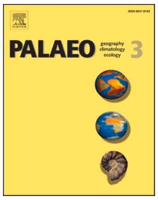
Palaeogeography, Palaeoclimatology, Palaeoecology 686 (2026) 113556

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo



Late Holocene vegetation dynamics, fire regimes, and human impact in Southern Brazil: A multi-proxy palaeoecological record from the Matematico Lake

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ARTICLE INFO

Editor: Yama Dixit

Keywords:
Palynology
Araucaria Forest
Grasslands
Charcoal
δ^2H isotopes
Southern Brazil
Human impact

ABSTRACT

The long-term interactions between forest and grassland in Southern Brazil remain poorly understood, despite the region's ecological importance and the ongoing debate about natural versus anthropogenic drivers of landscape dynamics. In this study we present a multi-proxy palaeoecological study of the Matematico sediment core from the Southern Brazilian highlands, with the aim of disentangling the roles of climate and human activity in shaping late Holocene Araucaria Forest and Campos (grassland) dynamics. We combined pollen, non-pollen palynomorphs (NPPs), charcoal, and compound-specific hydrogen isotopes (δ^2H) from leaf-wax *n*-alkanes, making this the first study in Southern Brazil to integrate these proxies within a single core. Between ∼3.500 and 2.100 cal yr BP (calibrated years before present), the landscape was dominated by Campos under relatively dry conditions, with low fire activity and limited forest cover. Subsequent Araucaria Forest expansion happened in two phases, which were identified at ∼1700 and ∼ 500 cal yr BP. Both phases correspond with shifts to more negative δ^2H values, indicating a forest expansion due to wetter climatic conditions. However, the earlier wet phase, corresponding to the wettest interval of the last 8000 years in Southern Brazil, did not trigger lasting forest establishment, suggesting that climate alone was insufficient to drive large-scale forest expansion. Meanwhile, the later expansion at ∼500 cal yr BP a coincides with increased charcoal influx and archaeological evidence of intensived occurrence of Southern Jê groups of the Taquara/Itararé Tradition, suggesting potential human influence in this latter expansion. This integrated multi-proxy approach provides new insights into the ecological and cultural legacies of the today's threatened Araucaria Forest–Campos mosaic.

1. Introduction

Anthropogenically-induced changes and destruction of tropical and subtropical ecosystems is a major global concern. This includes the increasing loss of forests due to human activities, which is known to be directly linked to a strong decline in biodiversity (Sala et al., 2000). While the decline in tropical and subtropical forests has attracted considerable scientific attention, subtropical grasslands, despite covering approximately 40% of the Earth's terrestrial surface and providing critical ecosystem services, remain underrepresented in global conservation discourse (Bardgett et al., 2021; Behling et al., 2024; Habel et al., 2013; Zhao et al., 2020). One important example of such an underrepresented region is the Brazilian Atlantic Forest Biome (Mata Atlântica), a global biodiversity hotspot that has suffered substantial

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https://doi.org/10.1016/j.palaeo.2026.113556
Received 7 October 2025; Received in revised form 6 January 2026; Accepted 7 January 2026

habitat loss due to agriculture, forestry, and urban expansion. Estimates range from approximately 72% to 89% habitat loss, depending on the source and methodology (Rezende et al., 2018; Ribeiro et al., 2009). The Mata Atlântica is uniquely characterized by both endangered subtropical forests as well as species-rich grassland ecosystems (Behling et al., 2024; Myers et al., 2000), with the temporal and spatial relationships between them being intensely debated.

Within this diverse biome, the Araucaria Forest (Portuguese: *Floresta Ombrófila Mista*) stands out due to its distinctive biodiversity, ecological significance, and high susceptibility to human impacts and climate change. These forests are located at higher elevations (500–1800 m a.s.l. (above sea level)) and are predominantly distributed in Paraná, Santa Catarina, and Rio Grande do Sul states where they create a distinctive mosaic landscape with diverse grassland vegetation, commonly referred to as Campos (Fig. 1) (Breshears, 2006; Overbeck et al., 2007). To investigate the development of Araucaria Forest-Campos vegetation several paleoenvironmental palynological studies have been conducted across Southern Brazil including sites in the States of Rio Grande do Sul (RS) (Aparados da Serra: Roth and Lorscheitter, 1993; São Francisco de Paula: Behling et al., 2001; Cambará do Sul: Behling et al., 2004; São José dos Ausentes: Jeske-Pieruschka et al., 2010; Rincão das Cabritas: Jeske-Pieruschka and Behling, 2011), Santa Catarina (SC) (Serra do Rio do Rastro, Morro da Igreja, Serra da Boa Vista: Behling, 1995; Ciama 2: Jeske-Pieruschka et al., 2010), and Paraná (PR) (Serra dos Campos Gerais: Behling, 1997; Lagoa Dourada: Piraquive-Bermúdez et al., 2024). They indicate that during the last Glacial period and early to mid-Holocene, Campos grasslands were dominant, primarily attributed to the cold and relatively dry glacial and warm and dry early to mid-Holocene climate. The formation and expansion of Araucaria Forests most likely began as gallery forests around 3210 cal yr BP (calibrated years before present), gradually spreading across the landscape, with accelerated growth around 1400 cal yr BP in Paraná and approximately 930 cal yr BP in Santa Catarina. However, the precise drivers behind this forest expansion remain unclear.

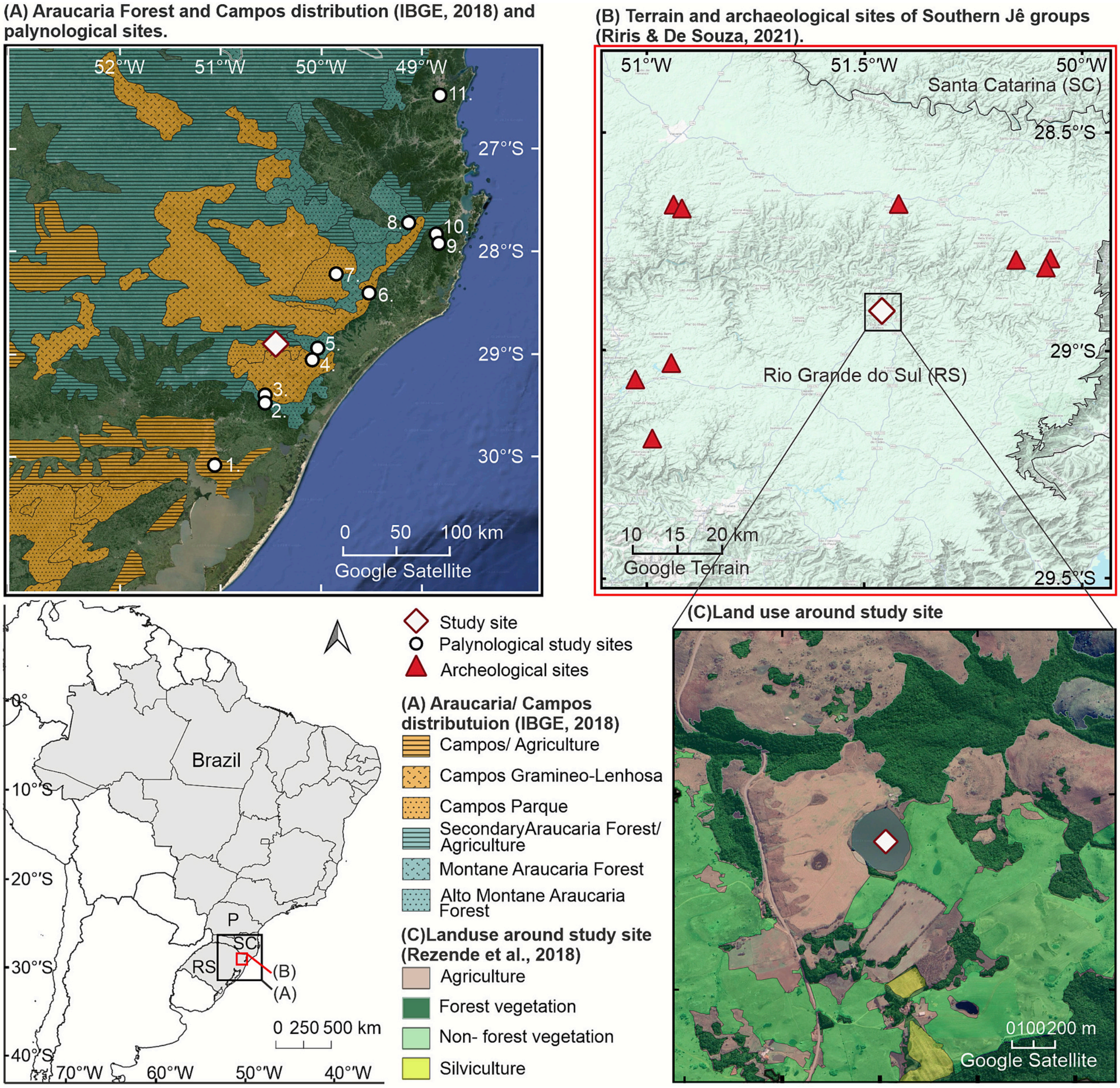

Fig. 1. Map of Southern Brazil: (A) Distribution map of Campos and Araucaria Forest (IBGE, 2018) and palynological study site: 1. Behling et al., 2007; 2. Jeske-Pieruschka and Behling, 2011, 3. Behling et al., 2001; 4. Behling et al., 2004; 5. Jeske-Pieruschka et al., 2010; 6. Behling et al., 1998; 7.-8. Behling, 1995; 9. Jeske-Pieruschka et al., 2013; 10. Behling and Oliveira, 2018; 11. Behling, 1997. (B) Terrain and distribution of archaeological study sites of Southern Jê groups (Riris and De Souza, 2021). (C) Satellite image of land use around the study site (Rezende et al., 2018).

