.J.,
 1738 Giardini, M., González, C., Gosling, W.D., Grigg, L.D., Grimm, E.C., Hayashi, R.,
 1739 Helmens, K., Heusser, L.E., Hill, T., Hope, G., Huntley, B., Igarashi, Y., Irino, T.,
 1740 Jacobs, B., Jiménez-Moreno, G., Kawai, S., Kershaw, A.P., Kumon, F., Lawson,
 1741 I.T., Ledru, M.-P., Lézine, A.-M., Liew, P.M., Magri, D., Marchant, R., Margari,
 1742 V., Mayle, F.E., McKenzie, G.M., Moss, P., Müller, S., Müller, U.C., Naughton,
 1743 F., Newnham, R.M., Oba, T., Pérez-Obiol, R., Pini, R., Ravazzi, C., Roucoux,
 1744 K.H., Rucina, S.M., Scott, L., Takahara, H., Tzedakis, P.C., Urrego, D.H., Van
 1745 Geel, B., Valencia, B.G., Vandergoes, M.J., Vincens, A., Whitlock, C.L., Willard,
 1746 D.A., Yamamoto, M.: The ACER pollen and charcoal database: a global
 1747 resource to document vegetation and fire response to abrupt climate changes
 1748 during the last glacial period. *Earth Syst. Sci. Data* 9, 679–695.
 1749 <https://doi.org/10.5194/essd-9-679-2017>, 2017.
- 1750 Sassoon, D., Combourieu-Nebout, N., Peyron, O., Bertini, A., Toti, F., Lebreton, V.,
 1751 Moncel, M.-H.: Pollen-based climatic reconstructions for the interglacial
 1752 analogues of MIS 1 (MIS 19, 11, and 5) in the southwestern Mediterranean:
 1753 insights from ODP Site 976. *Clim. Past* 21, 489–515.
 1754 <https://doi.org/10.5194/cp-21-489-2025>, 2025.
- 1755 Satkunas, J. and Grigienė, A.: Eemian-Weichselian palaeoenvironmental record from
 1756 the Mickūnai glacial depression (Eastern Lithuania), *Geologija*, 54, 35–51,
 1757 <https://doi.org/10.6001/geologija.v54i2.2482>, 2012.
- 1758 Seguinot, J., Ivy-Ochs, S., Juvet, G., Huss, M., Funk, M., Preusser, F.: Modelling last
 1759 glacial cycle ice dynamics in the Alps. *The Cryosphere* 12, 3265–3285.
 1760 <https://doi.org/10.5194/tc-12-3265-2018>, 2018.
- 1761 Šeirienė, V., Kūhl, N., Kisielienė, D.: Quantitative reconstruction of climate variability
 1762 during the Eemian (Merkinė) and Weichselian (Nemunas) in Lithuania. *Quat.*
 1763 *Res.* 82, 229–235. <https://doi.org/10.1016/j.yqres.2014.04.004>, 2014.
- 1764 Seltzer, A.M., Blard, P.-H., Sherwood, S.C., Kageyama, M.: Terrestrial amplification of
 1765 past, present, and future climate change. *Sci. Adv.* 9, eadf8119.
 1766 <https://doi.org/10.1126/sciadv.adf8119>, 2023.

- 1767 Sinopoli, G., Masi, A., Regattieri, E., Wagner, B., Francke, A., Peyron, O., Sadori, L.:
 1768 Palynology of the Last Interglacial Complex at Lake Ohrid:
 1769 palaeoenvironmental and palaeoclimatic inferences. *Quat. Sci. Rev.* 180, 177–
 1770 192. <https://doi.org/10.1016/j.quascirev.2017.11.013>, 2018.
- 1771 Sirocko, Frank; Knapp, Hannes; Dreher, Frank; Förster, Michael W; Albert, Johannes;
 1772 Brunck, Heiko; Veres, Daniel; Dietrich, Stephan; Zech, Michael; Hambach,
 1773 Ulrich; Röhner, Marieke; Rudert, Saskia; Schwiebus, Klaus; Adams, Christel;
 1774 Sigl, Petra.: The ELSA-Vegetation-Stack: Reconstruction of Landscape
 1775 Evolution Zones (LEZ) from laminated Eifel maar sediments of the last 60,000
 1776 years. *Global and Planetary Change*, 142, 108-135.
 1777 <https://doi.org/10.1016/j.gloplacha.2016.03.005>, 2016.
- 1778 Strahl, J.: Zur Pollenstratigraphie des Weichselspätglazials von Berlin-Brandenburg
 1779 [On the palynostratigraphy of the Late Weichselian in Berlin-Brandenburg],
 1780 Brand. Geowissensch. Beitr., 12, 87–112, 2005.
- 1781 Tarasov, P.E., Müller, S., Zech, M., Andreeva, D., Diekmann, B., Leipe, C.: Last glacial
 1782 vegetation reconstructions in the extreme-continental eastern Asia:
 1783 Potentials of pollen and n-alkane biomarker analyses. *Quat. Int.* 290–291.
 1784 253–263. <https://doi.org/10.1016/j.quaint.2012.04.007>, 2013.
- 1785 Tarasov, P.E., Peyron, O., Guiot, J., Brewer, S., Volkova, V.S., Bezusko, L.G.,
 1786 Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I.M., Panova, N.K.: Last Glacial
 1787 Maximum climate of the former Soviet Union and Mongolia reconstructed
 1788 from pollen and plant macrofossil data. *Clim. Dyn.* 15, 227–240.
