

Paleoceanography and Paleoclimatology*

RESEARCH ARTICLE

10.1029/2026PA005517

Key Points:

- Western Iberia hydroclimate shows an early to mid-Holocene trajectory from wet to arid conditions, with a more variable late Holocene
- Latitudinal temperature gradients shaped storm tracks and controlled long-term moisture in western Iberia
- Centennial-variability reflects ocean-atmosphere dynamics, including North Atlantic Oscillation influences and ocean circulation changes

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

U. Fernández-Pérez and A. Hernández,
m.eugenia.fernandezp@udc.es;
armand.hernandez@udc.es

Citation:

Fernández-Pérez, U., Santos, R. N., Rodrigues, T., Schefuß, E., Bao, R., Raposeiro, P. M., et al. (2026). North Atlantic ocean-atmosphere dynamics controlled the hydroclimate in western Iberia during the Holocene. *Paleoceanography and Paleoclimatology*, 41, e2026PA005517. <https://doi.org/10.1029/2026PA005517>

Received 14 APR 2026

Accepted 8 SEP 2026

Author Contributions:

Conceptualization: U. Fernández-Pérez, R. N. Santos, T. Rodrigues, E. Schefuß, A. Hernández

Data curation: U. Fernández-Pérez, A. Hernández

Formal analysis: U. Fernández-Pérez, R. N. Santos, T. Rodrigues, E. Schefuß, P. M. Raposeiro, A. Sáez, S. Giralt, C. Martín-Puertas, P. Francus, A. Hernández

© 2026 The Author(s). Paleoceanography and Paleoclimatology published by Wiley Periodicals LLC on behalf of American Geophysical Union.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs License](#), which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

North Atlantic Ocean–Atmosphere Dynamics Controlled the Hydroclimate in Western Iberia During the Holocene

U. Fernández-Pérez¹ , R. N. Santos² , T. Rodrigues^{3,4} , E. Schefuß⁵ , R. Bao¹ , P. M. Raposeiro^{6,7} , A. Sáez⁸ , S. Giralt⁹ , C. Martín-Puertas¹⁰ , P. Francus^{11,12} , R. M. Trigo^{13,14} , A. M. Ramos¹⁵ , and A. Hernández¹ 

¹Grupo de Investigación en Cambio Ambiental e Paleobiología (GRICA-BIOpast), Centro Interdisciplinar de Química e Biología (CICA), Universidade da Coruña, A Coruña, Spain, ²Department of Environmental Sciences, University of Basel, Basel, Switzerland, ³IPMA – Portuguese Institute of Sea and Atmosphere, Lisbon, Portugal, ⁴CCMAR – Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Faro, Portugal, ⁵MARUM – Center for Marine Environmental Sciences, University of Bremen, Bremen, Germany, ⁶Faculdade de Ciências e Tecnologia, Universidade dos Açores, Ponta Delgada, Portugal, ⁷CBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Ponta Delgada, Portugal, ⁸UB-Geomodels Research Institute, Department of Earth and Ocean Dynamics, Universitat de Barcelona, Barcelona, Spain, ⁹Geosciences Barcelona (GEO3BCN), CSIC, Barcelona, Spain, ¹⁰Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain, ¹¹Centre Eau Terre Environnement, Institut national de la recherche scientifique, Quebec, QC, Canada, ¹²GEOTOP Research Centre, Montreal, QC, Canada, ¹³Faculdade de Ciências, Instituto Dom Luiz (IDL), Universidade de Lisboa, Lisboa, Portugal, ¹⁴Departamento de Meteorologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, ¹⁵Institute of Meteorology and Climate Research Troposphere Research (IMKTRO), Karlsruhe Institute of Technology (KIT), Karlsruhe, Germany

Abstract Hydroclimate variability in western Iberia during the Holocene remains insufficiently resolved despite the high sensitivity of this region to the North Atlantic atmosphere and ocean dynamics. Here, we present the first source-resolved reconstruction of centennial- to millennial-scale moisture variability over the last 11,000 years using sediments from Lake Peixão (Portugal) based on compound-specific hydrogen and carbon isotopes of plant wax *n*-alkanes, supported by bulk organic geochemistry and continuous X-ray fluorescence elemental data. Terrestrial source-resolved isotope series, obtained using non-negative matrix factorization, primarily reflect precipitation isotopic composition and plant water use efficiency. The record indicates a wet early Holocene, a progressive mid-Holocene drying trend that culminated in maximum aridity at approximately 4,000 calibrated years before present, and a transition to generally wetter but more variable late Holocene conditions, partly overprinted by anthropogenic land-use change. These trends are interpreted as reflecting orbitally driven changes in Northern Hemisphere insolation that modified the latitudinal temperature gradient (LTG) and, in turn, influenced the North Atlantic storm track position and intensity. Enhanced early Holocene moisture reflects a higher LTG and southward-displaced storm tracks, whereas mid-Holocene aridity corresponds to a reduced LTG and northward-shifted westerlies. The late Holocene recovery of wetter conditions agrees with a higher LTG and increased storm-track influence over Iberia. Superimposed centennial-scale variability likely reflects changes in North Atlantic Oscillation phases, the position of the Azores Front, and the intensity of the subpolar gyre. These results demonstrate the dominant roles of the LTG and coupled ocean-atmosphere dynamics in shaping the western Iberian hydroclimate throughout the Holocene.

Plain Language Summary Rainfall in western Iberia depends strongly on North Atlantic atmospheric dynamics, but how it has changed over thousands of years is still not well known. Understanding this long-term variability is key to anticipating future water availability. We reconstructed 11,000 years of moisture variations using sediments from a mountain lake in Portugal. We analyzed chemical signals preserved in the plant-waxes, together with additional information from the lake sediments. Western Iberia was generally wetter during the early-Holocene, became progressively drier during the mid-Holocene, and reached its driest state approximately 4,000 years ago. Wetter conditions returned during the late-Holocene, although climate variability increased and humans began to leave a larger imprint on the landscape. These changes were driven mainly by shifts in the temperature contrast between low and high latitudes, which controlled the path of North Atlantic storms. Stronger contrasts pushed storms southward, bringing more rain to Iberia, whereas weaker contrasts led to drier conditions. High-frequency changes were likely linked to other atmospheric patterns such as the North Atlantic Oscillation. By revealing how large-scale climate dynamics shaped rainfall over thousands

Funding acquisition: R. M. Trigo, A. M. Ramos, A. Hernández
Investigation: U. Fernández-Pérez, R. N. Santos, T. Rodrigues, E. Schefuß, R. Bao, P. M. Raposeiro, A. Sáez, S. Giral, C. Martín-Puertas, P. Francus, R. M. Trigo, A. M. Ramos, A. Hernández
Methodology: U. Fernández-Pérez, R. N. Santos, T. Rodrigues, E. Schefuß, R. Bao, A. Sáez, S. Giral, C. Martín-Puertas, P. Francus, A. Hernández
Project administration: A. M. Ramos, A. Hernández
Resources: T. Rodrigues, E. Schefuß, R. Bao
Supervision: T. Rodrigues, E. Schefuß, R. Bao, A. Hernández
Validation: T. Rodrigues, E. Schefuß, R. Bao, C. Martín-Puertas, P. Francus
Visualization: U. Fernández-Pérez, R. N. Santos, R. Bao, A. Sáez, C. Martín-Puertas, A. Hernández
Writing – original draft: U. Fernández-Pérez, A. Hernández
Writing – review & editing: U. Fernández-Pérez, R. N. Santos, T. Rodrigues, E. Schefuß, R. Bao, P. M. Raposeiro, A. Sáez, S. Giral, C. Martín-Puertas, P. Francus, R. M. Trigo, A. M. Ramos, A. Hernández

of years, this study provides a key context for understanding how future water availability in western Iberia may respond to future climate change.

1. Introduction

The climate during the Holocene is often described as relatively stable but includes rapid hydroclimate shifts and high regional variability driven by changes in atmospheric and oceanic forcings (Wanner et al., 2008, 2011). Understanding this variability is crucial, as the Holocene provides a long-term context for placing current and predicted hydroclimate extremes within the envelope of natural variability (Kaufman et al., 2020; Mayewski et al., 2004). At mid-latitudes in the Northern Hemisphere (~30–60°N), the long-term variability in the Holocene hydroclimate is driven by orbital forcing through its control of the latitudinal temperature gradient (LTG) between the equator and poles, which modulates coupled tropical–extratropical circulation patterns (Routson et al., 2019). Specifically, over the North Atlantic sector and Iberia, this orbital-scale variability is superimposed by multi-decadal to centennial internal variability driven by various modes of climate variability, including the North Atlantic Oscillation (NAO) and the East Atlantic (EA) pattern, as well as shifts in ocean circulation patterns, such as the Azores Front and the strength of the subpolar gyre, which modulate sea-surface temperature gradients and westerly flow (Comas-Bru & McDermott, 2014; Hernández, Martín-Puertas, et al., 2020; Hernández, Sánchez-López, et al., 2020; Repschläger et al., 2017; Thornalley et al., 2009; Trigo et al., 2008).

NAO-like variability has been frequently invoked to explain Holocene hydroclimate changes in southwestern Europe (Ait Brahim et al., 2019; Hernández, Sánchez-López, et al., 2020), but the extent to which the combination of atmospheric and oceanic circulation shifts governed spatial heterogeneity across Iberia remains poorly understood. This uncertainty results partly from the nonstationarity of these shifts and partly from the unequal spatial distribution of proxy-based records and differences in seasonal sensitivity among archives (Hernández, Martín-Puertas, et al., 2020). Furthermore, the coupling between Atlantic and Mediterranean circulation systems introduces additional complexity into Iberian hydroclimate seasonality (Fernández-Alvarez et al., 2023; Lionello et al., 2006; Paredes et al., 2006; Ramos et al., 2014; Trigo et al., 2008).

The Iberian Peninsula occupies a strategic position to assess regional Holocene hydroclimate variability. Located at the interface between North Atlantic westerlies and Mediterranean influences, Iberia experiences steep west–east moisture gradients that respond to interactions operating at both millennial and centennial timescales, including Atlantic–Mediterranean seesaw dynamics, thereby creating complex spatial and temporal patterns of hydroclimate changes (Fernández-Pérez et al., 2025; García-Alix et al., 2021; Sáez et al., 2025; Sánchez-López et al., 2016; Santos et al., 2024). Existing paleoclimate records reveal orbital-scale trends consistent with broader Northern Hemisphere patterns (Moreno et al., 2017; Schirrmacher et al., 2019; Smith et al., 2016; Thatcher et al., 2020; Vegas et al., 2010), but west–central Iberia remains severely underrepresented in paleoclimate reconstructions (Moreno et al., 2023; Taylor et al., 2018; Thatcher et al., 2020). This gap is critical because this region, which is the first landmass intercepting North Atlantic westerlies, lies on the transitional boundary between Atlantic and Mediterranean climatic regimes, rendering it uniquely sensitive to coupled ocean–atmosphere dynamics. This data gap also reveals the fundamental limitations of conventional paleoclimate proxies (e.g., bulk organic geochemistry, XRF-derived elemental ratios), which often cannot distinguish among multiple hydroclimate signals or separate contributions from different environmental sources, limiting our ability to fully resolve centennial-scale variability superimposed onto millennial-scale orbital trends.

To mitigate this issue, compound-specific isotopes from plant-wax *n*-alkanes offer an effective tool for reconstructing past hydroclimate and vegetation dynamics, as demonstrated by regional applications across the Iberian Peninsula (Santos et al., 2024; Schäfer et al., 2018; Schirrmacher et al., 2020). Plant-wax $\delta^2\text{H}_{n\text{-alk}}$ values ($\delta^2\text{H}_{n\text{-alk}}$) ultimately reflect the isotopic composition of precipitation and are therefore valuable for inferring past hydroclimatic conditions (Freimuth et al., 2017). Moreover, the variations in plant-wax *n*-alkane $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{n\text{-alk}}$) provide key information on changes in vegetation composition and plant physiological responses to environmental conditions, particularly water availability (Diefendorf & Freimuth, 2017). However, plant-wax records preserved in lacustrine sediments typically contain mixtures of terrestrial and aquatic sources with distinct isotopic signatures, thus complicating the interpretation of $\delta^2\text{H}_{n\text{-alk}}$ and $\delta^{13}\text{C}_{n\text{-alk}}$ (Aichner et al., 2018; Castañeda & Schouten, 2011; Diefendorf et al., 2011). This occurs because changes in lake level, catchment vegetation, and

littoral habitat extent can modify the relative contribution of each source (Jambrina-Enríquez et al., 2016; Toney et al., 2020). Recent advances in the application of non-negative matrix factorization (NMF) in the analysis of *n*-alkane distributions have facilitated the quantitative unmixing of these sources and the isolation of endmember-specific isotopic signatures (Polissar et al., 2025). This approach represents a significant methodological advance, enabling more robust attribution of $\delta^2\text{H}_{n\text{-alk}}$ and $\delta^{13}\text{C}_{n\text{-alk}}$ variability.

We hypothesize that millennial-scale hydroclimate variability in western Iberia during the Holocene was largely controlled by changes in North Atlantic ocean-atmosphere interactions, including changes in the North Atlantic LTG, storm-track dynamics, and westerly moisture delivery. To test this hypothesis, we present the first Holocene hydroclimate reconstruction from the west-central Iberian Peninsula, resolving millennial to centennial scale isotopic signals into distinct source contributions on the basis of the compound-specific hydrogen and carbon isotopes of plant-wax *n*-alkanes in a multiproxy record spanning 11.1 calibrated thousand years before present (cal. ka BP) from Lake Peixão. Bulk organic matter geochemistry and X-ray fluorescence (XRF)-derived elemental ratios provide a complementary sedimentological context and independent support for inferred hydroclimatic evolution. This study provides new constraints on the regional expression of Holocene hydroclimate evolution in western Iberia and its connection to external forcing and internal climate variability.

2. Study Site and Previous Works

Lake Peixão (40°20'35"N, 7°36'19"W; 1,677 m above sea level) is a mountain lake located in the uplands of central Portugal (Figure 1). It occurs within a glacial cirque on the highest massif of mainland Portugal, that is, Serra da Estrela (Figure 1). Granite rocks dominate this massif, which constitutes the westernmost glaciated range of the Iberian Central System, oriented NE–SW in the central Iberian Peninsula (Vieira & Woronko, 2022). Lake Peixão formed after the retreat of glaciers from the Serra da Estrela plateau at 14.7 ± 0.3 cal. ka BP (Hernández et al., 2023). The lake is shallow (~ 5 m maximum depth) and small (0.015 km²; 176 m long and 138 m wide). Its catchment, with an area of ~ 0.30 km², is confined by steep granitic slopes with poorly developed soils and is drained by a few ephemeral streams. A small outlet to the south connects the basin with the Candieira valley (Figure 1). Lake Peixão is classified as a monomictic, oligotrophic, and slightly acidic lake (pH ~ 5.8) that is mostly filled with organic-rich terrigenous lacustrine silt overlying fluvioglacial silts and gravel particles (Hernández et al., 2023). The lake surroundings are characterized by an oroMediterranean vegetation mosaic of heathlands and grasslands (Rivas-Martínez et al., 2007), which are dominated by C₃ plants, with no evidence of C₄ vegetation either today or during the Holocene (Connor et al., 2012; Mendes et al., 2025; Santos et al., 2022, 2024; van der Knaap and van Leeuwen, 1997).

The regional climate of Serra da Estrela reflects a transitional setting between Atlantic and Mediterranean influences, as the range intercepts the path of westerlies carrying moisture from the Atlantic Ocean (Moreno et al., 2023). The altitude and slope orientation are the primary controls on the distribution of precipitation (Mora, 2010). An Atlantic climate dominates NW slopes, characterized by more frequent rainfall, whereas continental conditions prevail on SE slopes, leading to a drier climate with notable seasonal thermal contrasts (Moreno et al., 2023). The precipitation regime follows the typical biseasonal pattern of the western Iberian Peninsula, with the rainy season from October to April largely fed by Atlantic systems and notably modulated by the NAO (Cortesi et al., 2013). Across the plateau, the mean annual air temperature remains below 7°C and decreases to 4°C near the summit (Espinha Marques et al., 2011).

Existing work from the Serra da Estrela has provided a broad framework for analyzing Holocene environmental change in the region (Connor et al., 2012; Hernández et al., 2023; Moreno et al., 2023; van der Knaap & van Leeuwen, 1997). Specifically, previous work based on plant-wax biomarkers from Lake Peixão has demonstrated changes in Atlantic-driven hydroclimate and vegetation dynamics over the past two millennia (Santos et al., 2022, 2024). These studies have provided a robust baseline for interpreting lake-catchment responses to atmospheric circulation variability.