The ecological dynamics of these mosaic landscapes appear to have been shaped by complex interactions involving climatic variability, fire regimes, and possibly indigenous land-use practices. The archaeological context of Southern Brazil further enriches the study of this region, particularly through the historical presence of Southern Jê groups, who are archaeologically represented by the Taquara-Itararé Tradition (Fig. 1) (Brochado and Schmitz, 1972; Schmitz et al., 2002). These groups are characterized by semi-nomadic subsistence strategies involving foraging and cultivation practices, including the management of fire for slash-and-burn agriculture, as well as hunting (Corteletti et al., 2015). In addition, these communities intensively exploited and managed the *Araucaria angustifolia*, the pine nut (pinhão) for their nutrient-rich seeds, potentially influencing the spread and maintenance of the tree (Iriarte and Behling, 2007; Robinson et al., 2018). However, while archaeological evidence points to a presence of Southern Jê settlements during the late Holocene in a 50 km radius around the site, the extent and nature of their impact on regional vegetation dynamics remain uncertain. Thus, disentangling the role of climatic from anthropogenic influences in the transitions between Campos and Araucaria Forests is a central objective of this study.

To investigate the development of Araucaria Forest-Campos vegetation and the role of anthropogenic impacts more closely, we conducted a palaeoecological multiproxy analysis of the lacustrine core Matematico, which includes pollen, non-pollen palynomorphs (NPP), charcoal, and compound-specific hydrogen isotopes (δ^2H) from leaf-wax *n*-alkanes. To our knowledge, this is the first palaeoecological investigation in Southern Brazil combining pollen analysis and δ^2H within the same sediment core. This multi-proxy approach enables an integrated reconstruction of vegetation dynamics and hydrological change, providing unprecedented insight into the drivers of forest–grassland transitions in the region. In conducting a comprehensive comparison of different proxies, our objectives are to (1) investigate the dynamics of Araucaria Forest and Campos mosaic, (2) determine possible climatic factors driving vegetation changes, and (3) understand the link between possible past human impact and vegetation changes. Our findings aim to disentangle the relationship between past human impact and natural factors on current climate change and biodiversity loss in the Brazilian Atlantic Forest, which is crucial for improving conservation strategies and climate change predictions. Furthermore, we hope to contribute to a more comprehensive understanding of the ecological and cultural legacies influencing one of the world's most threatened biodiversity hotspots.

2. Study area

2.1. Geographical setting

The study site, Matematico, is situated in the Southern Brazilian highlands, specifically in the northeastern part of Rio Grande do Sul (28°53′32"S; 50°27′18"W, 837 m above sea level). The lacustrine sediment core was collected approximately 11 km west of the village of Jaquirana. The studied lake has a diameter ca. 350 m.

2.2. Climate

The Southern Brazilian highlands exhibit a humid subtropical climate, classified as Cfb according to the Köppen classification system (Alvares et al., 2013). The highland is dominated by subtropical climate, frosts can occur during the austral winter, particularly at higher elevations (Wrege et al., 2012). The South Atlantic Anticyclone, a semi-permanent high-pressure system, in combination with polar cold fronts, generates substantial rainfall throughout the year, resulting in an absence of a dry season (Hasenack et al., 2024; Hastenrath, 1991; Nimer, 1989). Years with exceptionally high precipitation are often associated with El Niño events, while colder years with reduced rainfall are linked to La Niña events (Fontana and Berlato, 1997; Martin et al., 1993.; McGlone et al., 1993.). The climate in the Jaquirana region is characterized as warm temperate, with an annual average minimum temperature of 7 °C and an annual average maximum temperature of 22 °C. The mean precipitation annual precipitation is 1830 mm and can vary between 100 and 400 mm per month (INMET, 2025).

2.3. Vegetation

The vegetation in close proximity of our study site was originally dominated by Araucaria Forest (Floresta Ombrófila Mista) and Campos (Fig. 1) (IBGE, 2018). The highly diverse Campos is generally characterized by non-arboreal species from the Poaceae, Cyperaceae, Asteraceae, Apiaceae, Rubiaceae, Fabaceae, and Eriocaulaceae families. Tall grasses such as *Andropogon* spp., *Aristida* spp., and *Schizachyrium* spp., dominate the landscape, intermixed with shrubs such as *Baccharis* spp., *Vernonia* spp. (Asteraceae), *Eryngium horridum* (Apiaceae), *Polygala* (Polygalaceae), *Xyris* (Xyridaceae), and *Plantago* (Plantaginaceae). Campos in this region can be classified into two categories: Campo Limpo (clean grassland) and Campo Sujo (dirty grassland). Campo Limpo, the most representative type of grassland in Southern Brazil, has been subjected to extensive management over many decades, and is dominated by species such as *Stipa*, *Andropogon*, *Aristida*, and *Erianthus*. Campo Sujo is mostly observed near Araucaria Forest plateaus. Within its arboreal upper stratum, consisting of sparse individuals, the most representative species belong to Lythraceae and Anacardiaceae, namely *Schinus* and *Lithraea*. The lower stratum is dominated by grasses such as *Paspalum*, *Axonopus*, *Andropogon*, and *Stipa* or Asteraceae such as *Baccaris* (IBGE, 2012).

The Araucaria Forest near our study site is classified as Montane Araucaria Forest (*Floresta Ombrófila Mista Montana*). The most representative species is *Araucaria angustifolia*, accompanied by *Ocotea*, *Ilex paraguariensis*, *Mimosa scabrella*, *Podocarpus lambertii*, *Nectandra*, *Cryptocarya, Dicksonia sellowiana* and members of the Myrtaceae family (*Myrceugenia* spp., *Eugenia* spp., *Myrciaria* spp.) (Hueck, 1953; IBGE, 2012; Negrelle and Da Silva, 1992). Nowadays, the Araucaria Forest-Campos formation has only been preserved in a few locations and much of the original vegetation has been replaced by large soybean and wheat plantation, or *Pinus* and *Eucalyptus* forestry. In the vicinity of our studied lake, large areas have recently been subjected to agricultural grazing activity. However, disturbed forest and non-forest vegetation, as well as forest managed through active forestry, can be found in close proximity to the lake (Rezende et al., 2018; IBGE, 2018) (Fig. 1). The Tropical Atlantic Rainforest (Floresta Ombrófila Densa) in Southern Brazil forms a 50–100 km wide belt along the coastal lowlands near the border of SC and RS states, extending up to elevations of 1000 m on the slopes of the Serra Campos Gerais mountains. This rainforest has an approximate distance of 70 km to our study site. Its plant composition is highly diverse, consisting of trees, shrubs, climbers, tree ferns, and epiphytes. The dominant trees belong to the Euphorbiaceae (*Alchornea*), Arecaceae (*Euterpe*), Myrtaceae, Moraceae, Bignoniaceae, Lauraceae, and Sapotaceae families (Hueck, 1966; IBGE, 2012).

2.4. Human settlements

Within a radius of 50 km around our study site 14 archaeological sites have been found (Fig. 1). Of those, 11 can be associated with Southern Jê groups, also known as the Taquara-Itararé, based on the characteristics and area of occurrence of this ceramic tradition. The remaining three sites have an unknown cultural affiliation (Brochado and Schmitz, 1972; Copé, 2006; Schmitz, 1969; Schmitz et al., 2002). Southern Jê groups practiced a form of semi-nomadic foraging, utilizing the diverse plant species for food, shelter, and medicinal purposes (Corteletti et al., 2015). It is posited that they might have employed fire as a tool for slash-and-burn horticulture and potentially for hunting practices (Behling et al., 2004; Iriarte and Behling, 2007; Schmitz and Becker, 1991). In 1900 the village Jaquirana, which is located approximately 11 km west of our study site, was founded.

3. Material and methods

3.1. Sampling

The 133 cm long sediment core was retrieved in 2009, approximately 20 m from the shore of the lake. Using a Russian corer, the core was retrieved in three sections of 50 cm length, extruded on-site, and wrapped in plastic foil. All sediment cores were stored under refrigeration (+4 °C) at the Albrecht-von-Haller Institute (University of Göttingen) and were subsequently sampled for laboratory processing. Due to water rich soft insufficient sediment material, the first 3 cm of the core could not be sampled and were therefore excluded from all analysis.