 1789 <https://doi.org/10.1007/s003820050278>, 1999.
- 1790 Tarasov, P.E., Volkova, V.S., Ili, T.W., Guiot, J., Andreev, A.A., Bezusko, L.G., Bykova,
 1791 G.V., Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I.M., Panova, N.K.,
 1792 Sevastyanov, D.V.: Black well Science, Ltd Last glacial maximum biomes
 1793 reconstructed from pollen and plant macrofossil data from northern Eurasia.
 1794 *J. Biogeogr.*, 27, 609-620. <https://doi.org/10.1046/j.1365-2699.2000.00429.x>,
 1795 2000.
- 1796 Ter Braak, C.J.F., Juggins, S.: Weighted averaging partial least squares regression (WA-
 1797 PLS): an improved method for reconstructing environmental variables from
 1798 species assemblages. *Hydrobiologia* 485–502.
 1799 <https://doi.org/10.1007/BF00028046>, 1993.
- 1800 Ter Braak, C.J.F., Looman, W.N.C.: Weighted Averaging, Logistic Regression and the
 1801 Gaussian Response Model. *Vegetation*, vol. 65, no. 1, pp. 3–11. JSTOR.
 1802 <http://www.jstor.org/bases-doc.univ-lorraine.fr/stable/20037257>, 1986.
- 1803 Tonkov, S., Lazarova, M., Bozilova, E., Ivanov, D., Snowball, I.: A 30,000-year pollen
 1804 record from Mire Kupena, Western Rhodopes Mountains (south Bulgaria).
 1805 *Rev. Palaeobot. Palynol.* 209, 41–51.
 1806 <https://doi.org/10.1016/j.revpalbo.2014.06.002>, 2014.
- 1807 Trasune, L., Välranta, M., Stivirs, N., Amon, L., Schenk, F., Salonen, J.S.: A
 1808 comparison of plant macrofossil-based quantitative climate reconstruction
 1809 methods: A case study of the lateglacial Baltic States. *Quat. Sci. Rev.* 33.
 1810 108811. <https://doi.org/10.1016/j.quascirev.2024.108811>, 2024.
- 1811 Tzedakis, P. C., Frogley, M. R., Lawson, I. T., Preece, R. C., Cacho, I., and de Abreu, L.:
 1812 Ecological thresholds and patterns of millennial-scale climate variability: The

- 1813 response of vegetation in Greece during the last glacial period, *Geology*, 32.
 1814 109–112, <https://doi.org/10.1130/G20118.1>, 2004.
- 1815 Vegas-Vilarrúbia, T., González-Sampériz, P., Morellón, M., GilRomera, G., Pérez-Sanz,
 1816 A., and Valero-Garcés, B.: Diatom and vegetation responses to late glacial and
 1817 early holocene climate changes at lake estanya (southern pyrenees, NE spain),
 1818 *Palaeogeogr. Palaeoclim. Palaeoecol.*, 392, 335–349.
 1819 <https://doi.org/10.1016/j.palaeo.2013.09.011>, 2013.
- 1820 Viau, A.E., Gajewski, K.: Reconstructing Millennial-Scale, Regional Paleoclimates of
 1821 Boreal Canada during the Holocene. *J. Clim.* 22, 316–330.
 1822 <https://doi.org/10.1175/2008JCLI2342.1>, 2009.
- 1823 Watts, W. A., Allen, J. R. M., and Huntley, B.: Vegetation history and palaeoclimate of
 1824 the last glacial period at Lago grande di Monticchio, southern Italy,
 1825 *Quaternary Sci. Rev.*, 15, 133–153. [https://doi.org/10.1016/0277-](https://doi.org/10.1016/0277-3791(95)00093-3)
 1826 [3791\(95\)00093-3](https://doi.org/10.1016/0277-3791(95)00093-3), 1996.
- 1827 Williams, J.W., Shuman, B.: Obtaining accurate and precise environmental
 1828 reconstructions from the modern analog technique and North American
 1829 surface pollen dataset. *Quat. Sci. Rev.* 27, 669–687.
 1830 <https://doi.org/10.1016/j.quascirev.2008.01.004>, 2008
- 1831 Wu, H., Guiot, J., Brewer, S., Guo, Z.: Climatic changes in Eurasia and Africa at the last
 1832 glacial maximum and mid-Holocene: reconstruction from pollen data using
 1833 inverse vegetation modelling. *Clim. Dyn.* 29, 211–229.
 1834 <https://doi.org/10.1007/s00382-007-0231-3>, 2007.
- 1835 Xu, Q., Zhang, S., Gaillard, M., Li, M., Cao, X., Tian, F., Li, F.: Studies of modern pollen
 1836 assemblages for pollen dispersal- deposition- preservation process
 1837 understanding and for pollen-based reconstructions of past vegetation,
 1838 climate, and human impact: A review based on case studies in China. *Quat.*
 1839 *Sci. Rev.* 149, 151–166. <https://doi.org/10.1016/j.quascirev.2016.07.017>,
 1840 2016.
- 1841 Zumaque, J., De Vernal, A., Fréchette, B., Guiot, J., Sánchez-Goñi, M.F., Barhoumi, C.,
 1842 Peyron, O., Peros, M., Burke, A., Camuera, J., Jiménez-Moreno, G., Ramos-
 1843 Román, M.J.: Decoupled winter and summer climate changes in southern
 1844 Europe during the Dansgaard-Oeschger cycles. *Quaternary Science Reviews.*
 1845 <https://doi.org/10.1016/j.quascirev.2025.109273>, 2025.