3. Materials and Methods

3.1. Core Retrieval, Lithology, and Chronology

Three parallel sediment sequences were retrieved from Lake Peixão in 2019 using a UWITEC® piston coring system, as described by Hernández et al. (2023). This study focuses on core PEX19-01, which was recovered from

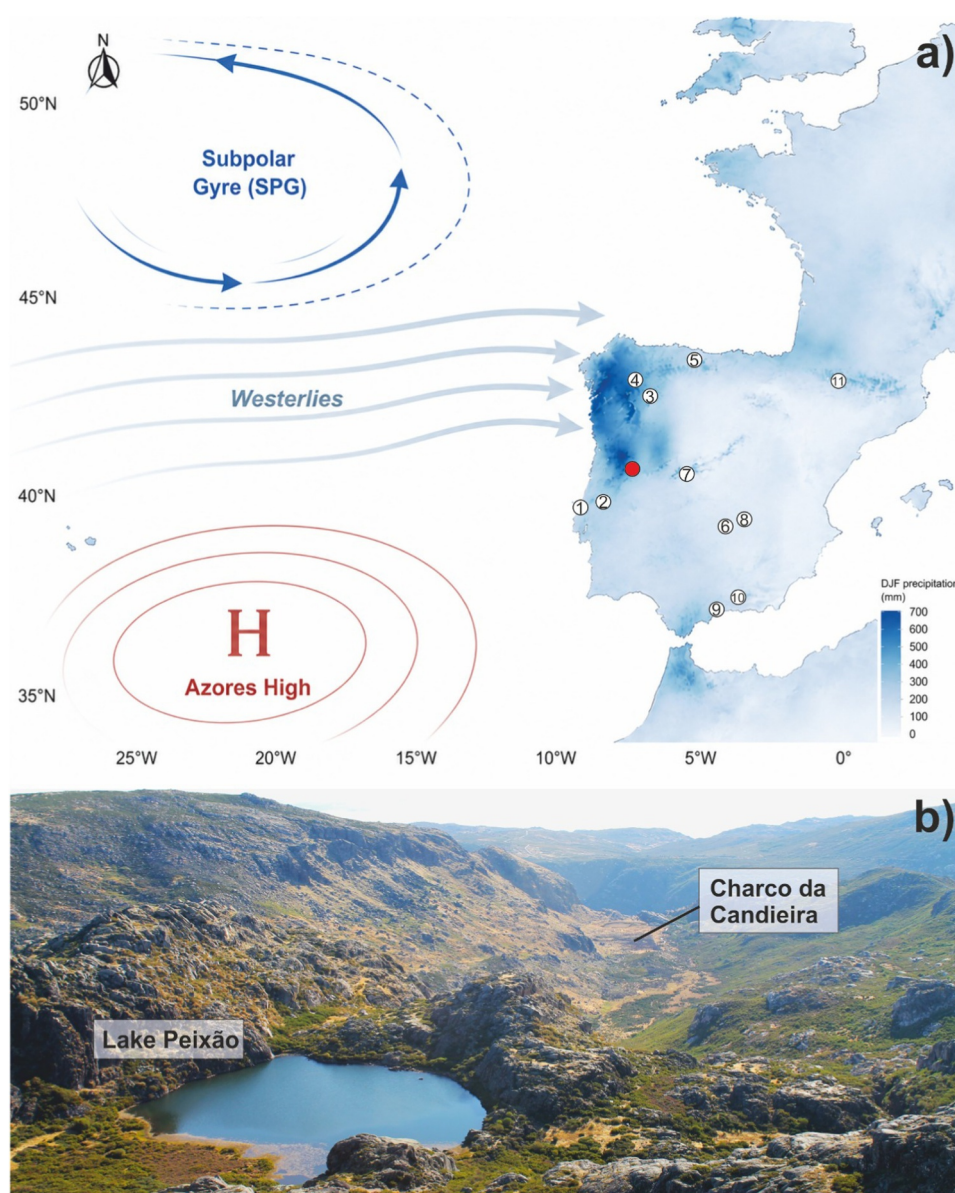


Figure 1. Location of Lake Peixão and reference sites in the Iberian Peninsula. (a) Accumulated December–February precipitation over western Iberia and the eastern North Atlantic, derived from WorldClim 2.1 monthly precipitation data. Colors indicate DJF precipitation totals in millimeters. The map highlights the pronounced winter precipitation maximum along western Iberia, consistent with Atlantic moisture delivery. The westerlies, North Atlantic Subpolar Gyre (SPG) and Azores High are included as schematic circulation features only, with oceanic circulation shown in dark blue, atmospheric circulation in sky blue and Sea Level Pressure (SLP) in red. Their locations and geometries are intentionally generalized and adjusted for figure layout and should not be interpreted as exact climatological positions or data-derived boundaries. The red circle marks the location of Lake Peixão; numbered sites indicate reference records from other studies: 1. Praia Rei Cortiço (Taylor et al., 2018); 2. Buraca Gloriosa (Thatcher et al., 2020); 3. Lake Sanabria (Jambrina-Enríquez et al., 2014); 4. Cova da Arcoia (Railsback et al., 2011); 5. Lake Enol (Moreno et al., 2011); 6. Campo de Calatrava Volcanic Field (Vegas et al., 2010); 7. Lake Cimera (Sánchez-López et al., 2016); 8. Las Tablas de Daimiel (Santisteban et al., 2019); 9. Refugio Cave (Walczak et al., 2015); 10. The Padul wetland (García-Alix et al., 2021); 11. Lake Basa de la Mora (Pérez-Sanz et al., 2013). (b) Aerial photograph showing Lake Peixão and Charco da Candieira within Serra da Estrela.

the deepest part of the lake. We adopt the age-depth model published by Hernández et al. (2023), which indicates continuous sedimentation over the past ~ 11.1 ka, with no evidence of major hiatuses (Figure S1 in Supporting Information S1). All ages are expressed in cal. ka BP. Full lithological descriptions and chronological details are provided in Supporting Information S1.

3.2. Plant-Wax *n*-Alkane Extraction and Analyses

Sedimentary plant waxes were analyzed to infer past vegetation and climate changes. This study included a total of 135 sediment samples (Figure S1a in Supporting Information S1), 60 previously reported by Santos et al. (2024), covering the uppermost 120 cm (~0–2 cal. ka BP) at a mean sampling interval of ~2 cm. An additional 75 samples were analyzed herein for the first time, with the record extending from 149 cm depth to 730 cm depth (~2–11.1 cal. ka BP). The new section was subsampled at variable intervals (range: 4–20 cm; mean: ~9 cm). This sampling strategy was designed to maximize temporal resolution in the most recent interval, where centennial- to decadal-scale variability was the main target. Moreover, it ensures adequate stratigraphic coverage throughout the full Holocene record, where the focus is on millennial-scale hydroclimate trends.

Sample preparation and extraction followed the protocols described by Santos et al. (2024) at the BioGeo-Chemistry Lab, Instituto Português do Mar e da Atmosfera (IPMA, Lisbon, Portugal) (see Supporting Information S1 for details). The *n*-alkane concentrations were quantified with a Varian gas chromatograph Model 3800 equipped with a programmable temperature vapourizer injector operated in split mode and a flame ionization detector. The concentration of each compound was determined using hexatriacontane as an internal standard (Villanueva et al., 1997). To characterize the distribution of *n*-alkanes, we calculated distributional indices, including the average chain length (ACL) (Poynter et al., 1989), the carbon preference index (CPI) (Bray & Evans, 1961; Marzi et al., 1993), and the proportion of aquatic plants (P_{aq}) (Ficken et al., 2000). These metrics provide simplified descriptions of complex molecular patterns and are typically applied to infer the dominant vegetation sources (ACL), the preservation state of plant waxes (CPI), and the relative contribution of aquatic versus terrestrial plants (P_{aq}). Equations for these indices are provided in Supporting Information S1.

Compound-specific isotope analyses of plant-wax *n*-alkanes ($\delta^{13}C_{n-alk}$ and δ^2H_{n-alk}) were performed via gas chromatography–isotope ratio mass spectrometry (GC–IRMS) at the MARUM Center for Marine Environmental Sciences, University of Bremen (Germany). The detailed analytical conditions and calibration procedures are provided in Supporting Information S1.

3.3. XRF and Bulk Organic Matter Analyses

Geochemical element profiles of core PEX19-01 were acquired directly at the split-core surface via the use of an ITRAX XRF core scanner (XRF-CS) equipped with a rhodium tube at the National Institute for Scientific Research (INRS) Center Eau Terre Environnement, Canada. Measurements were conducted under the following settings: 5-mm spatial resolution, 30-mA current, 30-s count time, and 30-kV voltage. XRF spectra were evaluated using the manufacturer's *Q-Spec* software. Elements exhibiting multiple zero values were not analyzed further. Twenty-six chemical elements were measured, but only 16 elements (Br, Ta, Ni, Cu, Ca, Ga, Zn, Mn, Si, Fe, Rb, K, Ti, Zr, Sr, and Y), along with the incoherent/coherent scatter ratio (inc/coh), were retained for analysis on the basis of median values of at least 650 counts per second (cps).

Core PEX19-01 was also sampled at 4-cm intervals for elemental and organic matter (OM) analysis. Total carbon (TC), total nitrogen (TN), and their respective stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) were measured with a DeltaV Advantage mass spectrometer, a Conflo IV interface, and a Flash IRMS EA IsoLink CNS elemental analyzer (Thermo Scientific), respectively, at Servicios de Apoyo á Investigación of the Universidade da Coruña (SAI-UDC; Spain). The TC and TN contents are expressed as percentages of the total dry weight. In the absence of carbonate minerals, TC was considered equivalent to total organic carbon (TOC). The TOC/TN atomic ratio was calculated for all the samples. Isotopic values are reported in conventional delta notation (‰) against Vienna Pee Dee Belemnite (VPDB) for carbon and against atmospheric nitrogen (N_2) for nitrogen. The analytical accuracy was assessed through repeated measurements of the acetanilide standard ($n = 10$), yielding an uncertainty of $\pm 0.15\text{‰}$.

3.4. Data Analysis

Statistical analyses were performed in R version 4.2.3. XRF elemental counts were centered on the log-ratio (clr) prior to multivariate analyses to reduce matrix-related nonlinearity and constant-sum effects and to increase the interpretability of downcore compositional changes (Weltje et al., 2015; Weltje & Tjallingii, 2008). Notably, clr transformation was conducted using the composition package in R (van den Boogaart and Tolosana-Delgado, 2008). Principal component analysis (PCA) was implemented with the prcomp function (data

centered and scaled to unit variance) and visualized using the factoextra, ggplot2, and base graphics packages in R (Kassambara & Mundt, 2017; R Development Core Team, 2015; Wickham et al., 2016). To determine the number of significant eigenvectors, we applied a broken-stick model (Jackson, 1993) using the vegan package (Oksanen et al., 2022). We also used the vegan package for similarity-based multivariate analyses (e.g., analysis of similarities (ANOSIM)).

We applied the NMF method, following the approach described by Polissar et al. (2025), to the Lake Peixão *n*-alkane data set. In this approach, the chain-length distributions of *n*-alkanes were analyzed, endmember distributions were extracted, and their individual contributions in all samples were quantified. This approach enabled us to (a) resolve distinct source components within the *n*-alkane pool, (b) evaluate which compounds carry an isotope signal most reflective of a given source, (c) calculate source-specific $\delta^{13}\text{C}_{n\text{-alk}}$ and $\delta^2\text{H}_{n\text{-alk}}$ values, and (d) reconstruct endmember $\delta^{13}\text{C}_{n\text{-alk}}$ and $\delta^2\text{H}_{n\text{-alk}}$ signatures for Lake Peixão. The model was first calibrated (~ 2.2 ka interval; Figure S4 in Supporting Information S1) against data published by Santos et al. (2024), considering recent biomarker information for the catchment (Santos et al., 2022) and the *n*-alkane indices of the ACL, CPI, and P_{aq} .

The decadal NAO-like index for the last 12,000 years was calculated via the TraCE-21K-II monthly sea level pressure (SLP) transient simulation model (He & Clark, 2022). To this end, the leading eigenvector of the empirical orthogonal function (EOF) for the area within 20°N–80°N and 40°E–70°W was calculated. The monthly data set was first converted into a decadal data series by calculating median values and then detrended through a loess function. To examine lower-frequency variability, decadal values were subsequently aggregated into 500-year bins, and the median NAO-like index was calculated for each bin. All calculations were performed in R software (R Development Core Team, 2015).

4. Results and Interpretation

4.1. Plant-Wax Biomarkers

4.1.1. Distribution and Sources of *n*-Alkanes

The distributions of plant-wax *n*-alkanes throughout the Holocene exhibited a notable odd-over-even predominance ($\text{CPI}_{21-35} = 4.7\text{--}11.1$; mean = 7.9 ± 1.4 ; $n = 135$) (Figure S3b in Supporting Information S1), indicating a primarily higher-plant origin and favorable molecular preservation (Eglinton & Eglinton, 2008; Sachse et al., 2012). Assemblages were dominated by long-chain homologs (here defined as *n*-C₂₇ to *n*-C₃₅), with *n*-C₃₁ being the most abundant compound, followed by *n*-C₂₉ and *n*-C₂₇ (Figure S2 in Supporting Information S1), which are usually produced in high quantities by terrestrial higher plants (Eglinton & Hamilton, 1967; Sachse et al., 2012). The average chain lengths (ACL_{21-35}) ranged from 28.1 to 29.9 (mean = 28.8 ± 0.4 ; $n = 135$) (Figure S3c in Supporting Information S1), with all values occurring within the terrestrial plant range, which is consistent with the TOC/TN and $\delta^{13}\text{C}_{\text{bulk}}$ patterns (Figure S9 in Supporting Information S1). The P_{aq} index remained consistently low (0.1–0.3; mean = 0.2 ± 0.05 ; $n = 135$) (Figure S3d in Supporting Information S1). Taken together, these indices indicate that the *n*-alkane assemblages are predominantly of terrestrial higher-plant origin throughout the Holocene, and that variations in chain-length distributions primarily reflect changes in the terrestrial vegetation composition rather than shifts in aquatic macrophyte contributions (Diefendorf & Freimuth, 2017; Sachse et al., 2012).

Long-chain *n*-alkane concentrations (odd $\sum n\text{-C}_{27}\text{--}n\text{-C}_{35}$) (Figure S3a in Supporting Information S1) were low during the earliest part of the record (11.1–9 cal. ka BP). They then increased progressively between 9 and 5.9 cal. ka BP, before declining from 5.9 cal. ka BP to the present, with several short-lived decreases superimposed on this longer-term trend.

4.1.2. Stable Isotopes From *n*-Alkanes

The concentration-weighted mean $\delta^2\text{H}$ values of the *n*-C₂₇, *n*-C₂₉, and *n*-C₃₁ alkanes followed similar trends throughout the Holocene (Figure 2a), although there were systematic offsets among homologs (Figure 2a). These offsets likely reflect a combination of differences in plant source assembly, chain-length-specific biosynthetic fractionation, and differential susceptibility to postdepositional degradation (Diefendorf et al., 2011; Häggi et al., 2021; Sachse et al., 2012; Sessions et al., 1999). The values were low during the earliest part of the record (11.1–9 cal. ka BP), with mean values of -168‰ for *n*-C₂₇, -178‰ for *n*-C₂₉, and -170‰ for *n*-C₃₁. After

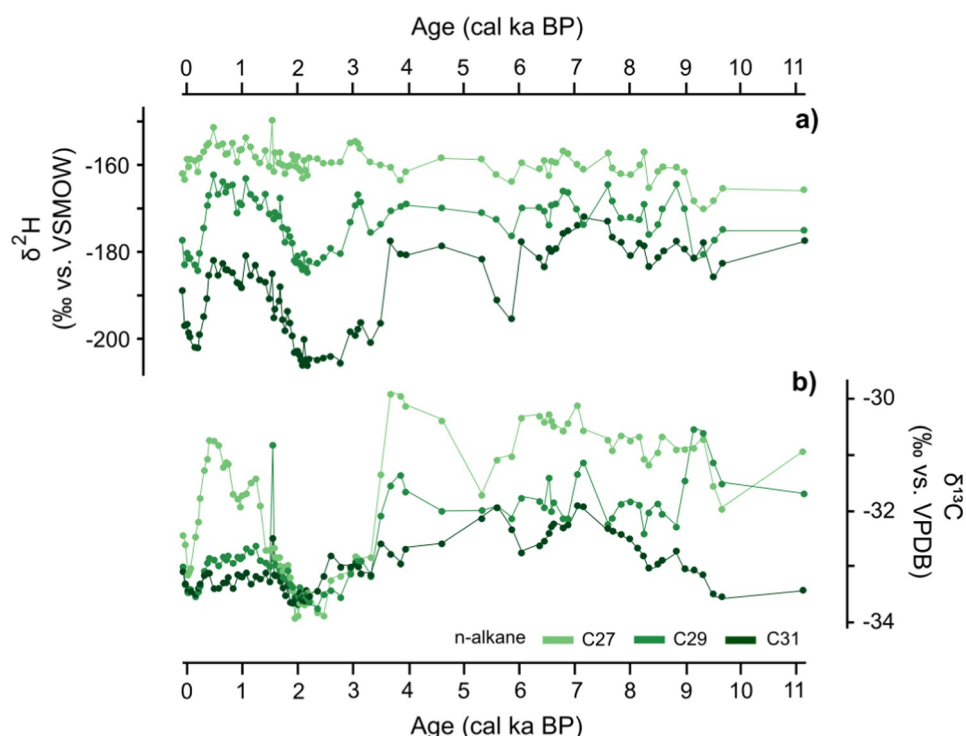


Figure 2. Compound-specific isotope record from long-chain plant-wax *n*-alkanes in Lake Peixão sediments. (a) Hydrogen isotope composition ($\delta^2\text{H}$, ‰ vs. VSMOW) of *n*-C₂₇, *n*-C₂₉, and *n*-C₃₁ alkanes. (b) Carbon isotope composition ($\delta^{13}\text{C}$, ‰ vs. VPDB) of *n*-C₂₇, *n*-C₂₉, and *n*-C₃₁ alkanes. Light green = *n*-C₂₇, green = *n*-C₂₉, dark green = *n*-C₃₁.