3.2. Radiocarbon dating

For the purpose of age-depth modelling, three bulk samples were submitted for AMS radiocarbon dating. Samples were submitted to the Poznan Radiocarbon Laboratory in Poland. The age-depth model was constructed using the R package 'BACON' (Blaauw and Christen, 2011), and calibrated with the SHCal20 curve (Hogg et al., 2020).

3.3. Pollen, NPP and charcoal analyses

Pollen, non-pollen palynomorphs (NPPs) such as spores, algae, and dung fungi, and microcharcoal analyses were undertaken on a total of 33 samples (0.25 cm^3) from the sediment core. Due to the low pollen concentration at the bottom of the core, sampling was conducted primarily between 4 and 80 cm, mostly at 2 cm intervals. For laboratory work the classical chemical pollen treatment method (Faegri and Iversen, 1989) was conducted at the Department of Palynology and Climate Dynamics (Georg-Augustu-University). To determine the pollen concentration, a tablet of the exotic marker *Lycopodium* (9666 +/− 200 spores, batch number: 1031) was added to each sample. Samples were initially treated with cold diluted hydrochloric acid (10% HCl) to remove calcium carbonates and were sieved at 120 μm to exclude large particles. Subsequently, the samples were subjected to cold diluted hydrofluoric acid (40% HF) for 24 h to dissolve siliceous material. Organic materials were broken down through acetolysis, using concentrated sulphuric acid and acetic anhydride. The samples were sieved again to remove small particles (< 5 μm).

Pollen, NPPs, algae, micro-charcoal, and *Lycopodium* spore markers were counted up to a total of 300 terrestrial pollen grains using a light microscope (Axiostar plus) at ×400 magnification. Pollen and spores were identified with Behling's personal reference collection, which includes approximately 2000 Brazilian pollen species and morphological descriptions (Behling, 1993). Dung fungi were identified with help of the NPP-ID - Non-Pollen Palynomorphs Image Database (Shumilovskikh et al., 2022). All identified taxa were further classified into ecological groups: Campos, Araucaria Forest, Atlantic Rainforest (ARF), Human Indicators (HI), Others, Aquatics, Ferns and Mosses, and Dung Fungi. For macro-charcoal analysis, a total of 76 samples (0.5 cm^3) were extracted from the sediment core. Sampling was conducted between 4 and 80 cm at 1 cm intervals and all samples were processed in the laboratory according to standard protocols (Stevenson and Haberle, 2018) at the Department of Palynology and Climate Dynamics (Georg-August-University). Each sample was treated with a 10% KOH solution for 24 h and was subsequently bleached with a chlorine cleaning agent for 24 additional hours. On the third day, all samples were sieved with distilled water at 120 μm to remove small particles. For the analysis, all samples were counted using a digital microscope at x5 magnification (Zeiss). In addition, grass-based charcoal was identified by morphological description (Enache and Cumming, 2006).

3.4. Leaf-wax n-alkanes

For leaf-wax n-alkane analysis a total of 11 samples were extracted from the sediment core. For total lipid extraction (TLE) and separation, the method described by Patalano et al. (2020) and Jha et al. (2020) was followed. Freeze dried (at −30 °C for 48 h) and homogenised samples were extracted by the Büchi Speed Extractor E-916 with using 9:1 (*v*/v) dichloromethane/methanol ratio at 100 °C and 103 bar (1500 psi) in three 10-min cycles. A Büchi SyncorePlus evaporator was used to concentrate the solvent containing the total lipid extract (TLE) to around 1 ml. Afterwards *n*-alkanes were separated from the TLEs, using a silica-gel chromatography eluted with hexane. Separated TLEs were analysed using a gas chromatography (GC) system (Agilent 7890B) equipped with an Agilent HP-5MS capillary column (30 m in length, 0.25 μm in film thickness, and 0.25 mm in column diameter) and coupled to an Agilent 5977 A Series Mass Selective Detector (interface temperature of 280 °C) at the Max Planck Institute of Geoanthropology. All samples were injected in splitless mode at 250 °C, and the GC oven was programmed from 60 °C (1 min hold) to 180 °C at 6 °C/min, then to 310 °C at 10 °C/min (12 min hold). Helium was used as the carrier gas, with a constant flow of 1.3 ml/min. The MS source was operated at 230 °C with 70 eV in the electron ionisation (EI) mode and a full scan rate of m/z 50–550 (Jha et al., 2024, 2020). Supelco C_8-C_{40} *n*-alkane standards and blanks were injected prior to, between, and posterior to the measurement of the 11 samples to detect the instrument stability, drift in retention times and/or to detect possible contamination. Specific *n*-alkane compounds were identified based on the retention times obtained from the *n*-alkane standards. *n*-alkane concentrations were calculated from peak areas in relation to those of the standards, which were prepared in six different dilutions (5, 10,20, 30, 40 and 50 ng/μl).

Furthermore, Compound Specific Isotope Analysis (CSIA) was conducted for the n-alkane fraction. CSIA of hydrogen from plant wax n-alkanes (C27-C33; δ2Hwax) were measured using a Thermo Scientific TRACE 1310 Gas Chromatograph fitted with a Thermo Scientific TraceGOLD TG-5MS capillary column (30 m length, 0. 25 μm in film thickness, 0.25 mm in column diameter) coupled via GC IsoLink II and ConFlo IV, with a reduction interface at 1420 °C in a pyrolysis furnace, to a Thermo Scientific MAT 253 Plus Isotope Ratio Mass Spectrometer at the Max Planck Institute of Geoanthropology. 1.0 μl of the sample was injected using an autosampler in splitless mode, and the GC oven was programmed from 40 °C (1-min hold) to 130 °C at a rate of 15 °C/min, then to 320 °C at a rate of 5 °C/min (10-min hold). Helium was supplied as the carrier gas at a constant flow rate of 1.2 ml/min. For evaluation, only peaks over 150 mV were evaluated. Results were calibrated against the international standard Indiana A7 (C_{16}-C_{30}), which was analysed after every six injections. The standard deviation of the C_{25}-C_{30} *n*-alkanes across all standard measurements was ≤7.8‰. All samples were measured in triplicate and mean, and standard deviations are reported here. Drift corrections were applied based on the Indiana A7 standards bracketing the samples within the Qtegra ISDS software (Thermo Fisher Scientific) and δ^2H_{wax} values are reported in per mil (‰) against Vienna Standard Mean Ocean Water (VSMOW). The H^{3+} factor was measured daily, with an average value of 7.505 ± 0.280 being recorded over the analysis period ($n = 12$).

3.5. Statistical analysis

For statistical analyses and figures, R Studio software (Version 1.4.1103) (R Core Team, 2025) with packages 'Rioja' (Juggins, 2024), 'PaleoMAS' (Correa-Metrio et al., 2011), and 'Vegan' (Oksanen et al., 2007) and graphic software CorelDraw (Version 24.2.1.446, 2022), were employed. Pollen, NPP, and algae percentages were calculated based on the total terrestrial pollen sum. The pollen record was subdivided into significant zones using constrained cluster analysis by Sum of Squares (CONISS) (Grimm, 1987) only including terrestrial pollen taxa. Furthermore, concentration and influx of pollen grains and microand macro-charcoal were calculated. Palynological richness was calculated as the number of distinct pollen taxa per sample and is used as an indicator of past vegetation diversity. To enable comparison among samples, richness values were standardized using rarefaction, implemented with 'Vegan' (Oksanen et al., 2007). Maps were created using QGIS 3.28 (QGIS Development Team, 2023) with Google Satellite and Google Terrain basemaps.

4. Results

4.1. Chronology and stratigraphy

A total of three radiocarbon dates were obtained from bulk sediment samples (Table 1, Fig. 2). As the age–depth model is only constrained by three radiocarbon dates it carries uncertainties that must be considered when interpreting rate-based indices such as influx. Chronological uncertainty is expected to be lowest in the dated interval in between 30 and 58 cm (205 ± 30 and 2505 ± 30 C^{14} yr BP), where the model is directly constrained. In contrast, uncertainty is higher in the uppermost section (0–30 cm), where no direct radiocarbon date is available and age estimates rely on extrapolation between the year of core retrieval and the first dated level at 30 cm. The basal part of the core, below the deepest dated level, should also be interpreted cautiously, as no radiocarbon date is available at the core base and ages are therefore only indirectly constrained through model extrapolation. These uncertainties do not prevent interpretation of major vegetation shifts, but they reduce confidence in precise estimates of rates and the exact timing of short-lived events. Between 30 and 80 cm, the age–depth model suggests comparatively higher accumulation rate, with 1 cm of sediment corresponding to approximately 90 years. The uppermost section (0–30 cm) is characterized by a lower accumulation, with 1 cm of sediment deposition corresponding to approximately 10 years. Because the upper and basal section lack direct radiocarbon dates, these values should be regarded as model-based estimates rather than exact rates. The first occurrences of introduced *Pinus* pollen grains were found at 8 cm (51 cal yr BP, i.e. AD 1905). German settlers, who potentially introduced *Pinus* to Southern Brazil, established their first known settlements on the lower slopes of the Serra Geral in Rio Grande do Sul around AD 1825 (Behling et al., 2004). Additionally, evidence of *Araucaria angustifolia* logging is documented in the pollen record, indicating that the top of the core represents the modern surface.