~9 cal. ka BP, the $\delta^2\text{H}$ values increase progressively, reaching their highest values between 8 and 6.7 cal. ka BP (mean = -160‰ for *n*-C₂₇, -170‰ for *n*-C₂₉, and -165‰ for *n*-C₃₁). A second interval of high values occurred between 5.3 and 3.7 cal. ka BP, with mean values of -160‰ for *n*-C₂₇, -170‰ for *n*-C₂₉, and -169‰ for *n*-C₃₁ (Figure 2a). A subsequent depletion after ~4 cal. ka BP reflects a return to lower $\delta^2\text{H}$ values in the longer-chain homologs (*n*-C₂₉, and *n*-C₃₁), interrupted by an interval of higher values between 1.5 and 0.5 cal. ka BP, with mean values of -167‰ for *n*-C₂₉ and -177‰ for *n*-C₃₁ (Figure 2a). In contrast, *n*-C₂₇ alkane remained relatively stable from 1.5 to 0.5 cal. ka BP, resembling the behavior of *n*-C₂₅ alkane (Figure S3e in Supporting Information S1), which possibly reflects a greater relative contribution of soil derived organic matter during this interval (Häggi et al., 2021). The most recent interval (0.5 cal. ka BP to the present) shows a return to more depleted $\delta^2\text{H}$ values across all *n*-alkanes (Figure 2a and Figure S3e in Supporting Information S1).

Throughout the Holocene, the measured compound-specific $\delta^{13}\text{C}$ records indicated a consistent offset between two groups of homologs: *n*-C₂₅ and *n*-C₂₇ alkanes versus *n*-C₂₉, *n*-C₃₁, and *n*-C₃₃ alkanes (Figure 2b and Figure S3f in Supporting Information S1). The shorter-chain homologs were consistently more ^{13}C -enriched than the longer-chain homologs were. With respect to all measured chain lengths, the interval 11.1–9 cal. ka BP was characterized by more ^{13}C -depleted values, with $\delta^{13}\text{C}$ values ranging from -31.8‰ to -33.0‰ , followed by progressively more ^{13}C -enriched values between 9 and 3.7 cal. ka BP with $\delta^{13}\text{C}$ values ranging from -31.2‰ to -32.7‰ , which resembles the slight enrichment trend of $\delta^2\text{H}$ values over the same interval. All chain lengths undergo rapid depletion from 3.6 to 2 cal. ka BP, all reaching values of $\sim -33\text{‰}$. *n*-C₂₉ and *n*-C₃₁ remain relatively depleted throughout the rest of the record, where *n*-C₂₇ and *n*-C₂₅ undergo enrichment from 2 to 0.4 cal. ka BP, and a subsequent abrupt depletion after 0.4 cal. ka BP. After 0.4 cal. ka BP, $\delta^{13}\text{C}$ values of all chain lengths converged toward similar values.

The $\delta^{13}\text{C}$ values obtained for all measured chain lengths fall within the range reported for C₃-dominated ecosystems (Chikaraishi & Naraoka, 2003; Diefendorf & Freimuth, 2017). The observed offset between shorter- and longer-chain homologs, as well as the temporal variability in $\delta^{13}\text{C}$, likely reflect a combination of factors: (a) changes in plant water use efficiency (WUE) (Diefendorf & Freimuth, 2017; Farquhar et al., 1989); (b) shifts in C₃ plant functional types with different intrinsic isotopic fractionation (Diefendorf et al., 2010); and (c) a greater

relative contribution of submerged macrophytes or soil-degraded organic matter to shorter chain lengths (Häggi et al., 2021).

The covariation between the long-chain $\delta^{13}\text{C}_{n\text{-alk}}$ and $\delta^2\text{H}_{n\text{-alk}}$ values throughout the Holocene suggests that both isotope systems responded to the same environmental forcing, likely climate-driven variations in moisture availability. Nevertheless, the distinct behavior of the shorter-chain *n*-alkanes, together with the potential influence of source mixing on the bulk isotopic signal, highlights the need to isolate the terrestrial vegetation component before interpreting these records in hydroclimatic terms. Thus, we applied a source unmixing approach based on the NMF method.

4.1.3. NMF Source Apportionment, Derived Isotope Record and Interpretation

The results of the NMF analysis revealed that three endmember distributions accounted for ~94% of the total variance in the *n*-alkane data set ($R^2 = 0.94$; Figure 3). The interpretation of each endmember is based on two complementary findings: (a) comparison with modern plant *n*-alkane distributions measured in the Lake Peixão catchment (Santos et al., 2022) supported by statistical analysis (see Supporting Information S1) and (b) chain length characteristics consistent with those reported in the literature for specific plant functional types (Eglinton & Hamilton, 1967; Ficken et al., 2000; Sachse et al., 2012). On the basis of these comparisons (Figure 3a), the endmembers can be interpreted as follows (Figure 3b): (a) Endmember 1 (EM1) is long-chain dominated, with high *n*-C₃₁ and secondary *n*-C₃₃ and *n*-C₂₉ values, and this endmember is interpreted as representing grasses and heathland vegetation; (b) Endmember 2 (EM2) is also long-chain dominated but centered on *n*-C₃₁ and *n*-C₂₇ and likely reflects a mixed terrestrial assemblage with increased contributions from shrubs and trees; and (c) Endmember 3 (EM3) is dominated by *n*-C₂₉, *n*-C₂₅, and *n*-C₂₇ and is interpreted as reflecting contributions from submerged macrophytes and shoreline vegetation. The relatively low CPI values of this endmember suggest the additional input of degraded plant waxes, which were potentially derived from soil organic matter erosion. Please refer to Supporting Information S1 for further details.

The relative contributions of the three endmembers vary throughout the Holocene record (Figure 3c), with gradual shifts in their dominance. During the earliest phase of the record (11.1–9 cal. ka BP), EM3 dominated (up to 80%), reflecting the combination of submerged macrophytes and shoreline graminoid vegetation along with increased delivery of soil-derived organic matter under sparse vegetation and active erosion conditions during the early postglacial phase (consistent with the XRF and bulk organic matter results; refer to Section 4.2). During the interval 9–3.7 cal. ka BP, EM2 (shrubs and trees) dominated (up to 70%) the terrestrial component (EM1 + EM2; 70%–90% of the total), with a brief increase in EM1 (grasses and heathlands) between 6 and 5.3 cal. ka BP, which is likely linked to hydroclimatic variability and incipient anthropogenic influence. This increase coincides with the onset of the “anthropogenic forest dynamics” phase (~6.4–5.3 cal. ka BP) recognized at nearby Charco da Candieira (Figure 1), during which time low-intensity grazing and small-scale deforestation began to affect montane forests (Connor et al., 2012; van der Knaap & van Leeuwen, 1995). Over the past 3700 years, EM1 dominated the record (60%–70% of the total), indicating that landscape opening was driven by combined climatic changes (Ausín et al., 2025; Santos et al., 2024) and intensified anthropogenic activity. In the Serra da Estrela, large-scale deforestation began ~3.4 cal. ka BP and is characterized by sharp declines in arboreal pollen, increased charcoal accumulation, and increased soil erosion (Connor et al., 2012; van der Knaap & van Leeuwen, 1995). This deforestation coincided with direct evidence of pastoral activity in the area: (a) Bronze Age (second millennium BC) faunal remains recovered from Buraco da Moura de São Romão, a site ~9 km away from Lake Peixão, documenting the presence of sheep and cattle herding in the region; and (b) human pressure intensified during the Medieval period, when historical sources attest to sheep grazing, rye cultivation, charcoal production, and deliberate agro-pastoral burning in the surroundings of the study area, with cereal pollen expanding shortly after fire events (Connor et al., 2012). This evidence indicates that grazing and fire acted alongside the climate to suppress forest recovery and maintain the open heathland and grassland landscape recorded by EM1, a trajectory of combined fire and pastoralism during the last ~4.2 ka also documented across the Iberian Central System (García Álvarez et al., 2017).

Since all endmembers are primarily of terrestrial origin, we combined EM1 and EM2 to derive source-specific isotope values representative of terrestrial vegetation ($\delta^2\text{H}_{\text{terr}}$ and $\delta^{13}\text{C}_{\text{terr}}$) following the approach of Polissar et al. (2025) (refer to the Supporting Information S1 for the detailed methodology). The NMF-derived $\delta^2\text{H}_{\text{terr}}$ index, defined as the hydrogen isotopic composition of the terrestrial vegetation endmember (EM1 + EM2)

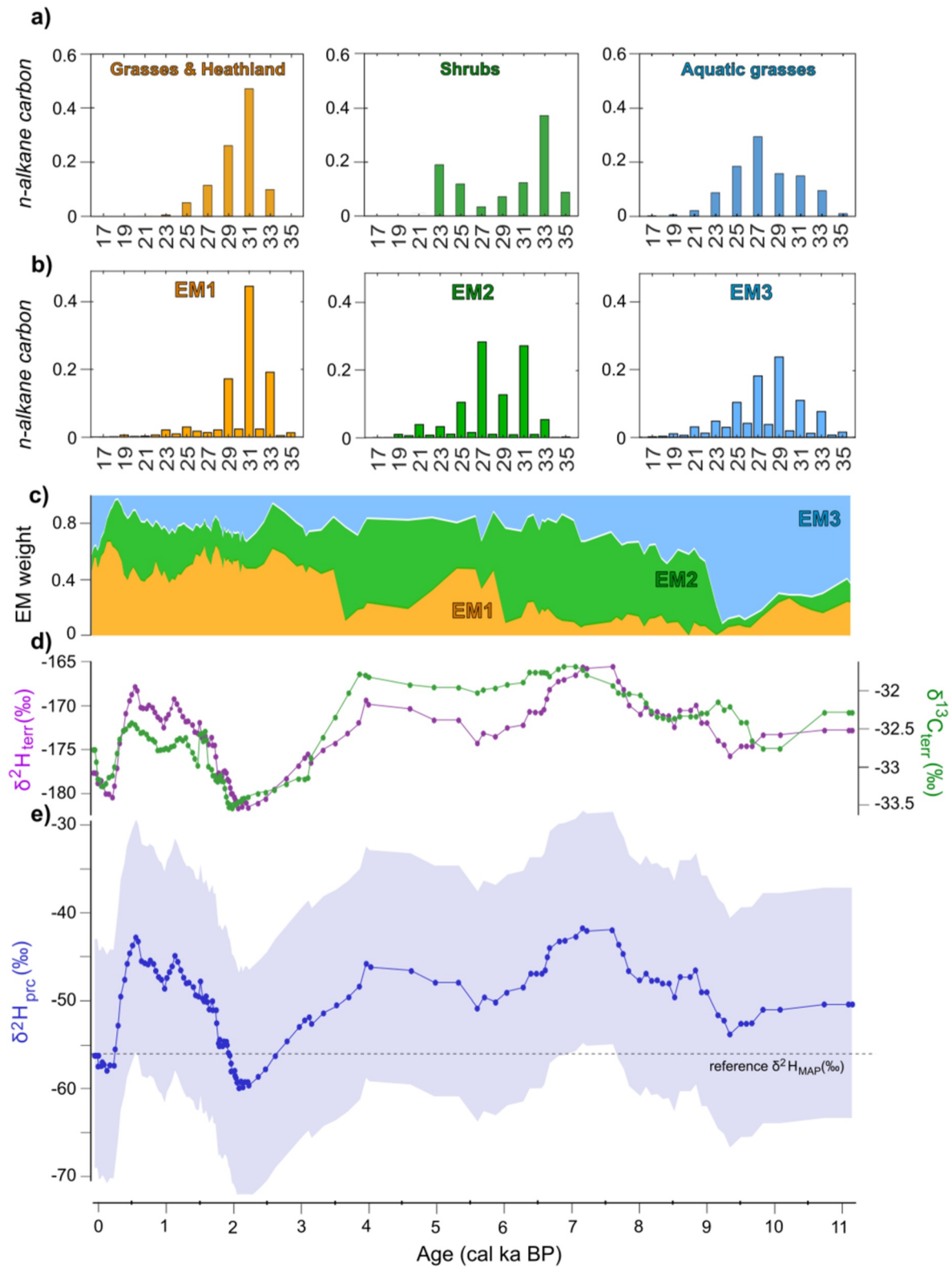


Figure 3.

isolated through NMF analysis, minimizes the contributions from degraded soil organic matter (Figure 3d) and reflects the isotopic composition of precipitation assimilated by plants.

The interpretation of $\delta^2\text{H}_{\text{terr}}$ requires consideration of both the controls on precipitation $\delta^2\text{H}$ and the processes that modify plant-water isotopic composition during leaf-wax biosynthesis. In this high-altitude Atlantic setting, precipitation $\delta^2\text{H}$ is controlled mainly by the isotopic evolution of Atlantic westerly moisture during transport to the catchment, including the effects of condensation temperature, progressive rainfall, precipitation amount, and distance from the moisture source (Santos et al., 2022, 2024; Thatcher et al., 2020). Colder and/or wetter conditions generally increase condensation and progressive rainfall during inland moisture transport, resulting in more $\delta^2\text{H}$ -depleted precipitation. Conversely, warmer and/or drier conditions, reduced rainfall, or a greater contribution from proximal and/or isotopically enriched moisture sources tend to produce higher $\delta^2\text{H}$ values. Although additional factors including growing-season evaporative enrichment, vegetation composition, rooting depth, and compound-specific biosynthetic fractionation can modulate the $\delta^2\text{H}_{\text{terr}}$ signal (Kahmen et al., 2013; Sachse et al., 2012; Santos et al., 2026), calibration work at Lake Peixão (Santos et al., 2022) and the overall stability of *n*-alkane source vegetation throughout most of the record (Santos et al., 2024) indicate that changes in $\delta^2\text{H}_{\text{terr}}$ at this site primarily reflect variations in precipitation $\delta^2\text{H}$. Accordingly, lower $\delta^2\text{H}_{\text{terr}}$ values are interpreted as reflecting relatively wetter and/or colder conditions, and/or more distal Atlantic moisture sources, whereas higher values indicate relatively drier and/or warmer conditions and/or more proximal or isotopically enriched moisture sources. Therefore, the NMF-derived $\delta^2\text{H}_{\text{terr}}$ index provides a useful proxy for Holocene hydroclimatic variability, particularly when interpreted together with independent sedimentological and geochemical indicators.

For comparison with modern observations and isotope-enabled climate model outputs, we estimated precipitation $\delta^2\text{H}$ values ($\delta^2\text{H}_{\text{prec}}$) from the NMF-derived $\delta^2\text{H}_{\text{terr}}$ record. The terrestrial endmembers represent a mixed pool of plant waxes delivered to the lake. Thus, the offset ($>100\%$) between $\delta^2\text{H}_{\text{terr}}$ and modern precipitation is best interpreted as a net apparent hydrogen-isotope offset. To estimate $\delta^2\text{H}_{\text{prec}}$, we applied the catchment-integrated apparent hydrogen-isotope fractionation between the *n*-alkanes and mean annual precipitation ($\epsilon_{\text{C}_{29}/\text{MAP}} = -129\% \pm 12\%$) determined by Santos et al. (2022) for the surface sediment of Lake Peixão. With respect to *n*-C₂₉, this lake-specific calibration captures the average apparent fractionation between catchment-derived terrestrial plant waxes and precipitation, including the mixture of vegetation sources preserved in the sediment. We applied this site-specific value as ϵ_{app} to estimate $\delta^2\text{H}_{\text{prec}}$. The resulting values (Figure 3e; $\sim -42\%$ to -60%) are consistent with the modern precipitation in the study area. They overlap with the OIPC3.1 mean annual value of $-56\% \pm 5\%$ (Santos et al., 2022) and $\delta^2\text{H}$ ($\sim -54\%$; corrected for the 300 m difference in elevation) of the nearest long-term GNIP station, Penhas Douradas, which is located 9.4 km from the lake (see Supporting Information S1). The youngest sediments approach this modern value, confirming the reliability of the correction and showing that the record is anchored to a realistic modern baseline. Because grasses/heathland (EM1) and shrubs/trees (EM2) may have different net hydrogen isotope fractionations, part of the $\delta^2\text{H}_{\text{terr}}$ variability could reflect changes in vegetation composition rather than precipitation $\delta^2\text{H}$ alone. However, two characteristics of Lake Peixão limit this potential bias. First, the NMF unmixing minimizes the contribution of the degraded soil- and aquatic-derived component (EM3), leaving $\delta^2\text{H}_{\text{terr}}$ dominated by the terrestrial plant-wax pool delivered to the lake. Second, modern plants from the main terrestrial ecological forms in the catchment show broadly consistent $\delta^{13}\text{C}$ and $\delta^2\text{H}$ behavior (Santos et al., 2022), suggesting that isotopic differences among vegetation types are relatively small. Accordingly, a fully quantitative, endmember-specific vegetation correction is not applied here. Such a correction would be difficult to justify because past EM1 and EM2 assemblages do not necessarily correspond to the modern plant taxa sampled for calibration (Santos et al., 2022). A more rigorous

Figure 3. NMF results for Lake Peixão using a three-endmembers solution and comparison with source-specific isotope records. (a) Concentration-weighted mean *n*-alkane chain-length distributions of modern catchment plants grouped by functional type (Santos et al., 2022): terrestrial grasses and heathland (*Agrostis* spp., *Nardus* spp., and *Erica* spp.; orange), shrubs (*Juniperus* spp. and *Cytisus* spp.; green), and aquatic grasses (*Antinoria* spp. and *Juncus* spp.; blue). Means were weighted by the total *n*-alkane concentration of each individual plant sample. (b) Chain-length distributions of the three NMF endmembers (bars): EM1 (orange) interpreted as grasses and heathlands, EM2 (green) as shrubs and trees, and EM3 (blue) as mostly soil-derived degraded terrestrial waxes. (c) Temporal changes in the relative contribution of the three NMF endmembers (EM1 = grasses + heathlands, EM2 = shrubs and trees, EM3 = mostly soil-derived degraded terrestrial waxes). (d) NMF-derived hydrogen and carbon isotope composition of the terrestrial vegetation component ($\delta^2\text{H}_{\text{terr}}$, purple; $\delta^{13}\text{C}_{\text{terr}}$, green), calculated from the combined EM1 + EM2 signal. (e) Reconstructed precipitation hydrogen isotopic composition ($\delta^2\text{H}_{\text{prec}}$, blue), obtained by correcting $\delta^2\text{H}_{\text{terr}}$ for the apparent fractionation factor; the shaded band denotes the uncertainty. Note that this record is uncorrected for changes in vegetation fractionation and global ice volume through time.

vegetation correction would require a method capable of robustly disentangling individual plant functional types, for example, separating grasses from heathland, together with a more comprehensive modern calibration covering those types individually. In addition, modern surface sediment already integrates the natural mixture of catchment vegetation delivered to the lake and shows only a small spread in apparent fractionation among the long-chain homologs that dominate EM1 and EM2 (Santos et al., 2022). See the Supporting Information S1 for further details.

In turn, the NMF-derived $\delta^{13}\text{C}_{\text{terr}}$ index (EM1 + EM2) reflects the carbon isotopic composition of terrestrial vegetation and can be used to infer water use efficiency (Farquhar et al., 1989). Under water stress, reduced stomatal conductance leads to lower isotopic discrimination and ^{13}C -enriched values, whereas wetter conditions result in more ^{13}C -depleted values (Diefendorf & Freimuth, 2017; Farquhar et al., 1989). Accordingly, higher (lower) $\delta^{13}\text{C}$ values can indicate drier (wetter) conditions and water stress (Li et al., 2024; Schirmacher et al., 2020). The NMF-derived $\delta^{13}\text{C}_{\text{terr}}$ (EM1 + EM2) broadly covaried with $\delta^2\text{H}_{\text{terr}}$ throughout the Holocene ($r = 0.83$, $p < 0.001$; Figure 3d), suggesting a common hydroclimatic control (Li et al., 2024; Schirmacher et al., 2020). However, part of the variability may also reflect shifts in the vegetation composition (Santos et al., 2026), particularly the increased contribution of ^{13}C -depleted grasses and heathlands (EM1), which were typically more ^{13}C -depleted than shrubs were during the late Holocene (Santos et al., 2022).

4.2. Geochemical Composition of the Sediments

We applied PCA to the clr-transformed XRF data set (Br, Ta, Ni, Cu, Ca, Ga, Zn, Mn, Si, Fe, Rb, K, Ti, Zr, Sr, and Y and the incoherent/coherent scatter ratio, inc/coh) at the original 0.5-cm sampling resolution to identify the main environmental processes controlling sediment deposition (Figure 4 and Supporting Information S1). PC1 and PC2 explained 46.4% and 10.9%, respectively, of the total variance, with only PC1 being statistically significant according to the broken-stick model (Figures 4a and 4b). Elements associated with the organic content (Br_{clr} , Cu_{clr} , Ni_{clr} , and inc/coh) attained positive loadings of PC1, and those associated with detrital sediments (Ti_{clr} , K_{clr} , Rb_{clr} , Fe_{clr} , Si_{clr} , and Zn_{clr}) attained negative loadings. Hence, the PCA results indicated that sediment composition was primarily controlled by variations in terrigenous input versus in-lake organic-associated components, which is well supported by the suitable match of PC1 with TOC, TOC/TN, and $\delta^{13}\text{C}_{\text{bulk}}$ (Figure 4d).

The three Holocene formal subdivisions, the Greenlandian (early Holocene; 11.1–8.2 cal. ka BP), Northgrippian (mid-Holocene; 8.2–4.2 cal. ka BP), and Meghalayan (late Holocene; since 4.2 cal. ka BP) are consistent with the PCA and geochemical proxy results (Figures 4a and 4b). The ANOSIM results confirmed that these three groups differed significantly ($R^2 = 0.3$, $p = 0.001$; Figure 4c). The PC1 loadings and organic matter content further support this pattern (Figure 4d). PC1 shifts from negative values and is dominated by terrigenous elements (11.1–9 cal. ka BP and 5–2 cal. ka BP), to positive values associated with organic inputs (9–5 cal. ka BP and after 2 cal. ka BP). High TOC/TN ratios indicate primarily terrestrial organic matter (Meyers, 1997; Meyers & Teranes, 2001).

Accordingly, Figure 4 shows that the interval between 11.1 and 10.5 cal. ka BP was characterized by low TOC and PC1 but high TOC/TN and $\delta^{13}\text{C}_{\text{bulk}}$ values, indicating that the dominance of terrigenous organic matter with substantial clastic input into the lake was related to enhanced watershed erosion and runoff (Martín-Puertas et al., 2011). Between 8 and 5 cal. ka BP, the TOC content and PC1 increased and stabilized, indicating a shift from a clastic-dominated to an organic-rich depositional regime. This organic enrichment, however, was not driven by algal productivity, as the TOC/TN ratio remained high, the P_{aq} was low, and the $\delta^{13}\text{C}_{\text{bulk}}$ became more negative, indicating that organic matter was dominated by vascular (higher) plants (Ficken et al., 2000; Meyers, 1997; Meyers & Teranes, 2001). In particular, the more negative $\delta^{13}\text{C}_{\text{bulk}}$ is consistent with the greater contribution of the ^{13}C -depleted C3 plant material. The most recent sediments encompassed the following two apparent subphases: from 5 to 2 cal. ka BP, the reduced TOC values and PC1 indicate increased terrigenous input and decreased organic accumulation, whereas after 2 cal. ka BP, higher TOC and PC1 values indicate renewed organic-rich sedimentation.

5. Discussion

A net increase in Northern Hemisphere mid-latitude precipitation has been broadly linked to a strengthening of the hemispheric LTG from the early to late Holocene (Routson et al., 2019) (Figure 5). However, regional variations in the LTG likely induced regional climate anomalies. In the North Atlantic, the large extension of the

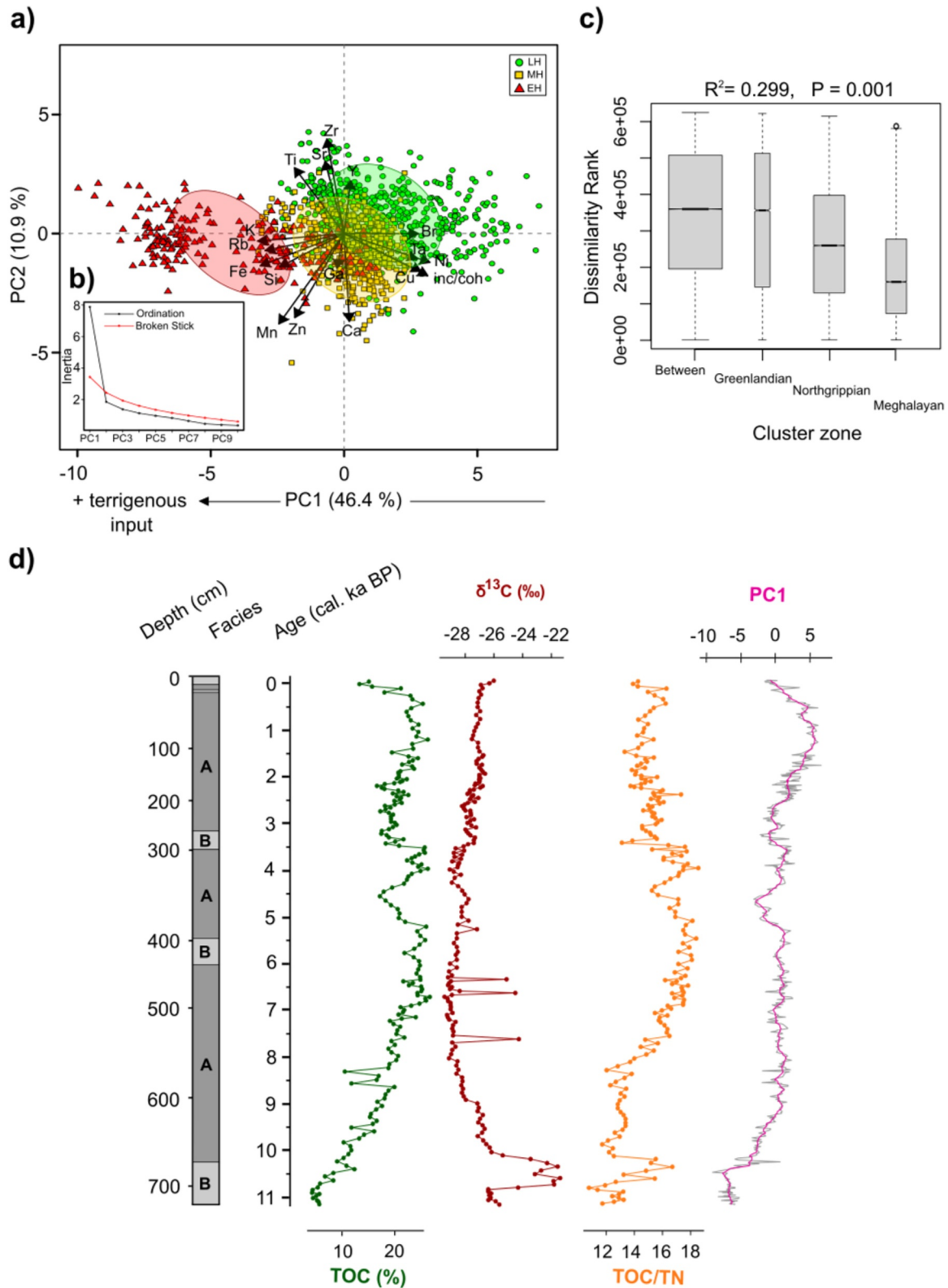


Figure 4.

Laurentide ice sheet caused a strengthening of the regional LTG during the Early Holocene (Martin-Puertas et al., 2025). A comparison of $\delta^2\text{H}_{\text{terr}}$ z-scores, interpreted here as a proxy for moisture conditions over western Iberia, with the regional LTG in the North Atlantic region is shown in Figure 5a. The favorable agreement between this potential driver and moisture supports the influence of the large-scale atmospheric dynamics suggested by Routson et al. (2019), but discrepancies highlight spatiotemporal differences relative to the evolution of the Northern Hemisphere mid latitude net precipitation during the Holocene. In western Iberia, the $\delta^2\text{H}_{\text{terr}}$ z-score record (Figure 5a) indicates three main hydroclimate phases: a wetter Phase 1 during the late Greenlandian until ~ 9 cal. ka BP; a predominantly arid Phase 2 from ~ 9 to 3.7 cal. ka BP, spanning the late Greenlandian and Northgrippian; and a return to wetter conditions during the Meghalayan, from ~ 3.7 cal. ka BP to present, with shorter-term variability superimposed. This pattern suggests that the Lake Peixão record reflects coupled North Atlantic ocean–atmosphere variability across multiple timescales. Changes in atmospheric circulation were likely linked to oceanic reorganizations, including variations in the subpolar gyre and the position of the Azores Front, which modulated sea-surface temperature gradients, moisture transport pathways, and ultimately hydroclimate variability over western Iberia.

5.1. Phase 1 (11.1–9 cal. ka BP)

Lake Peixão $\delta^2\text{H}_{\text{terr}}$ values slightly decreased from ~ 11 to 9.5 cal. ka BP, indicating a progressive shift toward wetter conditions, which became more pronounced between ~ 9.5 and 9 cal. ka BP (Figure 5a). Although the early Greenlandian is considered a humid period, the $\delta^2\text{H}_{\text{terr}}$ record also reveals an interval (11.1–9.7 cal. ka BP) corresponding to higher (i.e., drier) than average $\delta^2\text{H}$ values, which would only represent deviations from the long-term mean rather than an aridity phase (Figure 5a). This overall trend is further supported by decreasing $\delta^{13}\text{C}_{\text{terr}}$ values at the beginning of this period (Figure 3d), as more negative $\delta^{13}\text{C}$ values in C_3 plants reflect increased carbon isotope discrimination under reduced water stress (Diefendorf et al., 2010; Farquhar et al., 1989; Kohn, 2010). This wet phase coincided with the enhanced delivery of soil-derived degraded terrestrial waxes linked to inputs from lake-margin graminoid vegetation and submerged macrophytes (Figure 3b). A synchronously high terrigenous input indicates increased catchment erosion during early lake ontogeny (PC1; Figure 5b), when the sparse vegetation cover (Connor et al., 2012; van der Knaap & van Leeuwen, 1997) and poorly developed soils facilitated widespread mobilization of reworked organic matter into the lake (Arnaud et al., 2016). Despite the predominant trend toward wet conditions during this phase, this configuration suggests shallow-lake conditions at the early stages of ontogeny and catchment stabilization (Hernández et al., 2008). However, increased moisture availability did not translate into deeper water conditions. During these first stages of ontogeny, the lake level was governed more by the basin morphology and the local hydrological balance than by climate. As the basin progressively filled with sediment, the space available for water storage gradually decreased, indicating that increased water input was partly counterbalanced by basin shallowing (Cohen, 2003; Hernández et al., 2008).

Regional humid conditions during the early Greenlandian are broadly supported by lacustrine, speleothem, and pollen proxy-based records from across Iberia (Morellón et al., 2018; Moreno et al., 2011, 2017; Thatcher et al., 2020), although they indicate high heterogeneity in the Iberian Peninsula. Our records agree more closely with archives from northern ($>40^\circ\text{N}$) and western Iberia (Finné et al., 2019; Thatcher et al., 2020), whereas sites in eastern and southern Iberia often exhibit weaker or contrasting expressions of early Greenlandian humidity (García-Alix et al., 2021; Ilvonen et al., 2022). This pattern highlights a hydroclimatic see-saw trend across the Iberian Peninsula, with a likely more Atlantic-dominated signal in the northwestern sector than in the more Mediterranean-influenced response in the southeastern sector.