In addition to the chronology, a detailed stratigraphic description was conducted (Fig. 2). From 0 to 3 cm the limnic sediment was very soft material with a high-water content. From 4 to 13 cm the material consists out of soft, dark and less decomposed organic matter (detritus mud) with few plant remains. From 13 to 44 cm the organic material is more decomposed and more compact with a black colour. Very few plant remains can be found. From 44 to 57 cm the black soil material is fully decomposed, very compact with no plant remains present. From 57 to 70 cm the soil shows a slow transition from dark brown organic material to gray brown less organic mud material.

4.2. Pollen/ NPP/ charcoal data

In total, 77 terrestrial pollen taxa, five aquatic pollen taxa, one alga, and 36 NPPs were identified in 33 samples throughout the sediment core. Based on the constrained cluster analysis, the pollen record was subdivided into five pollen zones (MA-1a-c and MA-2a-b). Fig. 3 illustrates all distinct pollen taxa, including 44 terrestrial pollen taxa, 4 aquatic pollen taxa, 1 alga, and 19 NPPs. Fig. 4 summarizes the sum of pollen taxa according to their ecological groups, pollen concentration and influx, macro-charcoal (>120 μm) and micro-charcoal (<120 μm) influx, palynological richness, and a cluster analysis dendrogram. Given that the chronology is only constrained by three radiocarbon dates, the record provides robust insights into the direction and sequence of late-Holocene ecological change, but the exact ages of transitions should be interpreted as approximate, particularly in the undated uppermost section (0–30 cm) and lowest section (58–80 cm). In particularly, influx (e.g., particles cm^{-2} yr^{-1}) is estimated with the sedimentation rate and is therefore sensitive to age–depth model uncertainty and changes in accumulation rate. To improve transparency, we additionally present concentration data (e.g., particles cm^{-3}) alongside influx.

Table 1
Radiocarbon dating results.

Laboratory ID	Depth (cm)	Age (C^{14} yr BP)	Age (cal yr BP)
Poz-174,454	30	205 ± 30	298
Poz-175,112	46	1560 ± 30	1393
Poz-162,448	58	2505 ± 30	2497

4.2.1. MA-Ia (80–56 cm, 3680–2340 cal yr BP, 7 subsamples)

Within the lowermost zone, the pollen concentration increases from 65,000 to 400,000 grains per cm^3. The pollen influx remains consistently low at ca. 2500 grains per cm^{-2} yr^{-1}. A notable degree of pollen grain destruction was observed in the three lowest samples, particularly in the lowest one. This may introduce a bias into pollen observation, favouring taxa with more robust pollen walls, such as taxa belonging to the Asteraceae family. This first zone is characterized by a high occurrence of Campos pollen taxa (93–98%), primarily Poaceae (50–70%), Asteraceae (15–20%), Cyperaceae (5–15%), *Senecio* (1–6%), *Baccharis* (1–3%), *Eryngium* type (1–4%), and Apiaceae (1–2%). Other Campos taxa, due to their overall low occurrence are not shown in the diagram, include Lamiaceae, *Begonia*, and *Gunnera*. The overall occurrence of Araucaria Forest pollen taxa is low (1–4%), represented by *Araucaria angustifolia* (1–3%), *Myrsine* (0–1%), and single pollen grains of Myrtaceae, *Schinus, Weinmannia, Podocarpus, Ilex, Sebastiania commersoniana, Sebastiania brasiliensis*, and *Allophylus* (not shown in the diagram).

Atlantic Rain Forest (ARF) taxa have a low abundance (1–2%) and include Urticaceae-Moraceae (1–2%), *Piper* (0–1%), *Alchornea* (0–1%), two pollen grains of *Celtis*, and one pollen grain of *Trema*. Other taxa (1–4%) include Rubiaceae (0–1%), and taxa with under 1% not shown in the diagram, such as Araceae, *Oreopanax fulvum, Prockia, Alnus*, and Sapotaceae. The total amount of indeterminate pollen taxa does not exceed 5%. There is an overall low occurrence of aquatic pollen taxa, represented by a single pollen grain of *Persicaria* type and Potamogeton (not shown in the diagram). Among the spores, *Phaeoceros laevis* (5–10%), *Sphagnum* (0–3%), *Dicksonia sellowiana* (0–2%), Monolete verrucate spore (0–2%), Osmunda (0–1%), *Blechnum imperiale* (0–1%), and *Lycopodium cernuum* (0–2%) were observed. No dung fungi were found. Both macro-charcoal and micro-charcoal influx remain low, with approximately 0.002–0.2 particles per cm^{-2} $yr^{-1}$and between 1000 and 8000 particles per cm^{-2} yr^{-1}. Palynological richness increases from 10 to 25 pollen taxa throughout the zone.

4.2.2. MA-Ib (54–46 cm, 2170–1390 cal yr BP, 5 subsamples)

In the second zone, pollen concentration varies between 500,000 and 200,000 grains per cm^3, while pollen influx ranges between 2000 and 6000 grains per cm^{-2} yr^{-1}. Campos pollen taxa remain continuously dominant (90–95%), represented by Poaceae (ca. 50%), Cyperaceae (10–20%), Asteraceae (10–20%), *Senecio* (2–7%), *Baccharis* (1–5%) and *Eryngium* type (3–5%). Observed Campos taxa not displayed in the diagram include Lamiaceae, *Polygala*, *Begonia*, and Ericaceae. Araucaria Forest pollen taxa show a slight increase (3–7%), predominantly including *Araucaria angustifoilia* (1–3%) and *Myrsine* (0–3%). Additionally, one pollen grain of *Lamanonia speciosa* was identified, but not shown in the diagram. Atlantic Rain Forest (ARF) pollen taxa remain low (1–3%) and mainly include Urticaceae-Moraceae (0–2%), and *Piper* (0–1%), as well as single grain findings of *Matayba* and *Acalypha*. No pollen taxa indicating human impact were found. Other taxa (0–1%) include Anacardiaceae (0–1%) and, not shown in the diagram, Araceae and Prockia The total amount of indeterminate pollen taxa decreases to

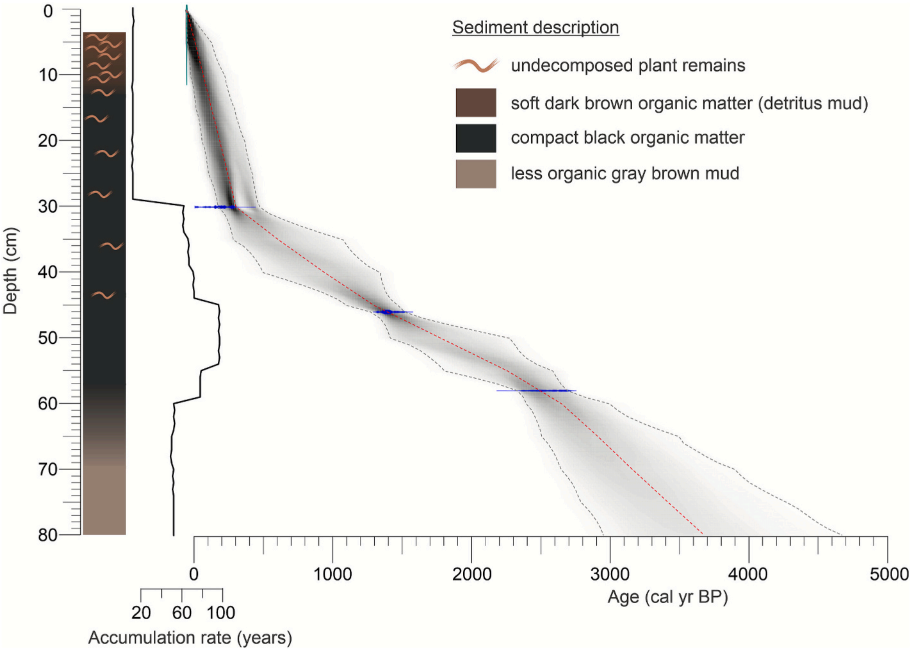

Fig. 2. Age-Depth-Model, accumulation rate and soil description of lacustrine sediment core Matematico (28°53′32"S; 50°27′18"W, 837 m above sea level) in Rio Grande do Sul, Southern Brazil (cal yr BP = calibrated years before present).