Figure 4. (a) PCA biplot of the XRF data set shows samples grouped into three periods: Greenlandian; Northgrippian; and Meghalayan. Ellipses and markers represent the three distinct phases. Black vectors represent the loadings of geochemical variables. PC1 (46.4%) represents a gradient from higher terrigenous input to more autochthonous elements. (b) Broken-stick model for the PCA of the XRF data set. The black line represents the ordination values for the components (PC1 to PC10), while the red line shows the broken-stick threshold. (c) ANOSIM test results for the classification of samples into three climate phases in the PCA biplot. The boxplot displays dissimilarities between the three groups, and numbers (1–3) representing the within-group dissimilarities. The ANOSIM test produced a high R -value ($R^2 = 0.3$) with a significant p -value ($P = 0.001$). This analysis validates the statistical separation of the three phases identified in the PCA biplot. (d) Simplified stratigraphic log (derived from Figure S1 in Supporting Information S1) showing the alternation of Facies A (lighter gray) and Facies B (darker gray) along the core, plotted alongside downcore variations of TOC, $\delta^{13}\text{C}_{\text{bulk}}$, TOC/TN ratio and PC1 scores against depth and calibrated age (cal. ka BP). For the PC1 panel, the gray line shows the raw scores at sample resolution and the magenta line a 200-year smoothing, plotted to emphasize the long-term trend.

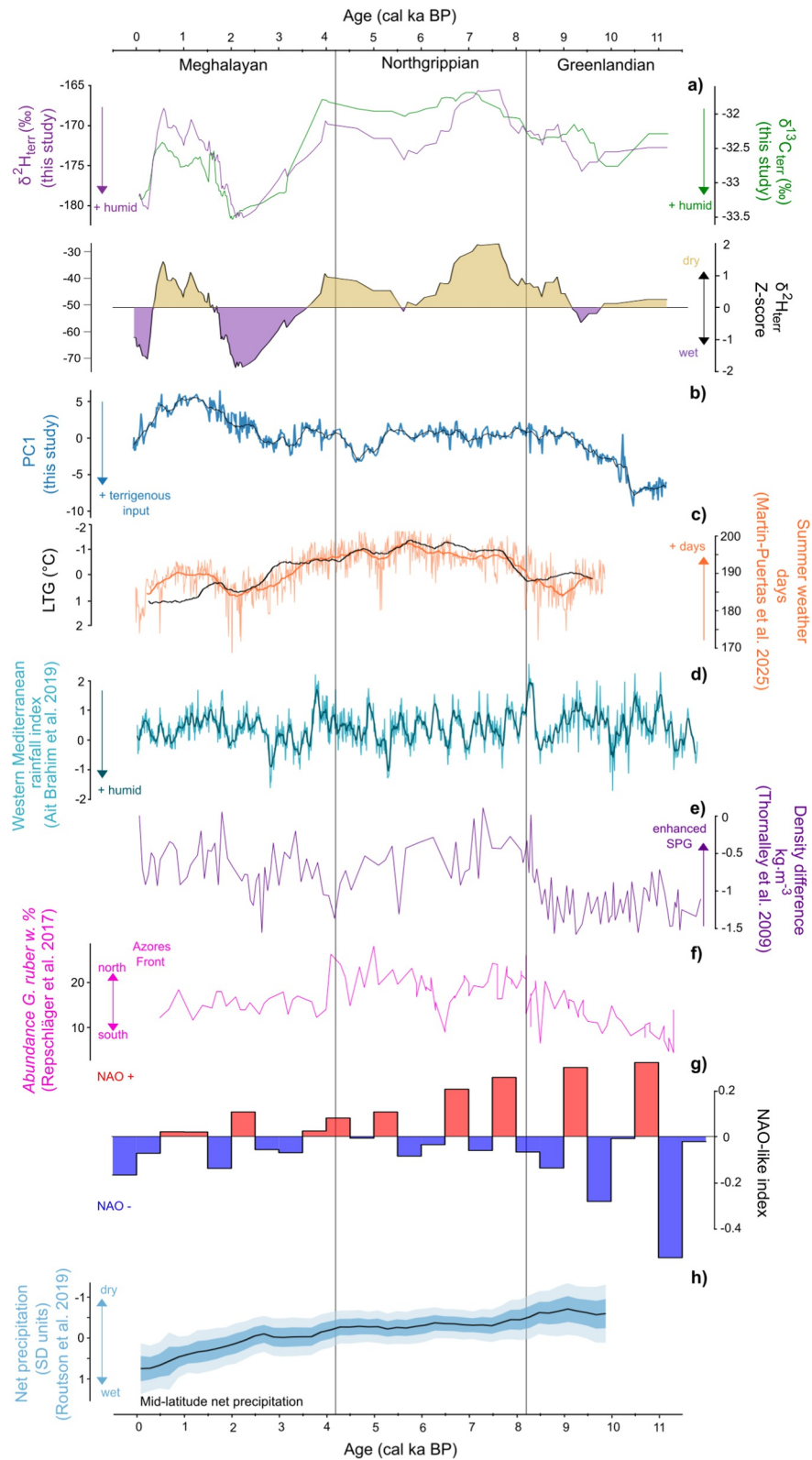


Figure 5.

Previous North Atlantic reconstructions (Blaschek et al., 2015; Repschläger et al., 2017; Thornalley et al., 2009) have indicated that the Greenlandian was characterized by relatively weak subpolar gyre circulation and a southward-displaced Azores Front (Figures 5e and 5f). This oceanic configuration is dynamically consistent with a more persistent negative NAO-like state and a southward shift in storm track positions (Figure 5g), which promotes enhanced winter moisture delivery to Iberia (Smith et al., 2016; Thatcher et al., 2020). Furthermore, the Greenlandian was characterized by an increased number of winterlike days (Martin-Puertas et al., 2025) (Figure 5c), extending the period over which more persistent negative NAO-like conditions modulated precipitation patterns, thereby likely increasing precipitation over the Iberian Peninsula. Independent speleothem records from the western Mediterranean support the prevalence of negative NAO-like conditions within this interval (Ait Brahimi et al., 2019) (Figure 5d), in agreement with the lower $\delta^2\text{H}_{\text{terr}}$ values observed at Lake Peixão (Figure 5a). These depleted values are consistent with several mutually reinforcing mechanisms: a southward storm track and more distal (Atlantic) moisture sources lengthen the transport pathway, promoting greater rainfall and isotopically lighter precipitation, while the associated increase in precipitation further depletes $\delta^2\text{H}_{\text{terr}}$ through the amount effect and, by sustaining more humid conditions, reduces evaporative ^2H -enrichment of soil and plant water.

5.2. Phase 2 (9–3.7 cal. ka BP)

The aridification trend initiated in the late Greenlandian intensified across the Northgrippian, as reflected in the progressive increase in $\delta^2\text{H}_{\text{terr}}$ values (Figure 5a), which is consistent with hydroclimate reconstructions from central and northwestern Iberia (Jambrina-Enríquez et al., 2014; Moreno et al., 2011, 2017; Thatcher et al., 2020; Vegas et al., 2010). This progressive weakening of Atlantic moisture influence reflects the combined effect of decreasing Northern Hemisphere summer insolation and a reduction in the regional North Atlantic LTG following the decay of the Laurentide ice sheet at ~ 8 cal. ka BP (Kaufman & Broadman, 2023; Martin-Puertas et al., 2025; Routson et al., 2019). This reduction in the regional LTG shifted the European seasonal balance toward a greater number of summer days (Figures 5c and 5h). This atmospheric reconfiguration, coupled with a sustained northward position of the Azores Front (Repschläger et al., 2017) (Figure 5f) and primarily positive NAO-like conditions (Figure 5g) and broader oceanic circulation variations (e.g., enhanced subpolar gyre circulation; Figure 5e) (Repschläger et al., 2017; Smith et al., 2016; Thornalley et al., 2009), collectively reduced humidity advection to southwestern Europe and shifted Atlantic storm tracks northward, away from Iberia (Ait Brahimi et al., 2019; Thatcher et al., 2020). The resulting increase in $\delta^2\text{H}$ values is consistent with several complementary mechanisms. A northward-shifted storm track likely favored more proximal moisture sources and shorter transport pathways, reducing progressive moisture loss and producing isotopically heavier precipitation. In turn, drier conditions increase the evaporative ^2H -enrichment of soil and plant water (Dansgaard, 1964; Sachse et al., 2012).

This drying trend culminated in a notable aridity maximum between ~ 7.6 and 6.7 cal. ka BP, which has also been identified in other regional records (García-Alix et al., 2021; Jambrina-Enríquez et al., 2014; Walczak et al., 2015). Proxy-based evidence suggests that the Atlantic Ocean sustained relatively humid conditions across inland Iberia until ~ 6 cal. ka BP (Ausín et al., 2025), but the northern sectors ($>40^\circ\text{N}$) experienced earlier drying, which is in agreement with the Lake Peixão record (Benito et al., 2023; Jambrina-Enríquez et al., 2014; Moreno

Figure 5. Proxy-based climate reconstructions over the last 11.1 cal. ka BP compared to the geochemical record of Lake Peixão. (a) Hydrogen ($\delta^2\text{H}_{\text{terr}}$, purple) and carbon ($\delta^{13}\text{C}_{\text{terr}}$, green) isotope composition of the terrestrial vegetation component derived from the NMF-combined EM1 + EM2 signal (upper subpanel), and corresponding $\delta^2\text{H}_{\text{terr}}$ z-score (lower subpanel) from Lake Peixão. Purple shading indicates wet conditions (negative z-scores) and yellow shading indicates dry conditions (positive z-scores). (b) PC1 from XRF geochemistry (this study), with more negative values indicating increased terrigenous input. (c) North Atlantic–European equator-to-pole latitudinal temperature gradient (LTG, $^\circ\text{C}$; black line) and reconstructed European summer weather days per year from varved lake sediments; dark line shows 500-year moving average, light orange shows variability at higher resolution (Martin-Puertas et al., 2025). (d) Western Mediterranean rainfall index from Ait Brahimi et al. (2019). (e) Density difference of upper-water-column stratification of North Atlantic Ocean based on the inferred water density difference between *G. bulloides* and *G. inflata* which is used as a proxy for the intensity of the subpolar gyre (SPG) (Thornalley et al., 2009). (f) *G. ruber* w. abundance from a marine core near the Azores archipelago (Repschläger et al., 2017) as indicator for the Azores Front position. (g) Decadal NAO-like index derived from the leading EOF of sea level pressure over the North Atlantic domain from the TraCE-21K-II transient simulation (He & Clark, 2022). Bars represent median values aggregated into 500-year bins; red and blue shading indicate positive and negative NAO phases, respectively. (h) Standardized mid-latitude (30°N – 50°N) net precipitation composite (black line) with one- and two-standard deviation uncertainty envelopes (blue shading) (Routson et al., 2019). Solid vertical lines delimit the three Holocene phases: Greenlandian (ca. 11.1–8.2 cal. ka BP), Northgrippian (ca. 8.2–4.2 cal. ka BP) and Meghalayan (ca. 4.2 cal. ka BP–present).

et al., 2011, 2017). This spatial configuration once again reflects the hydroclimatic see-saw pattern across the Iberian Peninsula centered on $\sim 40^{\circ}\text{N}$ and is likely linked to adjustments in the Azores High.

Between ~ 6.7 and 5.6 cal. ka BP, a transient shift toward wetter conditions interrupted the overall drying trend (Figure 5a). This interval corresponds to one of the rapid climate change events identified by Mayewski et al. (2004) and is recognized in northern Iberia and European records ($>40^{\circ}\text{N}$) (Lincoln et al., 2025; Railsback et al., 2011; Thatcher et al., 2020). The wetter signal observed at Lake Peixão is supported by lower $\delta^2\text{H}$ values in long-chain *n*-alkanes in the Praia Rei Cortiço record from the western Portuguese margin (Taylor et al., 2018), as well as by multiple Iberian lacustrine and speleothem archives (Aranbarri et al., 2014; Moreno et al., 2017; Ortiz et al., 2010). However, the west-central Portugal speleothem record studied by Thatcher et al. (2020) shows a more muted expression of this variability, likely reflecting altitudinal differences at the site and/or the seasonal sensitivity of records (Anderson et al., 2011; Kwiecien et al., 2022).

Several oceanic and atmospheric changes converged within this interval (~ 6.7 and 5.6 cal. ka BP). Subpolar gyre circulation first strengthened before weakening after ~ 6 cal. ka BP (Thornalley et al., 2009) (Figure 5e), and the brief southward excursion of the Azores Front between ~ 6.7 and 6.2 cal. ka BP is consistent with wetter conditions and Atlantic storm track displacement toward lower latitudes (Repschläger et al., 2017) (Figure 5f). In the study area, Moreno et al. (2023) reported intermittent peaks in marine-derived halogen input at Lake Peixão within this interval, reflecting enhanced atmospheric deposition of sea-salt aerosols associated with increased advection of high-latitude moisture sources (isotopically depleted in deuterium). On a broader scale, this reorganization coincides with the establishment of a more meridional circulation regime over northern Europe, which was driven by persistent blocking anticyclones over Scandinavia in response to a low LTG (Yu & Harrison, 1995). These changes are consistent with a shift to more negative NAO-like conditions within this interval (Figure 5g), which could have enhanced winter precipitation over western Iberia.

The Lake Peixão record reveals renewed dry conditions between 5.6 and 3.5 cal. ka BP (Figure 5a), which is consistent with numerous Iberian and western Mediterranean records indicating increased aridity during this period (Moreno et al., 2011; Pérez-Sanz et al., 2013; Schirrmacher et al., 2019; Thatcher et al., 2020; Vegas et al., 2010). This aridification broadly coincides with the end of the Holocene Thermal Maximum across Europe and the progressive decrease in summer insolation (Santos et al., 2026).

Superimposed on this hydroclimatic variability, organic matter productivity and vegetation indicators increased during the Northgrippian (Figure 4d), with the highest plant-wax concentrations suggesting maximum vegetation cover conditions (Figure S3a in Supporting Information S1) (e.g., Schwab et al., 2025). This period coincides broadly with the Holocene Thermal Maximum in western Iberia (between ~ 9 and 6 cal. ka BP), when the optimal temperature and moisture balance promoted vegetation development and enhanced lake productivity (Connor et al., 2012; Jambriña-Enríquez et al., 2014; van der Knaap & van Leeuwen, 1997). At Lake Peixão, the warmer conditions promoted the expansion of woody vegetation (Figure 3b), consistent with the concurrent $\delta^{13}\text{C}_{\text{terr}}$ enrichment, which reflects increased water use efficiency under a drier setting where moisture nonetheless remained sufficient to sustain woody plants. This configuration was linked to the northward positioning of the Azores High, which weakened Atlantic moisture advection from boreal sources (Cresswell-Clay et al., 2022), and it simultaneously opened a meridional corridor that channeled isotopically enriched moisture toward the region (Schirrmacher et al., 2019, 2020). This well-developed vegetation cover also modulated the catchment response. The XRF-based PC1 does not covary with the $\delta^2\text{H}_{\text{terr}}$ record throughout the Northgrippian (Figures 5a and 5b), remaining relatively stable and only shifting toward higher terrigenous input after ~ 5 cal. ka BP. This pattern suggests that catchment sediment delivery was partly decoupled from hydroclimate during this period and was instead buffered by the well-developed vegetation cover established under the Holocene Thermal Maximum. Importantly, when the influence of changing vegetation composition is removed, the $\delta^2\text{H}_{\text{prc}}$ record still preserves the main precipitation changes described above (Figures 3e, 5a, and 5b), indicating that vegetation and precipitation responded to the same climatic forcing throughout this phase.

5.3. Phase 3 (3.7 cal. ka BP to the Present)

During Phase 3 (Meghalayan), the $\delta^2\text{H}_{\text{terr}}$ values decreased progressively, with the most depleted values occurring between ~ 3.5 and 1.5 cal. ka BP (Figure 5a). While lower $\delta^2\text{H}_{\text{terr}}$ values indicate mainly increased precipitation, recent work has demonstrated that transitions from woody vegetation to herbaceous vegetation produce a decrease in $\delta^2\text{H}$ through changes in isotopic fractionation (Santos et al., 2022, 2026). At Lake Peixão,

the concurrent decrease in $\delta^{13}\text{C}_{\text{terr}}$ values (Figure 3d) supports the occurrence of cooler/wetter conditions, which is consistent with reduced water use efficiency in terrestrial C_3 vegetation (Diefendorf et al., 2010; Farquhar et al., 1989). This interpretation is further corroborated by an increase in terrigenous input into the lake (Figure 5b) and a shift toward greater herbaceous dominance over shrub taxa, which agrees with the vegetation changes revealed by the NMF model (Figure 3b). The corrected record retains the main $\delta^2\text{H}$ decrease (Figure 3e), showing that the wetting signal persists once vegetation-driven fractionation changes are removed. These findings suggest that both hydroclimate change and vegetation reorganization contributed to the depleted isotopic signal observed during the late Holocene, and that vegetation and precipitation responded to the same climatic forcing.