0–2%. Aquatic pollen taxa remain low, represented only by *Hydrocotyle* (0–1%) and one grain of *Potamogeton*. The algae *Botryococcus* was first observed in this zone (0–2%). Within the spore taxa, mainly *Phaeoceros laevis* (2–14%), *Sphagnum* (1–5%) and *Dicksonia sellowiana* (1–3%), were observed. Additionally, one dung fungi spore of *Delitschia* was found. Macro-charcoal influx remains low, between 0.09 and 0.6 particles per cm^{-2} yr^{-1} and micro-charcoal influx remains between 5000 and 7000 particles per cm^{-2} yr^{-1}. Palynological richness remains around approximately 25 taxa.

4.2.3. *MA-Ic (44–32 cm, 1230–420 cal yr BP, 7 subsamples)*

In the third zone, the overall pollen concentration varies between 10,000 and 20,000 grains per cm^3, while the pollen influx ranges from 1000 to 4000 grains per cm^{-2} yr^{-1}. The proportion of Campos (87–92%) pollen taxa remains dominant, although its composition changes towards the end of the zone. Specifically, the amount of Poaceae taxa decreases from ca. 50 to 40%, while Cyperaceae increases from ca. 10 to 20%. Other dominant Campos pollen taxa include Asteraceae (ca. 10%), *Senecio* (3–7%), *Baccharis* (1–4%), *Eryngium* type (3–7%), Apiaceae (1–2%). Additionally, single grains of *Plantago*, Lamiaceae, and *Gunnera* were found but are not included in the pollen diagram. Araucaria Forest pollen taxa further increase to 5–10%, mainly represented by *Araucaria angustifoilia* (3–6%), *Myrsine* (1–3%). Furthermore, small amounts of *Allophylus*, *Sapium*, and *Ocotea* were identified but are not shown in the diagram. Atlantic Rain Forest (ARF) pollen taxa remain low (1–4%) and include Urticaceae-Moraceae (1–2%), *Piper* (ca. 1%), and less than 1% of *Alchornea*, *Celtis*, *Trema*, and two grains of *Matayba*. No pollen taxa indicating human impact were found. Aquatic taxa include *Ludwigia* (0–2%) and *Persicaria* type (0–1%). Spores are mainly represented by *Sphagnum* (5–13%), *Phaeoceros laevis* (2–5%) and *Dicksonia sellowiana* (1–2%). Additionally, fungi spores of *Gelasinospora* (0–1%) were observed. The overall amount of dung fungi spores increases from 0 to 4%, represented by *Coniochaeta*, *Podospora* type, *Delitschia*, *Sordaria*, *Apiosordaria*, *Cercophora* type, and *Arnium* all ranging between 0 and 2%. The macro-charcoal influx slightly increases from 0.3 to 0.9 particles per cm^{-2} yr^{-1}, while the micro-charcoal influx fluctuates between 5000 and 30,000 particles per cm^{-2} yr^{-1}. Palynological richness varies between 25 and 35 taxa.

4.2.4. *MA-IIa (30–12 cm, 300–90 cal yr BP, 10 subsamples)*

In the fourth zone, the pollen concentration varies between 100,000 and 300,000 grains per cm^3, while the pollen influx has a peak up to 40,000 grains per cm^{-2} yr^{-1}. The overall abundance of Campos pollen taxa decreases from 87 to ca. 75% and is dominated by Poaceae (ca. 30–35%) and Cyperaceae (ca. 30–20%). Other abundant Campos taxa include *Asteraceae* (4–8%), *Senecio* (1–4%), *Baccharis* (1–5%) and *Eryngium* type (2–4%). Additionally, single grains of *Verbena*, *Plantago*, *Eupatorium*, and *Cuphea* were found. *Araucaria* Forest taxa increase from 10% to 15–20%, mainly including *Araucaria angustifoilia* (8–13%), *Myrsine* (1–4%), *Schinus* (0–2%), *Weinmannia* (0–2%). Not included in the diagram is the occurrence of ca. 1% *Sapium* and single grains of *Lamanonia speciosa*, *Buddleja*, *Ocotea*, *Drimys brasiliensis*, and *Phyllanthus*. The abundance of Atlantic Rain Forest (ARF) taxa slightly increases to 2–6%, including Urticaceae-Moraceae (0–1.5%), *Piper* (1–2%), *Alchornea* (0.5–2%), less than 1% of *Celtis* and *Trema* and single grains of *Matayba*, *Cecropia*, *Pera*, and *Pouteria*. No pollen taxa indicating human impact were found. Other pollen taxa (1–2%) include Rubiaceae, Melastomataceae, and Anacardiaceae with less than 1%, as well as single grains of *Oreopanax fulvum*, Rhamnaceae, *Chrysophyllum dusenii*, *Dodonaea* type, *Phrygilanthus*, and *Alnus*. The amount of undetermined pollen taxa varies between 0% and 1%. Aquatic taxa such as *Hydrocotyle* (1–3%), *Ludwigia* (0–2%), *Echinodorus* (0–1%), and *Botryococcus* (0–2%) slightly increase. Observed spores mainly include *Sphagnum* (4–10%), *Phaeoceros laevis* (1–2%), *Dicksonia sellowiana* (1–2%), Psilate trilete *spore (1–2%),* Monolete verrucate spore (1–2%), and two spore findings of *Gelasinospora*. The overall amount of dung fungi spores varies between 1 and 5%, represented by *Coniochaeta*, *Podospora* type, *Delitschia*, *Sordaria*, *Apiosordaria*, *Cercophora* type, and *Arnium* (all between 0 and 2%). The macro-charcoal influx fluctuates between approximately 1 and 7 particles per cm^{-2} yr^{-1}, while the micro-charcoal influx varies between 15,000 and 270,000 particles per cm^{-2} yr^{-1}. The palynological richness varies between 25 and 35 species.

4.2.5. *MA-IIb (10–4 cm, 60 – (−10) cal yr BP, 4 subsamples)*

In the uppermost zone, the pollen concentration is approximately 80,000 grains per cm^3, with a pollen influx of about 7000 grains per cm^2 per cm^{-2} yr^{-1}. The abundance of Campos pollen taxa (78–75%)

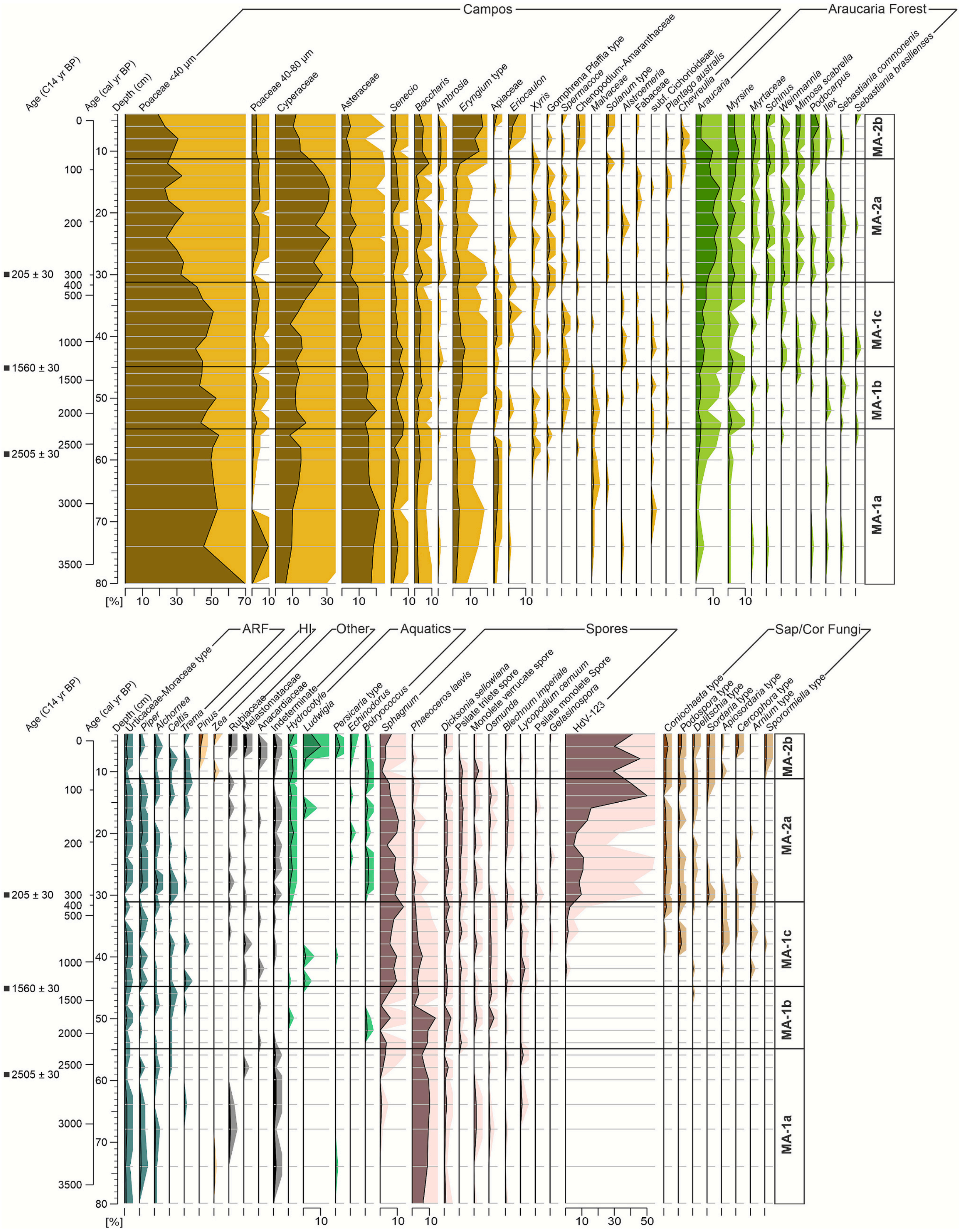

Fig. 3. Pollen percentage diagram for the Matematico core (Rio Grande do Sul, Southern Brazil) displayed against depth and age (cal yr BP = calibrated years before present, C14 yr BP = C14 years before present). The pollen diagram is divided into 5 significant pollen zones by cluster analysis. The light-coloured pollen curves correspond to exaggerated curves by a factor 5. ARF=Atlantic Rainforest, HI = Human Impact, Sap/Cor = Saprotrophs/Coprophilous.

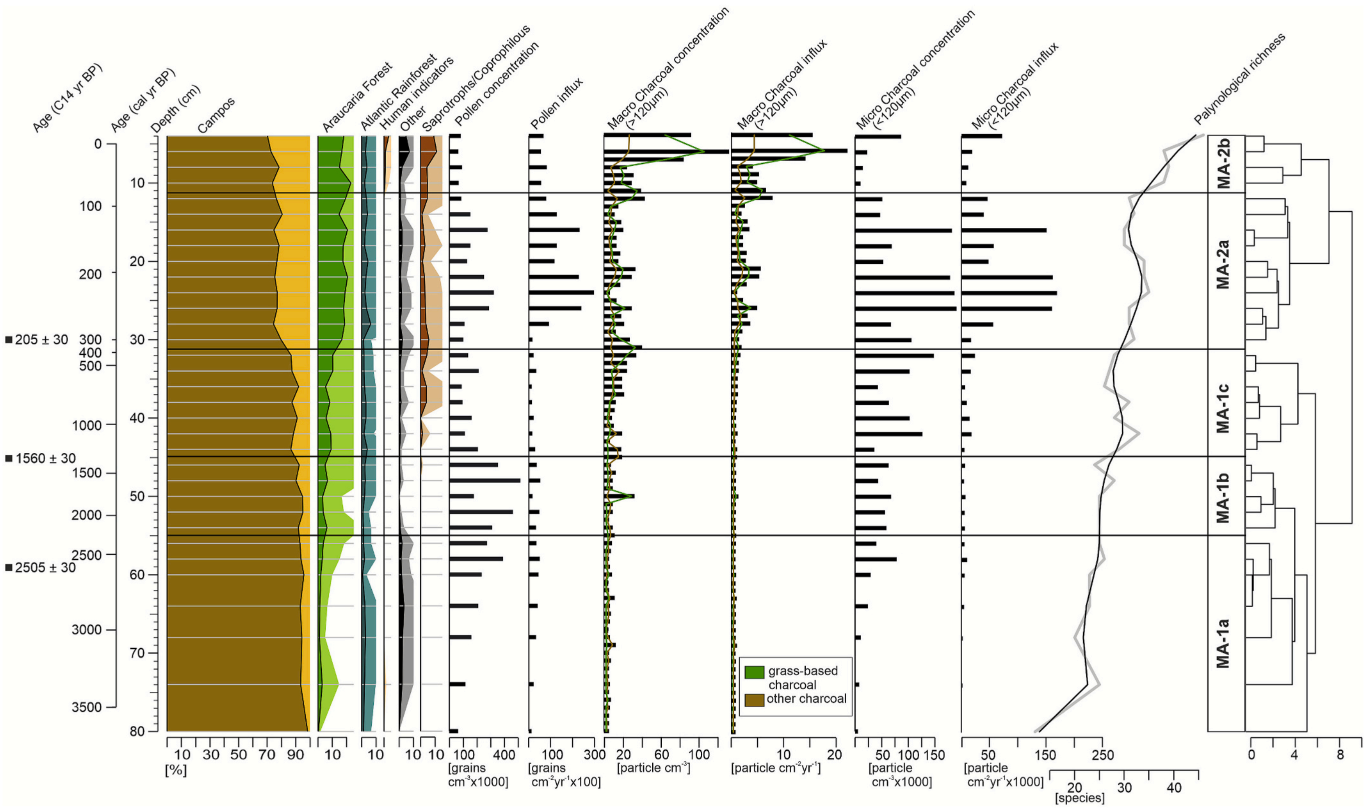

Fig. 4. Pollen percentage diagram for Matematico core (Rio Grande do Sul, Southern Brazil) displayed against depth and age (cal yr BP = calibrated years before present, C14 yr BP = C14 years before present). The pollen diagram shows the summary of pollen taxa according to their ecological groups, pollen concentration and influx, macro-charcoal (>120 μm) and micro-charcoal (<120 μm) influx and concentration, palynological richness (gray line: number of taxa per sample; black line: smoothed spline of taxon richness) and the cluster analysis dendrogram dividing the pollen diagram into 5 significant zones.

continues to decline. Specifically, the abundance of Poaceae *(20–30%) and* Cyperaceae (20–10%) decreases, while other Campos pollen taxa, such as *Eryngium* type (ca. 17%) and *Eriocaulon* (ca. 6%), increase. Additional Campos taxa include *Asteraceae* (3–5%), *Senecio* (1–3%), *Baccharis* (3–5%), *Ambrosia* (0–2%), Apiaceae (0–2%), *Chenopodium*-Amaranthaceae (0–2%), and with 0–1% *Xyris*, *Gomphrena-Pfaffia* type, *Spermacoce*, *Solanum* type, *Alstroemeria*, Fabaceae, *Plantago australis*, and *Chevreulia*. Furthermore, three grains of *Plantago* and two grains of *Begonia* were identified. Araucaria Forest taxa decrease from 23% to 15%, primarily due to a reduction in *Araucaria angustifoilia* pollen from 10% to 3%. Other taxa present include *Myrsine* (4–6%), Myrtaceae (1–3%), *Schinus* (1–2%), *Mimosa scabrella* (1–2%), *Podocarpus* (1–5%), and with 0–1% *Weinmannia*, *Ilex*, *Sebastiania commersoniana*, *Sebastiania brasiliensis*, three grains of *Allophylus*, and two grains of *Lamanonia speciosa*. ARF pollen taxa (2–4%) are composed of Urticaceae/Moraceae (1–2%) and with less than 1% of *Piper*, *Alchornea*, *Celtis*, *Trema*, and *Matayba*. Pollen taxa indicative of human impact increase from 1% to 3.5%, dominated by an increase in *Pinus* (2%) and *Zea* (1%). Additionally, one pollen grain of *Eucalyptus* was identified. Other taxa increase to 4–7%, including Rubiaceae (ca. 2%), Melastomataceae (ca. 2%), Anacardiaceae (approximately 1%), and indeterminate pollen taxa (1–2%). Several single pollen grains, such as *Oreopanax fulvum*, *Rhamnaceae*, *Prockia*, *Cupania*, *Alnus*, and *Trichilia*, were identified but not included in the pollen diagram. Aquatic taxa primarily include *Hydrocotyle* (approximately 2%), *Ludwigia* (0–10%), and the algae *Botryococcus* (ca. 1%). Spores are represented by *Sphagnum* (3–6%), *Phaeoceros laevis* (0–1%), *Monolete verrucate* spore (1–3%), and *Blechnum* (0–2%). Additionally, one fungal spore of *Gelasinospora* (0–1%) was found. The amount *HdV.123* varies between 30% and 45%. The overall quantity of dung fungal spores increases from 4% to 11%, including *Coniochaeta* (1–2%), *Podospora* type (1–2%), *Delitschia* (ca. 1%), *Sordaria* (1–2%), *Apiosordaria* (0–1%), *Cercophora* type (0–2%), *Sporormiella* (ca.1%), and *Chaetomium* (not included in the diagram). The overall macro-charcoal influx increases from approximately 5 to 29 particles per cm^{-2} yr^{-1}, while the abundance of micro-charcoal varies between 10,000 and 70,000 particles per cm^{-2} yr^{-1}. Palynological richness increases from 30 to 45 taxa.