This vegetation shift toward grassland and heathland conditions coincides with documented environmental changes at nearby Charco da Candieira, where Connor et al. (2012) attributed large-scale deforestation to intensive pastoral activities and deliberate fires. Similar patterns are also documented in the Sierra de Gredos (García Álvarez et al., 2017). Large-scale deforestation in Serra da Estrela began ~ 3.4 cal. ka BP, documented by declines in arboreal pollen, increased charcoal accumulation, and increased soil erosion, and coincided with direct evidence of pastoral activity in the area (Connor et al., 2012; van der Knaap & van Leeuwen, 1995). The synchronous vegetation change at our study site therefore suggests two potentially coupled drivers for the Northgrippian-Meghalayan transition: (a) regional climate reorganization involving increased Atlantic Ocean moisture delivery and (b) sustained pastoral pressure and/or increased fire frequency, reflecting the complex regional interplay between climate change and land use pressure during this period.

At the regional scale, multiple proxy-based records indicate that dry conditions persisted across much of the Iberian Peninsula between ~ 4.0 and ~ 2.7 cal. ka BP, followed by a transition toward wetter conditions between ~ 2.7 and ~ 1.5 cal. ka BP (Cisneros et al., 2021; Martín-Puertas et al., 2011), which matches the wettest period (3.5 and 1.5 cal. ka BP) in the Lake Peixão record (Figure 5a). Despite minor differences in the timing and magnitude among individual records, broad regional agreement exists for late Holocene hydroclimatic evolution. Moreover, the transition from dry to wet conditions at Lake Peixão aligns with western Mediterranean rainfall index data (Ait Brahimi et al., 2019) (Figure 5d) and circum-Mediterranean evidence suggesting enhanced moisture availability between 4 and 3 cal. ka BP (Hu et al., 2022).

This Meghalayan wetting trend is consistent with the long-term Holocene temperature decrease reported by Kaufman et al. (2020) and a higher LTG (Martín-Puertas et al., 2025). Moreover, Martín-Puertas et al. (2025) reported a progressive reduction in the number of European summer weather days between ~ 4 and 2 cal. ka BP (Figure 5c), suggesting a longer winter season and an extended temporal window for NAO-driven precipitation over western Iberia. Thus, we suggest that the wet interval between ~ 4 and 2 cal. ka BP at Lake Peixão reflects a shift from a largely strong positive NAO-like state prior to ~ 4.0 cal. ka BP toward negative NAO-like phases thereafter (Figure 5g). This transition promoted a southward displacement of Atlantic westerlies, thereby enhancing winter precipitation over western Iberia (Ait Brahimi et al., 2019; Sáez et al., 2025) (Figure 5d). Analogously, the wet episode between 0.4 and 0.2 cal. ka BP, associated with the Little Ice Age, reflects persistent NAO-negative-like states that enhanced precipitation across the Iberian Peninsula (Ait Brahimi et al., 2019; Santos et al., 2024; Thatcher et al., 2020) (Figures 5d and 5g). Thus, hydroclimate variability is governed primarily by the sign and persistence of NAO-like phases, potentially interacting with other modes of North Atlantic variability, such as the East Atlantic pattern (e.g., Sánchez-López et al. (2016)), and is modulated by the Azores Front/subpolar gyre state.

However, discrepancies emerge between ~ 2.0 and 0.5 cal. ka BP. Although the detailed expression of the last ~ 2 millennia at Lake Peixão has been previously addressed by Santos et al. (2024), our record revealed a transition toward drier conditions; however, some western Mediterranean archives indicate relatively humid phases peaking at ~ 1.5 and 1.3 cal. ka BP, which is typically linked to NAO negative-like conditions (Ait Brahimi et al., 2019). In contrast, Hu et al. (2022) described a multicentennial positive NAO phase between ~ 2.2 and 1.2 cal. ka BP, which was characterized by wet and warm conditions across large parts of Europe. This dry event recorded at Lake Peixão is consistent with a positive NAO phase (Figure 5g), which typically suppresses winter precipitation over southwestern Iberia by displacing the storm track northward. These differences between a positive NAO phase and the humid signals recorded in other Mediterranean archives reflect the modulating role of the EA pattern. A positive NAO combined with a negative East Atlantic pattern would explain the spatially heterogeneous hydroclimate responses observed (Hernández, Sánchez-López, et al., 2020; Sánchez-López et al., 2016; Santos et al., 2024). These findings are consistent with an intensified subpolar gyre and a southward-displaced Azores

Front (Figures 5e and 5f) and an increase in the number of European summer days in between (Martin-Puertas et al., 2025) (Figure 5c).

Finally, the $\delta^2\text{H}_{\text{terr}}$ record identifies both the Greenlandian (Phase 1) and the Meghalayan (this Phase 3) as wet phases, although they show contrasting terrigenous inputs in the XRF-based PC1 record (Figure 5b). Between ~ 11.1 and 9 cal. ka BP, the recently deglaciated catchment was sparsely vegetated and hosted abundant unconsolidated material. Under these conditions, even moderate increases in moisture could generate strong erosion and sediment delivery, explaining the highest terrigenous input of the record (Arnaud et al., 2016; Hernández et al., 2023; Moreno et al., 2023). In contrast, during Phase 3 the catchment had been stabilized by several millennia of vegetation and soil development under the Holocene Thermal Maximum. This reduced the availability of erodible material, and the return to wetter conditions resulted in lower terrigenous input. This contrast supports the hypothesis that the $\delta^2\text{H}_{\text{terr}}$ mainly records hydroclimate variability, whereas PC1 reflects the catchment response to hydroclimate, modulated by vegetation cover, soil development, and sediment availability.

6. Conclusions

Our results revealed the following three main phases of Holocene hydroclimate variability in western Iberia at millennial scales: (a) a mostly wet Greenlandian (11.1–9 cal. ka BP), (b) a generally dry Northgrippian (8.2–4.2 cal. ka BP), and (c) a predominantly wetter Meghalayan (4.2–2 cal. ka BP) with a trend toward aridification, which is superimposed onto anthropogenic influence, over the last two millennia.

Millennial-scale variability was likely driven by orbitally forced changes in Northern Hemisphere insolation, which contributed to the final retreat of the Laurentide ice sheet and thereby modified North Atlantic ocean–atmosphere dynamics, including the LTG, storm track position, and westerly influence. These interpretations are supported by a source-resolved biomarker approach based on NMF analysis of plant-wax n -alkanes, which facilitates the isolation of terrestrial signals ($\delta^2\text{H}_{\text{terr}}$) and their conversion into precipitation-equivalent $\delta^2\text{H}$ values ($\delta^2\text{H}_{\text{prec}}$) using a catchment-integrated apparent fractionation factor, further constrained by bulk geochemical and XRF data. By providing precipitation-equivalent isotopic values that converge on the modern observed baseline, this record provides a robust basis for separating hydroclimatic signals, thereby offering a benchmark for model–data comparisons and for contextualizing modern hydroclimate extremes within the range of natural Holocene variability.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

The XRF data, bulk organic matter data, and downcore sedimentary plant wax data set generated in this study are archived at PANGAEA (Fernández-Pérez et al., 2026a, 2026b, 2026c). The scripts used for data analysis and figure generation are archived in open access at Zenodo (Fernández-Pérez, 2026).

References

- Aichner, B., Ott, F., Słowiński, M., Noryskiewicz, A. M., Brauer, A., & Sachse, D. (2018). Leaf wax n -alkane distributions record ecological changes during the Younger Dryas at Trzechowskie paleolake (northern Poland) without temporal delay. *Climate of the Past*, 14(11), 1607–1624. <https://doi.org/10.5194/cp-14-1607-2018>
- Ait Ibrahim, Y., Wassenburg, J. A., Sha, L., Cruz, F. W., Deininger, M., Sifeddine, A., et al. (2019). North Atlantic ice-rafting, ocean and atmospheric circulation during the Holocene: Insights from western Mediterranean Speleothems. *Geophysical Research Letters*, 46(13), 7614–7623. <https://doi.org/10.1029/2019GL082405>
- Anderson, R. S., Jiménez-Moreno, G., Carrión, J. S., & Pérez-Martínez, C. (2011). Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Nevada, southern Spain. *Quaternary Science Reviews*, 30(13), 1615–1629. <https://doi.org/10.1016/j.quascirev.2011.03.005>
- Aranbarri, J., González-Sampériz, P., Valero-Garcés, B., Moreno, A., Gil-Romera, G., Sevilla-Callejo, M., et al. (2014). Rapid climatic changes and resilient vegetation during the Lateglacial and Holocene in a continental region of south-western Europe. *Global and Planetary Change*, 114, 50–65. <https://doi.org/10.1016/j.gloplacha.2014.01.003>
- Arnaud, F., Poulenard, J., Giguet-Covex, C., Wilhelm, B., Révillon, S., Jenny, J.-P., et al. (2016). Erosion under climate and human pressures: An alpine lake sediment perspective. *Quaternary Science Reviews*, 152, 1–18. <https://doi.org/10.1016/j.quascirev.2016.09.018>
- Ausin, B., García-Alix, A., Hernández, A., González-Rouco, J. F., & Montoya, M. (2025). Atmospheric and oceanic changes since the last glacial maximum: Review of proxy-based and climate model simulation reconstructions in the Iberian Peninsula. In I. Cacho & A. Moreno (Eds.), *The CLIVAR-Spain report on the Climate in Spain* (pp. 18–83). Subsecretaría Gabinete Técnico (MITECO).

Acknowledgments

This research has been supported through the HOLMODRIVE (PTDC/CTA-GEO/29029/2017), funded by the Portuguese Foundation for Science and Technology – FCT, and by the MEDIATIC project (PID2022-139775OB-I00), funded by MCIN/AEI/10.13039/501100011033 and co-funded by “ERDF A way of making Europe.” Xunta de Galicia also supports this work through project ED431F 2022/18 and project ED431B 2024/03 from the programme “Axudas para a consolidación e estruturación de unidades de investigación competitivas e outras accións de fomento nas universidades do Sistema universitario de Galicia (SUG).” This work was also supported by project RED24-153734-T (PALEONET), funded by the Ministerio de Ciencia e Innovación of Spain, the Agencia Estatal de Investigación and the Fondo Europeo de Desarrollo Regional FEDER. Funding for open access charge: Universidade da Coruña/CISUG. AH is funded by the Spanish Ministry of Science and Innovation through the Ramón y Cajal Scheme [RYC2020-029253-I]; PF was supported by the Fonds de recherche du Québec (FRQ) [<https://doi.org/10.6977/341269>]; AMR is funded by the Helmholtz Program “Changing Earth”; IPMA’s Biogeochemistry Lab was supported by EMSO-PT - PINFRA/22157/2016 and CCMAR FCT Research Unit - project UIDB/04326/2020. The monthly sea level pressure transient simulation model (TraCE-21K-II) was downloaded from the Transient Climate Simulation Lab (<https://trace-21k.nelson.wisc.edu/portal.html>). Last time accessed: 30 March 2026.

- Benito, G., Greenbaum, N., Medialdea, A., Calle, M., Sanchez-Moya, Y., Machado, M., et al. (2023). Late Pleistocene–Holocene multi-decadal patterns of extreme floods in NW Iberia: The Duero River palaeoflood record. *Quaternary Science Reviews*, 321, 108356. <https://doi.org/10.1016/j.quascirev.2023.108356>
- Blaschek, M., Renssen, H., Kissel, C., & Thornalley, D. (2015). Holocene North Atlantic overturning in an atmosphere-ocean-sea ice model compared to proxy-based reconstructions. *Paleoceanography*, 30(11), 1503–1524. <https://doi.org/10.1002/2015PA002828>
- Bray, E. E., & Evans, E. D. (1961). Distribution of n-paraffins as a clue to recognition of source beds. *Geochimica et Cosmochimica Acta*, 22(1), 2–15. [https://doi.org/10.1016/0016-7037\(61\)90069-2](https://doi.org/10.1016/0016-7037(61)90069-2)
- Castañeda, I. S., & Schouten, S. (2011). A review of molecular organic proxies for examining modern and ancient lacustrine environments. *Quaternary Science Reviews*, 30(21), 2851–2891. <https://doi.org/10.1016/j.quascirev.2011.07.009>
- Chikaraishi, Y., & Naraoka, H. (2003). Compound-specific δD – $\delta^{13}C$ analyses of n-alkanes extracted from terrestrial and aquatic plants. *Phytochemistry*, 63(3), 361–371. [https://doi.org/10.1016/S0031-9422\(02\)00749-5](https://doi.org/10.1016/S0031-9422(02)00749-5)
- Cisneros, M., Cacho, I., Moreno, A., Stoll, H., Torner, J., Català, A., et al. (2021). Hydroclimate variability during the last 2700 years based on stalagmite multi-proxy records in the central-western Mediterranean. *Quaternary Science Reviews*, 269, 107137. <https://doi.org/10.1016/j.quascirev.2021.107137>
- Cohen, A. S. (2003). *Paleolimnology: The history and evolution of lake systems*. Oxford University Press.
- Comas-Bru, L., & McDermott, F. (2014). Impacts of the EA and SCA patterns on the European twentieth century NAO–winter climate relationship. *Quarterly Journal of the Royal Meteorological Society*, 140(679), 354–363. <https://doi.org/10.1002/qj.2158>
- Connor, S. E., Araújo, J., van der Knaap, W. O., & van Leeuwen, J. F. N. (2012). A long-term perspective on biomass burning in the Serra da Estrela, Portugal. *Quaternary Science Reviews*, 55, 114–124. <https://doi.org/10.1016/j.quascirev.2012.08.007>
- Cortesi, N., Trigo, R. M., Gonzalez-Hidalgo, J. C., & Ramos, A. M. (2013). Modelling monthly precipitation with circulation weather types for a dense network of stations over Iberia. *Hydrology and Earth System Sciences*, 17(2), 665–678. <https://doi.org/10.5194/hess-17-665-2013>
- Cresswell-Clay, N., Ummenhofer, C. C., Thatcher, D. L., Wanamaker, A. D., Denniston, R. F., Asmerom, Y., & Polyak, V. J. (2022). Twentieth-century Azores High expansion unprecedented in the past 1,200 years. *Nature Geoscience*, 15(7), 548–553. <https://doi.org/10.1038/s41561-022-00971-w>
- Dansgaard, W. (1964). Stable isotopes in precipitation. *Tellus*, 16(4), 436–468. <https://doi.org/10.1111/j.2153-3490.1964.tb00181.x>
- Diefendorf, A. F., Freeman, K. H., Wing, S. L., & Graham, H. V. (2011). Production of n-alkyl lipids in living plants and implications for the geologic past. *Geochimica et Cosmochimica Acta*, 75(23), 7472–7485. <https://doi.org/10.1016/j.gca.2011.09.028>
- Diefendorf, A. F., & Freimuth, E. J. (2017). Extracting the most from terrestrial plant-derived n-alkyl lipids and their carbon isotopes from the sedimentary record: A review. *Organic Geochemistry*, 103, 1–21. <https://doi.org/10.1016/j.orggeochem.2016.10.016>
- Diefendorf, A. F., Mueller, K. E., Wing, S. L., Koch, P. L., & Freeman, K. H. (2010). Global patterns in leaf $\delta^{13}C$ discrimination and implications for studies of past and future climate. *Proceedings of the National Academy of Sciences*, 107(13), 5738–5743. <https://doi.org/10.1073/pnas.0910513107>
- Eglinton, G., & Hamilton, R. J. (1967). Leaf epicuticular waxes. *Science*, 156(3780), 1322–1335. <https://doi.org/10.1126/science.156.3780.1322>
- Eglinton, T. I., & Eglinton, G. (2008). Molecular proxies for paleoclimatology. *Earth and Planetary Science Letters*, 275(1), 1–16. <https://doi.org/10.1016/j.epsl.2008.07.012>
- Espinha Marques, J., Carvalho, A., Marques, J. M., Chaminé, H. I., Guerner, A., Moura, R., et al. (2011). A methodology for assessing the impact of the use of road salt on groundwater resources in a mountain environment (Serra da Estrela, Central Portugal). *CAD. LAB. XEOL. LAXE.*, 36, 78–79.
- Farquhar, G. D., Hubick, K. T., Condon, A. G., & Richards, R. A. (1989). Carbon isotope fractionation and plant water-use efficiency. In P. W. Rundel, J. R. Ehleringer, & K. A. Nagy (Eds.), *Stable isotopes in ecological research* (pp. 21–40). Springer. https://doi.org/10.1007/978-1-4612-3498-2_2
- Fernández-Alvarez, J. C., Pérez-Alarcón, A., Eiras-Barca, J., Rahimi, S., Nieto, R., & Gimeno, L. (2023). Projected changes in atmospheric moisture transport contributions associated with climate warming in the North Atlantic. *Nature Communications*, 14(1), 6476. <https://doi.org/10.1038/s41467-023-41915-1>
- Fernández-Pérez, U. (2026). Uxia94/PEX-01_Holocene: PEX-01 Holocene analysis workflows for paleoclimate reconstruction (v1.0.2) [Software]. *Zenodo*. <https://doi.org/10.5281/zenodo.21064795>
- Fernández-Pérez, U., Hernández, A., Sáez, A., Carballeira, R., Altrogge, R., Santos, L., et al. (2025). Late Holocene climate changes in the Northwest Iberian Peninsula reflect fluctuations in the relative dominance of Atlantic and Mediterranean climate zones. *Palaogeography, Paleoclimatology, Palaeoecology*, 674, 113034. <https://doi.org/10.1016/j.palaeo.2025.113034>
- Fernández-Pérez, U., Santos, R. N., Rodrigues, T., Schefuß, E., Bao, R., Raposeiro, P. M., et al. (2026a). Concentrations and compound-specific hydrogen (δ^2H) and carbon ($\delta^{13}C$) isotope compositions of plant wax n-alkanes from sediment core PEX19-01, Lake Peixão, Serra da Estrela, Portugal [Dataset]. *PANGAEA*. <https://doi.org/10.1594/PANGAEA.993909>
- Fernández-Pérez, U., Santos, R. N., Rodrigues, T., Schefuß, E., Bao, R., Raposeiro, P. M., et al. (2026b). XRF core-scanning elemental data and bulk organic matter analyses from sediment core PEX19-01, Lake Peixão, Serra da Estrela, Portugal [Dataset]. *PANGAEA*. <https://doi.org/10.1594/PANGAEA.993913>
- Fernández-Pérez, U., Santos, R. N., Rodrigues, T., Schefuß, E., Bao, R., Raposeiro, P. M., et al. (2026c). Holocene hydrogen isotope composition of precipitation (δ^2H) reconstructed from sedimentary leaf wax n-alkanes in Lake Peixão, Serra da Estrela, Portugal [Dataset]. *PANGAEA*. <https://doi.org/10.1594/PANGAEA.995820>
- Ficken, K. J., Li, B., Swain, D. L., & Eglinton, G. (2000). An n-alkane proxy for the sedimentary input of submerged/floating freshwater aquatic macrophytes. *Organic Geochemistry*, 31(7), 745–749. [https://doi.org/10.1016/S0146-6380\(00\)00081-4](https://doi.org/10.1016/S0146-6380(00)00081-4)
- Finné, M., Woodbridge, J., Labuhn, I., & Roberts, C. N. (2019). Holocene hydro-climatic variability in the Mediterranean: A synthetic multi-proxy reconstruction. *The Holocene*, 29(5), 847–863. <https://doi.org/10.1177/0959683619826634>
- Freimuth, E. J., Diefendorf, A. F., & Lowell, T. V. (2017). Hydrogen isotopes of n-alkanes and n-alkanoic acids as tracers of precipitation in a temperate forest and implications for paleorecords. *Geochimica et Cosmochimica Acta*, 206, 166–183. <https://doi.org/10.1016/j.gca.2017.02.027>
- García-Alix, A., Camuera, J., Ramos-Román, M. J., Toney, J. L., Sachse, D., Schefuß, E., et al. (2021). Paleohydrological dynamics in the Western Mediterranean during the last glacial cycle. *Global and Planetary Change*, 202, 103527. <https://doi.org/10.1016/j.gloplacha.2021.103527>
- García Álvarez, S., Bal, M. C., Allée, P., García-Amorena, I., & Rubiales, J. M. (2017). Holocene treeline history of a high-mountain landscape inferred from soil charcoal: The case of Sierra de Gredos (Iberian Central System, SW Europe). *Quaternary International, Anthracology: Local to Global Significance of Charcoal Science - Part 1*, 457, 85–98. <https://doi.org/10.1016/j.quaint.2017.04.019>
- Hägg, C., Pätzold, J., Bouillon, S., & Schefuß, E. (2021). Impact of selective degradation on molecular isotope compositions in oxic and anoxic marine sediments. *Organic Geochemistry*, 153, 104192. <https://doi.org/10.1016/j.orggeochem.2021.104192>

- He, F., & Clark, P. U. (2022). Freshwater forcing of the Atlantic Meridional Overturning Circulation revisited. *Nature Climate Change*, 12(5), 449–454. <https://doi.org/10.1038/s41558-022-01328-2>
- Hernández, A., Bao, R., Giral, S., Leng, M. J., Barker, P. A., Sáez, A., et al. (2008). The palaeohydrological evolution of Lago Chungará (Andean Altiplano, northern Chile) during the Lateglacial and early Holocene using oxygen isotopes in diatom silica. *Journal of Quaternary Science*, 23(4), 351–363. <https://doi.org/10.1002/jqs.1173>
- Hernández, A., Martín-Puertas, C., Moffa-Sánchez, P., Moreno-Chamarro, E., Ortega, P., Blockley, S., et al. (2020). Modes of climate variability: Synthesis and review of proxy-based reconstructions through the Holocene. *Earth-Science Reviews*, 209, 103286. <https://doi.org/10.1016/j.earscirev.2020.103286>
- Hernández, A., Sáez, A., Santos, R. N., Rodrigues, T., Martín-Puertas, C., Gil-Romera, G., et al. (2023). The timing of the deglaciation in the Atlantic Iberian mountains: Insights from the stratigraphic analysis of a lake sequence in Serra da Estrela (Portugal). *Earth Surface Processes and Landforms*, 48(2), 233–242. <https://doi.org/10.1002/esp.5536>
- Hernández, A., Sánchez-López, G., Pla-Rabes, S., Comas-Bru, L., Parnell, A., Cahill, N., et al. (2020). A 2,000-year Bayesian NAO reconstruction from the Iberian Peninsula. *Scientific Reports*, 10(1), 1. <https://doi.org/10.1038/s41598-020-71372-5>
- Hu, H.-M., Trouet, V., Spötl, C., Tsai, H.-C., Chien, W.-Y., Sung, W.-H., et al. (2022). Tracking westerly wind directions over Europe since the middle Holocene. *Nature Communications*, 13(1), 7866. <https://doi.org/10.1038/s41467-022-34952-9>
- Iivonen, L., López-Sáez, J. A., Holmström, L., Alba-Sánchez, F., Pérez-Díaz, S., Carrión, J. S., et al. (2022). Spatial and temporal patterns of Holocene precipitation change in the Iberian Peninsula. *Boreas*, 51(4), 776–792. <https://doi.org/10.1111/bor.12586>
- Jackson, D. A. (1993). Stopping rules in principal components analysis: A comparison of heuristic and statistical approaches. *Ecology*, 74(8), 2204–2214. <https://doi.org/10.2307/1939574>
- Jambrina-Enríquez, M., Rico, M., Moreno, A., Leira, M., Bernárdez, P., Prego, R., et al. (2014). Timing of deglaciation and postglacial environmental dynamics in NW Iberia: The Sanabria Lake record. *Quaternary Science Reviews*, 94, 136–158. <https://doi.org/10.1016/j.quascirev.2014.04.018>
- Jambrina-Enríquez, M., Sachse, D., & Valero-Garcés, B. L. (2016). A deglaciation and Holocene biomarker-based reconstruction of climate and environmental variability in NW Iberian Peninsula: The Sanabria Lake sequence. *Journal of Paleolimnology*, 56(1), 49–66. <https://doi.org/10.1007/s10933-016-9890-6>
- Kahmen, A., Hoffmann, B., Schefuß, E., Arndt, S. K., Cernusak, L. A., West, J. B., & Sachse, D. (2013). Leaf water deuterium enrichment shapes leaf wax n -alkane δD values of angiosperm plants II: Observational evidence and global implications. *Geochimica et Cosmochimica Acta, Hydrogen Isotopes*, 111, 50–63. <https://doi.org/10.1016/j.gca.2012.09.004>
- Kassambara, A., & Mundt, F. (2017). Package ‘factoextra’. Extract and visualize the results of multivariate data analyses (version 1.0.7) [Computer software]. <https://cran.r-project.org/web/packages/factoextra/index.html>
- Kaufman, D., McKay, N., Routson, C., Erb, M., Dätwyler, C., Sommer, P. S., et al. (2020). Holocene global mean surface temperature, a multi-method reconstruction approach. *Scientific Data*, 7(1), 201. <https://doi.org/10.1038/s41597-020-0530-7>
- Kaufman, D. S., & Broadman, E. (2023). Revisiting the Holocene global temperature conundrum. *Nature*, 614(7948), 425–435. <https://doi.org/10.1038/s41586-022-05536-w>
- Kohn, M. J. (2010). Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. *Proceedings of the National Academy of Sciences*, 107(46), 19691–19695. <https://doi.org/10.1073/pnas.1004933107>
- Kwiecien, O., Braun, T., Brunello, C. F., Faulkner, P., Hausmann, N., Helle, G., et al. (2022). What we talk about when we talk about seasonality – A transdisciplinary review. *Earth-Science Reviews*, 225, 103843. <https://doi.org/10.1016/j.earscirev.2021.103843>
- Li, W., Cao, X., Stoof-Leichsenring, K., Hou, X., Yu, S.-Y., Tian, F., & Herzschuh, U. (2024). Holocene lake response to glacier and catchment changes on the eastern Tibetan Plateau from quantitative conductivity reconstructions based on sedaDNA-derived macrophyte records. *Quaternary Science Reviews*, 338, 108806. <https://doi.org/10.1016/j.quascirev.2024.108806>
- Lincoln, P., Tjallingii, R., Kosonen, E., Ojala, A., Abrook, A. M., & Martín-Puertas, C. (2025). Disruption of boreal lake circulation in response to mid-Holocene warmth: evidence from the varved sediments of Lake Nautajärvi, southern Finland. *Science of the Total Environment*, 964, 178519. <https://doi.org/10.1016/j.scitotenv.2025.178519>
- Lionello, P., Malanotte-Rizzoli, P., Boscolo, R., Alpert, P., Artale, V., Li, L., et al. (2006). The Mediterranean climate: An overview of the main characteristics and issues. In P. Lionello, P. Malanotte-Rizzoli, & R. Boscolo (Eds.), *Developments in Earth and environmental sciences* (Vol. 4, pp. 1–26). Elsevier. [https://doi.org/10.1016/S1571-9197\(06\)80003-0](https://doi.org/10.1016/S1571-9197(06)80003-0)
- Martin-Puertas, C., Boyall, L., Hernandez, A., Ojala, A. E. K., Abrook, A., Kosonen, E., et al. (2025). Consistent response of European summers to the latitudinal temperature gradient over the Holocene. *Nature Communications*, 16(1), 9969. <https://doi.org/10.1038/s41467-025-65804-x>
- Martin-Puertas, C., Valero-Garcés, B. L., Mata, M. P., Moreno, A., Giral, S., Martínez-Ruiz, F., & Jiménez-Espejo, F. (2011). Geochemical processes in a Mediterranean Lake: A high-resolution study of the last 4,000 years in Zofar Lake, southern Spain. *Journal of Paleolimnology*, 46(3), 405–421. <https://doi.org/10.1007/s10933-009-9373-0>
- Marzi, R., Torkelson, B. E., & Olson, R. K. (1993). A revised carbon preference index. *Organic Geochemistry*, 20(8), 1303–1306. [https://doi.org/10.1016/0146-6380\(93\)90016-5](https://doi.org/10.1016/0146-6380(93)90016-5)
- Mayewski, P. A., Rohling, E. E., Stager, J. C., Karlén, W., Maasch, K. A., Meeker, L. D., et al. (2004). Holocene climate variability. *Quaternary Research*, 62(3), 243–255. <https://doi.org/10.1016/j.yqres.2004.07.001>
- Mendes, I., Mora, C., & Rodríguez-Echeverría, S. (2025). Mapa de alta resolução da vegetação dos vales e planaltos superiores da Serra da Estrela (Portugal). *Finisterra*, 60(130), e38919. <https://doi.org/10.18055/Finis38919>
- Meyers, P. A. (1997). Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes. *Organic Geochemistry*, 27(5), 213–250. [https://doi.org/10.1016/S0146-6380\(97\)00049-1](https://doi.org/10.1016/S0146-6380(97)00049-1)
- Meyers, P. A., & Teranes, J. L. (2001). Sediment organic matter. In W. M. Last & J. P. Smol (Eds.), *Tracking environmental change using lake sediments: Physical and geochemical methods* (pp. 239–269). Springer. https://doi.org/10.1007/0-306-47670-3_9
- Mora, C. (2010). A synthetic map of the climatopes of the Serra da Estrela (Portugal). *Journal of Maps*, 6(1), 591–608. <https://doi.org/10.4113/jom.2010.1112>
- Morellón, M., Aranbarri, J., Moreno, A., González-Sampériz, P., & Valero-Garcés, B. L. (2018). Early Holocene humidity patterns in the Iberian Peninsula reconstructed from lake, pollen and speleothem records. *Quaternary Science Reviews*, 181, 1–18. <https://doi.org/10.1016/j.quascirev.2017.11.016>
- Moreno, A., López-Merino, L., Leira, M., Marco-Barba, J., González-Sampériz, P., Valero-Garcés, B. L., et al. (2011). Revealing the last 13,500 years of environmental history from the multiproxy record of a mountain lake (Lago Enol, northern Iberian Peninsula). *Journal of Paleolimnology*, 46(3), 327–349. <https://doi.org/10.1007/s10933-009-9387-7>
- Moreno, A., Pérez-Mejías, C., Bartolomé, M., Sancho, C., Cacho, I., Stoll, H., et al. (2017). New speleothem data from Molinos and Ejulve caves reveal Holocene hydrological variability in northeast Iberia. *Quaternary Research*, 88(2), 223–233. <https://doi.org/10.1017/qua.2017.39>