4.3. Compound-specific hydrogen isotopes (δ^{2}H) from leaf-wax n-alkanes

Measurements of compound specific hydrogen isotope values (δ^{2}H) of *n*-alkanes (*n*-C$_{27}$ to *n*-C$_{33}$) are presented in Fig. 5. δ^{2}H values of *n*-C$_{29}$ and *n*-C$_{31}$ were the most consistently attained throughout the core and are therefore used as the main basis for interpretation. All δ^{2}H values range between −200‰ and − 140‰. A distinct decrease in δ^{2}H values is observed at 49 cm across *n*-C$_{27}$ to *n*-C$_{31}$, reaching values near −200‰. This is followed by a marked increase in δ^{2}H values rising to approximately −140‰ in *n*-C$_{29}$ to *n*-C$_{33}$ and − 175‰ in *n*-C$_{27}$. At 20 cm depth, all compounds again show a pronounced decrease in δ^{2}H to around −200‰, followed by a slight increase towards the core top. Such variations in δ^{2}H values are typically interpreted as changes in moisture availability, with more negative values indicating wetter conditions and less negative values suggesting drier phases (Sachse et al., 2012; Jha et al., 2020; Patalano et al., 2023).

4.4. Interpretation and discussion

In this study, we conducted a multiproxy analysis using pollen, charcoal, and δ^{2}H isotope analyses from the Matematico sediment core to reconstruct vegetation dynamics and fire history in Southern Brazil (Fig. 6). Palynological evidence reveals that, between ~3500 and 2500 cal yr BP, the landscape was dominated by open Campos grasslands, as

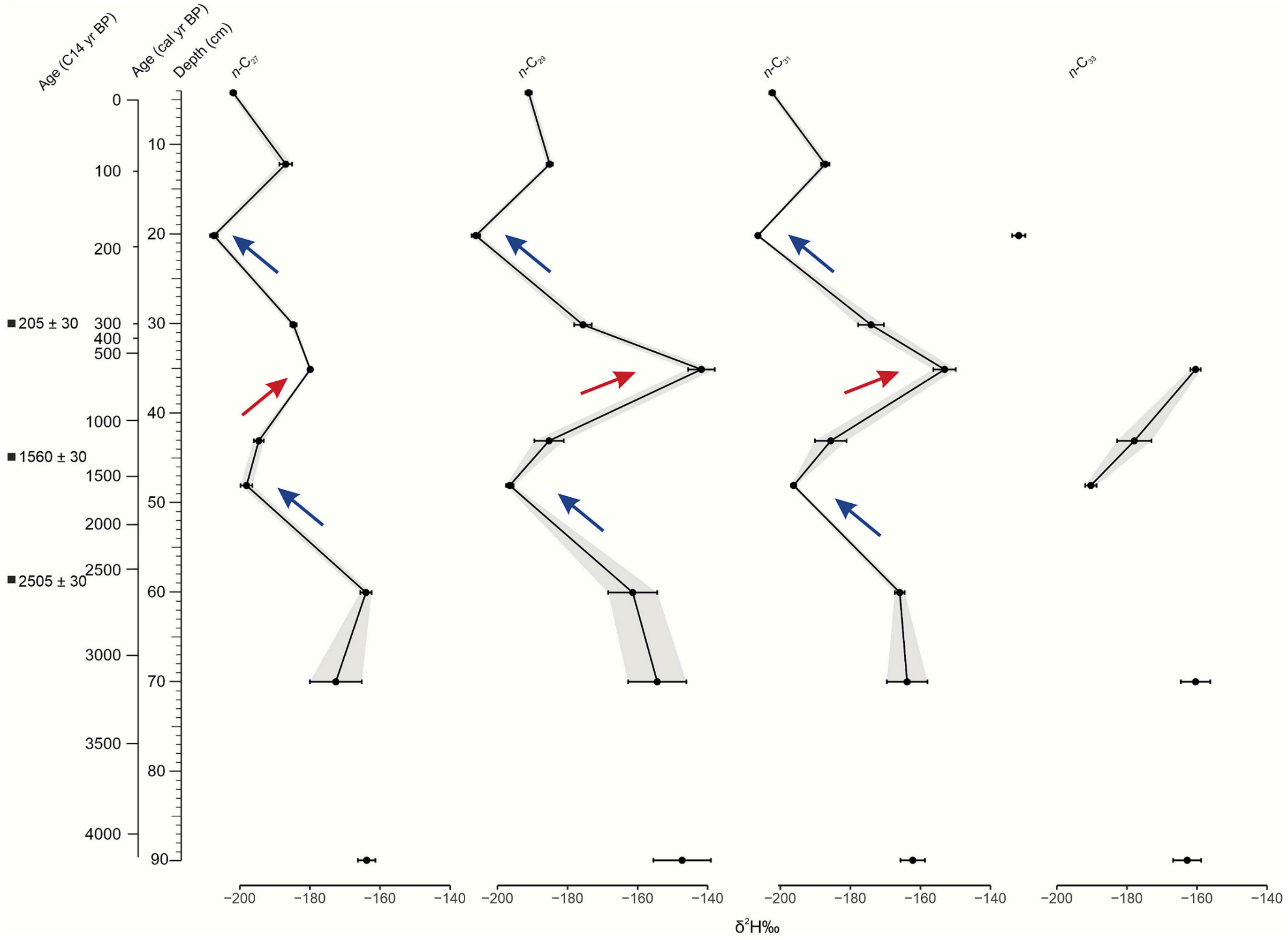

Fig. 5. Hydrogen isotope values (δ^{2}H) of long-chain n-alkanes (n-C_{27} to n-C_{33}) extracted from the Matematico sediment core. Values are plotted against depth (cm) and age (cal yr BP = calibrated years before present, C14 yr BP = C14 years before present). δ^{2}H values of n-C_{29} and n-C_{31} were consistently detected throughout the profile and are used as the primary basis for palaeohydrological interpretation. Shaded areas represent standard deviation based on replicate measurements. Blue arrows indicate wetter conditions, and red arrows indicate drier conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indicated by high proportions of herbaceous pollen, especially Poaceae, various Asteraceae types, and *Eryngium*. Although, the Matematico record indicates a Campos flora dominated by wind-pollinated grasses, palynological richness is relatively stable during this phase (Fig. 4), suggesting that Campos supported structurally simple but taxonomically rich communities. Forest taxa, such *as Araucaria angustifolia* and Urticaceae–Moraceae type, are only sparsely present, suggesting a landscape of predominantly open vegetation with only scattered woody plants. Charcoal influx during this period is low, indicating infrequent natural fire occurrence under grassland conditions. Similarly, early– to mid-Holocene dominance of Campos grasslands is documented in other highland and foreland records from Rio Grande do Sul, Santa Catarina and Paraná, pointing to a regionally extensive, climatically controlled grassland vegetation during this time (Behling et al., 2004; Jeske-Pieruschka and Behling, 2011; Jeske-Pieruschka et al., 2013).

As observed in other palynological records, the expansion of Araucaria Forest, in particular *Araucaria angustifolia* but also forest taxa such as *Myrsine* and Myrtaceae, occurred in two phases (Behling et al., 2024). The first increase is evident at ~1700 cal yr BP and the second, slightly sharper expansion occurs at ~500 cal yr BP. *Araucaria* Forest pollen, mostly absent before, increase while Campos taxa decline, indicating the formation of a Forest–Grassland mosaic. Notably, the timing of Araucaria Forest expansion at Matematico is slightly later than in other sites, where the first increase often occurs at ~3000 cal yr BP and the second at ~1400 cal yr BP in Paraná and Rio Grande do Sul and at ~900 cal yr BP in Santa Catarina (Behling et al., 2024; Jeske-Pieruschka and Behling, 2011; Piraquive-Bermúdez et al., 2024). Additionally, the maximum abundance of *Araucaria angustifolia* pollen in this record (~10%) is lower than that found at sites located within continuous forest. Species distribution models indicate that the modern occurrence of *Araucaria angustifolia* in Brazil is primarily controlled by mean annual precipitation of approximately 1680 ± 180 mm (Pinaya et al., 2019). At Matematico, which is situated slightly more inland than other palynological sites, present-day precipitation averages around 1800 mm, placing the site only slightly above this ecological threshold. This implies that even modest reductions in rainfall in the past could have constrained Araucaria Forest establishment and dispersal at this location. In contrast, palynological sites situated closer to the coast generally receive higher annual precipitation. Consequently, short-term or moderate drying events would have had less severe impacts on the forest expansion (Behling, 1997; Behling et al., 2004, 2001).