- Moreno, J., Ramos, A. M., Raposeiro, P. M., Santos, R. N., Rodrigues, T., Naughton, F., et al. (2023). Identifying imprints of externally derived dust and halogens in the sedimentary record of an Iberian alpine lake for the past ~13,500 years – Lake Peixão, Serra da Estrela (Central Portugal). *Science of the Total Environment*, 903, 166179. <https://doi.org/10.1016/j.scitotenv.2023.166179>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., et al. (2022). Vegan: Community ecology package (version 2.6-4) [Computer software]. <https://cran.r-project.org/web/packages/vegan/index.html>
- Ortiz, J. E., Gallego, J. L. R., Torres, T., Díaz-Bautista, A., & Sierra, C. (2010). Palaeoenvironmental reconstruction of Northern Spain during the last 8000 cal yr BP based on the biomarker content of the Roñanzas peat bog (Asturias). *Organic Geochemistry*, 41(5), 454–466. <https://doi.org/10.1016/j.orggeochem.2010.02.003>
- Paredes, D., Trigo, R. M., García-Herrera, R., & Trigo, I. F. (2006). Understanding precipitation changes in Iberia in early spring: Weather typing and storm-tracking approaches. *Journal of Hydrometeorology*, 7(1), 101–113. <https://doi.org/10.1175/JHM472.1>
- Pérez-Sanz, A., González-Sampériz, P., Moreno, A., Valero-Garcés, B., Gil-Romera, G., Rieradevall, M., et al. (2013). Holocene climate variability, vegetation dynamics and fire regime in the central Pyrenees: The Basa de la Mora sequence (NE Spain). *Quaternary Science Reviews*, 73, 149–169. <https://doi.org/10.1016/j.quascirev.2013.05.010>
- Polissar, P. J., Karp, A. T., & D'Andrea, W. J. (2025). Mixed messages: Unmixing sedimentary molecular distributions reveals source contributions and isotopic values. *Geochimica et Cosmochimica Acta*, 396, 122–134. <https://doi.org/10.1016/j.gca.2025.03.001>
- Poynter, J. G., Farrimond, P., Robinson, N., & Eglinton, G. (1989). Aeolian-derived higher plant lipids in the marine sedimentary record: Links with palaeoclimate. In M. Leinen & M. Sarnthein (Eds.), *Paleoclimatology and paleometeorology: Modern and past patterns of global atmospheric transport* (pp. 435–462). Springer. https://doi.org/10.1007/978-94-009-0995-3_18
- Railsback, L. B., Liang, F., Vidal Romaní, J. R., Grandal-d'Anglade, A., Vaqueiro Rodríguez, M., Santos Fidalgo, L., et al. (2011). Petrographic and isotopic evidence for Holocene long-term climate change and shorter-term environmental shifts from a stalagmite from the Serra do Courel of northwestern Spain, and implications for climatic history across Europe and the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 305(1), 172–184. <https://doi.org/10.1016/j.palaeo.2011.02.030>
- Ramos, A. M., Cortesi, N., & Trigo, R. M. (2014). Circulation weather types and spatial variability of daily precipitation in the Iberian Peninsula. *Frontiers in Earth Science*, 2. <https://doi.org/10.3389/feart.2014.00025>
- R Development Core Team. (2015). *A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Repschläger, J., Garbe-Schönberg, D., Weinelt, M., & Schneider, R. (2017). Holocene evolution of the North Atlantic subsurface transport. *Climate of the Past*, 13(4), 333–344. <https://doi.org/10.5194/cp-13-333-2017>
- Rivas-Martínez, S. (2007). Mapa de seires, geoseries y geopermaseries de vegetación de España [Memoria del mapa de vegetación potencial de España]. Parte I. *Itinera Geobotanica*, 17, 5–46.
- Routson, C. C., McKay, N. P., Kaufman, D. S., Erb, M. P., Goosse, H., Shuman, B. N., et al. (2019). Mid-latitude net precipitation decreased with Arctic warming during the Holocene. *Nature*, 568(7750), 83–87. <https://doi.org/10.1038/s41586-019-1060-3>
- Sachse, D., Billault, I., Bowen, G. J., Chikaraishi, Y., Dawson, T. E., Feakins, S. J., et al. (2012). Molecular paleohydrology: Interpreting the hydrogen-isotopic composition of lipid biomarkers from photosynthesizing organisms. *Annual Review of Earth and Planetary Sciences*, 40(1), 221–249. <https://doi.org/10.1146/annurev-earth-042711-105535>
- Sáez, A., Hernández, A., Pimentel, A., Andrade, M., Bao, R., Raposeiro, P. M., et al. (2025). Westerlies migrations and volcanic records over the past 4000 years from the Azores lacustrine sequences. Exploring correlations and impacts on Western Europe. *Global and Planetary Change*, 246, 104698. <https://doi.org/10.1016/j.gloplacha.2025.104698>
- Sánchez-López, G., Hernández, A., Pla-Rabes, S., Trigo, R. M., Toro, M., Granados, I., et al. (2016). Climate reconstruction for the last two millennia in central Iberia: The role of East Atlantic (EA), North Atlantic Oscillation (NAO) and their interplay over the Iberian Peninsula. <https://doi.org/10.13039/501100001871>
- Santisteban, J. I., Mediavilla, R., Galán de Frutos, L., & López Cilla, I. (2019). Holocene floods in a complex fluvial wetland in central Spain: Environmental variability, climate and time. *Global and Planetary Change*, 181, 102986. <https://doi.org/10.1016/j.gloplacha.2019.102986>
- Santos, R. N., Nelson, D. B., Klatt, A., Schubert, C. J., Dubois, N., De Jonge, C., & Ladd, S. N. (2026). Central European hydroclimate since the younger dryas inferred from vegetation-corrected sedimentary plant wax δ^{2H} values. *Paleoceanography and Paleoclimatology*, 41(3), e2025PA005401. <https://doi.org/10.1029/2025PA005401>
- Santos, R. N., Rodrigues, T., Naughton, F., Schefuß, E., Oliveira, D., Moreno, J., et al. (2024). Understanding the Atlantic influence on climate and vegetation dynamics in western Iberia over the last 2000 years. *Quaternary Science Reviews*, 337, 108796. <https://doi.org/10.1016/j.quascirev.2024.108796>
- Santos, R. N., Schefuß, E., Cordeiro, L. G. M. S., Oliveira, D., Hernández, A., Ramos, A. M., & Rodrigues, T. (2022). Leaf wax biomarkers of a high-mountain lake area in western Iberia—Implications for environmental reconstructions. *Frontiers in Environmental Science*, 10, 994377. <https://doi.org/10.3389/fenvs.2022.994377>
- Schafer, Bliedner, M., Wolf, D., Kolb, T., Zech, J., Faust, D., & Zech, R. (2018). A $\delta^{13}C$ and δ^{2H} leaf wax record from the Late Quaternary loess-paleosol sequence El Paraíso, Central Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 507, 52–59. <https://doi.org/10.1016/j.palaeo.2018.06.039>
- Schirmacher, J., Andersen, N., Schneider, R. R., & Weinelt, M. (2020). Fossil leaf wax hydrogen isotopes reveal variability of Atlantic and Mediterranean climate forcing on the southeast Iberian Peninsula between 6000 to 3000 cal. BP. *PLoS One*, 15(12), e0243662. <https://doi.org/10.1371/journal.pone.0243662>
- Schirmacher, J., Weinelt, M., Blanz, T., Andersen, N., Salgueiro, E., & Schneider, R. R. (2019). Multi-decadal atmospheric and marine climate variability in southern Iberia during the mid-to late-Holocene. *Climate of the Past*, 15(2), 617–634. <https://doi.org/10.5194/cp-15-617-2019>
- Schwab, M. S., Haghipour, N., & Eglinton, T. I. (2025). Hydrodynamic, seasonal, and climatic factors affecting the terrestrial-to-aquatic export of plant-derived biomarkers. *Geochimica et Cosmochimica Acta*, 391, 31–48. <https://doi.org/10.1016/j.gca.2024.12.009>
- Sessions, A. L., Burgoyne, T. W., Schimmelmann, A., & Hayes, J. M. (1999). Fractionation of hydrogen isotopes in lipid biosynthesis. *Organic Geochemistry*, 30(9), 1193–1200. [https://doi.org/10.1016/S0146-6380\(99\)00094-7](https://doi.org/10.1016/S0146-6380(99)00094-7)
- Smith, A. C., Wynn, P. M., Barker, P. A., Leng, M. J., Noble, S. R., & Tych, W. (2016). North Atlantic forcing of moisture delivery to Europe throughout the Holocene. *Scientific Reports*, 6(1), 24745. <https://doi.org/10.1038/srep24745>
- Taylor, A. K., Benedetti, M. M., Haws, J. A., & Lane, C. S. (2018). Mid-Holocene Iberian hydroclimate variability and paleoenvironmental change: Molecular and isotopic insights from Praia Rei Cortiço, Portugal. *Journal of Quaternary Science*, 33(1), 79–92. <https://doi.org/10.1002/jqs.3000>
- Thatcher, D. L., Wanamaker, A. D., Denniston, R. F., Asmerom, Y., Polyak, V. J., Fullick, D., et al. (2020). Hydroclimate variability from western Iberia (Portugal) during the Holocene: Insights from a composite stalagmite isotope record. *The Holocene*, 30(7), 966–981. <https://doi.org/10.1177/0959683620908648>

- Thornalley, D. J. R., Elderfield, H., & McCave, I. N. (2009). Holocene oscillations in temperature and salinity of the surface subpolar North Atlantic. *Nature*, 457(7230), 711–714. <https://doi.org/10.1038/nature07717>
- Toney, J. L., García-Alix, A., Jiménez-Moreno, G., Anderson, R. S., Moossen, H., & Seki, O. (2020). New insights into Holocene hydrology and temperature from lipid biomarkers in western Mediterranean alpine wetlands. *Quaternary Science Reviews*, 240, 106395. <https://doi.org/10.1016/j.quascirev.2020.106395>
- Trigo, R. M., Valente, M. A., Trigo, I. F., Miranda, P. M. A., Ramos, A. M., Paredes, D., & García-Herrera, R. (2008). The impact of North Atlantic Wind and cyclone trends on European precipitation and significant wave height in the Atlantic. *Annals of the New York Academy of Sciences*, 1146(1), 212–234. <https://doi.org/10.1196/annals.1446.014>
- van den Boogaart, K. G., & Tolosana-Delgado, R. (2008). “Compositions”: A unified R package to analyze compositional data. *Computers & Geosciences*, 34(4), 320–338. <https://doi.org/10.1016/j.cageo.2006.11.017>
- van der Knaap, W. O., & van Leeuwen, J. F. N. (1995). Holocene vegetation succession and degradation as responses to climatic change and human activity in the Serra de Estrela, Portugal. *Review of Palaeobotany and Palynology*, 89(3), 153–211. [https://doi.org/10.1016/0034-6667\(95\)00048-0](https://doi.org/10.1016/0034-6667(95)00048-0)
- van der Knaap, W. O., & van Leeuwen, J. F. N. (1997). Late Glacial and early Holocene vegetation succession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology*, 97(3), 239–285. [https://doi.org/10.1016/S0034-6667\(97\)00008-0](https://doi.org/10.1016/S0034-6667(97)00008-0)
- Vegas, J., Ruiz-Zapata, B., Ortiz, J. E., Galán, L., Torres, T., García-Cortés, Á., et al. (2010). Identification of arid phases during the last 50 cal. Ka BP from the Fuentillejo maar-lacustrine record (Campo de Calatrava Volcanic Field, Spain). *Journal of Quaternary Science*, 25(7), 1051–1062. <https://doi.org/10.1002/jqs.1262>
- Vieira, G., & Woronko, B. (2022). Chapter 4.16—The glaciers of Serra da Estrela. In M. Oliva, D. Palacios, & J. M. Fernández-Fernández (Eds.), *Iberia, land of glaciers* (pp. 417–435). Elsevier. <https://doi.org/10.1016/B978-0-12-821941-6.00020-7>
- Villanueva, J., Grimalt, J. O., Cortijo, E., Vidal, L., & Labeyrie, L. (1997). A biomarker approach to the organic matter deposited in the North Atlantic during the last climatic cycle. *Geochimica et Cosmochimica Acta*, 61(21), 4633–4646. [https://doi.org/10.1016/S0016-7037\(97\)83123-7](https://doi.org/10.1016/S0016-7037(97)83123-7)
- Walczak, I. W., Baldini, J. U. L., Baldini, L. M., McDermott, F., Marsden, S., Standish, C. D., et al. (2015). Reconstructing high-resolution climate using CT scanning of unsectioned stalagmites: A case study identifying the mid-Holocene onset of the Mediterranean climate in southern Iberia. *Quaternary Science Reviews*, 127, 117–128. <https://doi.org/10.1016/j.quascirev.2015.06.013>
- Wanner, H., Beer, J., Büttikofer, J., Crowley, T. J., Cubasch, U., Flückiger, J., et al. (2008). Mid- to late Holocene climate change: An overview. *Quaternary Science Reviews*, 27(19), 1791–1828. <https://doi.org/10.1016/j.quascirev.2008.06.013>
- Wanner, H., Solomina, O., Grosjean, M., Ritz, S. P., & Jetel, M. (2011). Structure and origin of Holocene cold events. *Quaternary Science Reviews*, 30(21), 3109–3123. <https://doi.org/10.1016/j.quascirev.2011.07.010>
- Weltje, G. J., Bloemsa, M. R., Tjallingii, R., Heslop, D., Röhl, U., & Croudace, I. W. (2015). Prediction of geochemical composition from XRF core scanner data: A new multivariate approach including automatic selection of calibration samples and quantification of uncertainties. In I. W. Croudace & R. G. Rothwell (Eds.), *Micro-XRF studies of sediment cores: Applications of a non-destructive tool for the environmental sciences* (pp. 507–534). Springer. https://doi.org/10.1007/978-94-017-9849-5_21
- Weltje, G. J., & Tjallingii, R. (2008). Calibration of XRF core scanners for quantitative geochemical logging of sediment cores: Theory and application. *Earth and Planetary Science Letters*, 274(3), 423–438. <https://doi.org/10.1016/j.epsl.2008.07.054>
- Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., et al. (2016). ggplot2: Create elegant data visualisations using the grammar of graphics (Version 3.5.0) [Computer Software]. Retrieved from <https://cran.r-project.org/web/packages/ggplot2/index.html>
- Yu, G., & Harrison, S. P. (1995). Holocene changes in atmospheric circulation patterns as shown by lake status changes in northern Europe. *Boreas*, 24(3), 260–268. <https://doi.org/10.1111/j.1502-3885.1995.tb00778.x>

References From the Supporting Information

- Appleby, P. G. (2001). Chronostratigraphic techniques in recent sediments. In W. M. Last & J. P. Smol (Eds.), *Tracking environmental change using lake sediments: Basin analysis, coring, and chronological techniques* (pp. 171–203). Springer. https://doi.org/10.1007/0-306-47669-X_9
- Bennett, K. D., & Willis, K. J. (2001). Pollen. In J. P. Smol, H. J. B. Birks, W. M. Last, R. S. Bradley, & K. Alverson (Eds.), *Tracking environmental change using lake sediments: Terrestrial, algal, and siliceous indicators* (pp. 5–32). Springer. https://doi.org/10.1007/0-306-47668-1_2
- Bertrand, S., Tjallingii, R., Kylander, M. E., Wilhelm, B., Roberts, S. J., Arnaud, F., et al. (2024). Inorganic geochemistry of lake sediments: A review of analytical techniques and guidelines for data interpretation. *Earth-Science Reviews*, 249, 104639. <https://doi.org/10.1016/j.earscirev.2023.104639>
- Binford, M. W. (1990). Calculation and uncertainty analysis of 210Pb dates for PIRLA project lake sediment cores. *Journal of Paleolimnology*, 3(3), 253–267. <https://doi.org/10.1007/BF00219461>
- Blaauw, M., & Christen, J. A. (2011). Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis*, 6(3), 457–474. <https://doi.org/10.1214/11-BA618>
- Blaauw, M., Christen, J. A., Bennett, K. D., & Reimer, P. J. (2018). Double the dates and go for Bayes—Impacts of model choice, dating density and quality on chronologies. *Quaternary Science Reviews*, 188, 58–66. <https://doi.org/10.1016/j.quascirev.2018.03.032>
- Bush, R. T., & McInerney, F. A. (2013). Leaf wax *n*-alkane distributions in and across modern plants: Implications for paleoecology and chemotaxonomy. *Geochimica et Cosmochimica Acta*, 117, 161–179. <https://doi.org/10.1016/j.gca.2013.04.016>
- Carreira, P. M., Nunes, D., Valério, P., & Araújo, M. F. (2009). A 15-year record of seasonal variation in the isotopic composition of precipitation water over continental Portugal. *Journal of Radioanalytical and Nuclear Chemistry*, 281(1), 153–156. <https://doi.org/10.1007/s10967-009-0064-0>
- Davies, S., Lamb, H., & Roberts, S. (2015). Micro-XRF core scanning in palaeolimnology: Recent developments. *Developments in Paleo-environmental Research*, 17, 189–226. https://doi.org/10.1007/978-94-017-9849-5_7
- Kahmen, A., Schefuß, E., & Sachse, D. (2013). Leaf water deuterium enrichment shapes leaf wax *n*-alkane δD values of angiosperm plants I: Experimental evidence and mechanistic insights. *Geochimica et Cosmochimica Acta, Hydrogen Isotopes*, 111, 39–49. <https://doi.org/10.1016/j.gca.2012.09.003>
- Konecky, B. L., McKay, N. P., Churakova, O. V., Comas-Bru, L., Dassié, E. P., DeLong, K. L., et al. (2020). The Iso2k database: A global compilation of paleo- $\delta^{18}O$ and δ^2H records to aid understanding of Common Era climate. *Earth System Science Data*, 12(3), 2261–2288. <https://doi.org/10.5194/essd-12-2261-2020>

- Meyers, P. A. (2003). Applications of organic geochemistry to paleolimnological reconstructions: A summary of examples from the Laurentian Great Lakes. *Organic Geochemistry*, 34(2), 261–289. [https://doi.org/10.1016/S0146-6380\(02\)00168-7](https://doi.org/10.1016/S0146-6380(02)00168-7)
- Mudelsee, M. (2014). Correlation. In M. Mudelsee (Ed.), *Climate time series analysis: Classical statistical and bootstrap methods* (pp. 271–319). Springer International Publishing. https://doi.org/10.1007/978-3-319-04450-7_7
- Carla Vaz de Oliveira, A., & da Silva Lima, A. (2010). Spatial variability in the stable isotopes of modern precipitation in the northwest of Iberia. *Isotopes in Environmental and Health Studies*, 46(1), 13–26. <https://doi.org/10.1080/10256010903388154>
- Reimer, P. J., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Ramsey, C. B., et al. (2020). The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*, 62(4), 725–757. <https://doi.org/10.1017/RDC.2020.41>
- Rozanski, K., Araguás-Araguás, L., & Gonfiantini, R. (1993). Isotopic patterns in modern global precipitation. In *Climate change in continental isotopic records* (pp. 1–36). American Geophysical Union (AGU). <https://doi.org/10.1029/GM078p0001>
- Schwark, L., Zink, K., & Lechterbeck, J. (2002). Reconstruction of postglacial to early Holocene vegetation history in terrestrial Central Europe via cuticular lipid biomarkers and pollen records from lake sediments. *Geology*, 30(5), 463–466. [https://doi.org/10.1130/0091-7613\(2002\)030<0463:ROPTEH>2.0.CO;2](https://doi.org/10.1130/0091-7613(2002)030<0463:ROPTEH>2.0.CO;2)
- Wang, Y., & Sessions, A. L. (2008). Memory effects in compound-specific D/H analysis by gas chromatography/pyrolysis/isotope-ratio mass spectrometry. *Analytical Chemistry*, 80(23), 9162–9170. <https://doi.org/10.1021/ac801170v>