With forest expansion at ~500 cal yr BP, there is a noticeable increase in saprotrophic/ coprophilous fungi. While these fungi are sometimes interpreted as indicators of pastoralism, many taxa can also grow on decaying wood and are not exclusively linked to dung (Shumilovskikh and van Geel, 2020). At the same time, charcoal

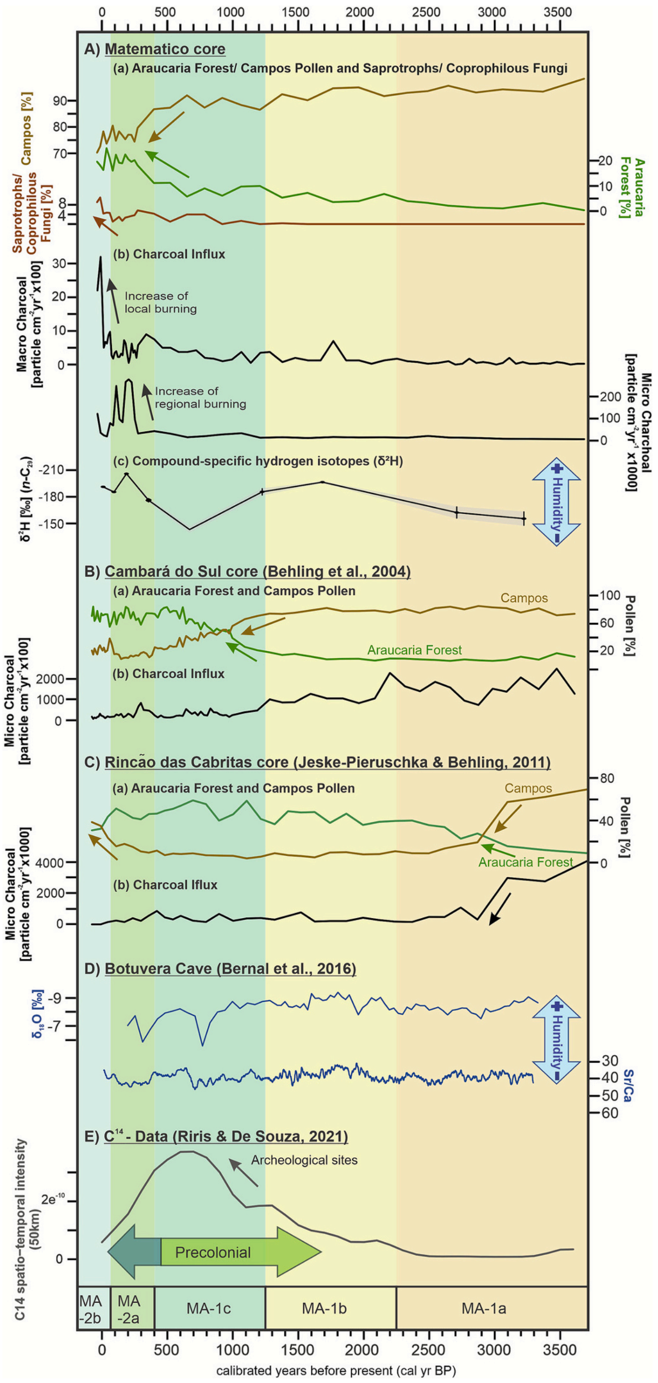

Fig. 6. (A) Overview of data from the Matematico core (Rio Grande do Sul, Southern Brazil): (a) percentages of Araucaria Forest and Campos pollen and saprotrophs/coprophilous fungi; (b) charcoal index; and (c) compound-specific hydrogen isotopes (δ^2H). (B) Overview of data from the Cambará do Sul core (Behling et al., 2004): (a) percentages of Araucaria Forest and Campos pollen and (b) charcoal index. (C) Overview of data from the Rincão das Cabritas core (Jeske-Pieruschka and Behling, 2011): (a) percentages of Araucaria Forest and Campos pollen and (b) charcoal index. (D) Stable oxygen isotope (δ^{18}O) and Sr/Ca records from Botuverá Cave (Bernal et al., 2016). (E) Spatio-temporal intensity of ^{14}C dates from archaeological sites within a 50 km radius of the Matematico site (Riris and De Souza, 2021).

accumulation increases, indicating more frequent or intense burnings. The expansion of forest coupled with an increased fire activity suggests a shift in disturbance regime: either climatic conditions became more conducive to fire, or possibly humans, began using fire more actively e.g. as a land-management tool (Iriarte and Behling, 2007). After ~100 cal yr BP, several indicators suggest increasing anthropogenic disturbance, likely due to intensified land use resulting from European settlement. *Eryngium* type increases sharply, a taxon commonly also associated with disturbance due to fire or pasture (Behling et al., 2024). Throughout most of the core, the relative proportions of grass-derived and non-grass microcharcoal remain broadly similar (Fig. 4), indicating that both Campos and woody vegetation contributed to the fire regime. After ~100 cal yr BP, however, grass-derived microcharcoal increases strongly relative to other charcoal types, pointing to a greater emphasis on burning open grassland. This shift is consistent with anthropogenic pasture management, where repeated burning is used to maintain Campos for livestock grazing (Overbeck et al., 2007). Although overall Araucaria Forest pollen values remain relatively stable, *Araucaria angustifolia* itself declines after ~100 cal yr BP possibly reflecting selective logging pressure, as documented elsewhere in Southern Brazil (Enright and Hill, 1995). Additionally, the occurrence of pollen of cultivated crops such as *Zea mays* and exotic species such as *Pinus*, further support the interpretation of modern land-use impact. From a grassland perspective, these late Holocene changes illustrate a shift from relatively undisturbed Campos, characterized by a composition of Poaceae, Cyperaceae, Asteraceae, Apiaceae, and Malvaceae families, to more strongly managed pastures marked by enhanced *Eryngium*, higher frequencies of disturbance-tolerant/ early-successional plants such as Chenopodium–Amaranthaceae and *Solanum* type (Lando et al., 2018; Medina et al., 2017) and enhanced grass-charcoal signals. Notably, palynological richness increases slightly during this interval, suggesting not only a contraction of Campos area due to forest and agriculture, but also a diversification in Campos community composition under intensified grazing and fire management. Taken together, these comparisons emphasise that Campos are not a single homogeneous vegetation type, but a set of communities whose structure and functioning depend strongly on local fire, grazing and soil conditions (Overbeck et al., 2007).

A notable contrast emerges when comparing our fire history with other Araucaria–Campos records from southern Brazil. For example, at Cambará do Sul and Rincão das Cabritas charcoal influx peaks during phases dominated by Campos and subsequently declines once Araucaria Forest is established, reflecting frequent grass-fuelled fires that become locally suppressed as forest expands (Behling et al., 2004; Jeske-Pieruschka and Behling, 2011). At Matematico, charcoal influx remains low during the earlier Campos-dominated phase and increases only after ~500 cal yr BP, contemporaneous with Araucaria Forest expansion and intensified human presence. This opposite pattern suggests that local fire regimes were not solely controlled by regional climate, but also by site position within the forest–grassland mosaic and by the timing and intensity of human land use.

Hydrological proxy data provide additional context for these ecological changes. The δ^2H values of sedimentary *n*-alkanes exhibit shifts concurrent with the pollen transitions. Prior to ~1700 cal yr BP, δ^2H values remain relatively high (i.e., less negative), consistent with drier or more evapotranspiration-intensive conditions during the grassland-dominated phase. Around both forest expansion phases (~1700 and ~ 500 cal yr BP), δ^2H values shift towards more negative values, suggesting increased effective moisture availability at Matematico. This could reflect greater precipitation, reduced evapotranspiration, or shifts in rainfall seasonality (Sachse et al., 2012; Jha et al., 2020; Patalano et al., 2023). Taken together, the multiproxy dataset presents a coherent narrative: a transition during the late Holocene from dry Campos with low fire activity to a wetter Forest–Grassland mosaic characterized by more frequent disturbance.

It is possible that climatic shifts during the late Holocene are responsible for the observed ecological transitions at Matematico, which are similarly reported across Southern Brazil. The hydrogen isotope evidence points to a hydrological change that roughly corresponds to the two expansions of Araucaria Forest. A trend towards wetter conditions or a change towards little or no dry season would favour tree growth and the spread of *Araucaria angustifolia*, which is known to thrive under the cooler and moisture-rich climate of the Southern Brazilian highlands (Behling et al., 2004; Bitencourt, 2007; Robinson et al., 2018). Indeed, regional palaeoclimate records support the notion of increased late Holocene precipitation. For example, speleothem records from the nearby Botuverá Cave indicate a generally stable or slightly wetter climate over the past ~1000 years (Bernal et al., 2016; Cruz et al., 2005). Comparable associations between hydrological shifts and *Araucaria* expansion have been inferred from lake-sediment records at the high-resolution Lagoa Dourada record, where stepwise changes in precipitation regimes appear to coincide with gradual woodland development and later forest consolidation (Piraquive-Bermúdez et al., 2024). Thus, a shift towards wetter and increasingly moist climatic conditions could explain the expansion of Araucaria Forest.

However, several lines of evidence suggest that climate variability alone is insufficient to explain the pronounced vegetation changes. Notably, earlier in the mid-Holocene and late Holocene, there were other periods of significant climate fluctuation that did not produce a lasting conversion of grassland to forest. For instance, a wet phase between ~2000–1750 cal yr BP, that was identified as the wettest interval in Southern Brazil over the last 8000 years (Bernal et al., 2016; Robinson et al., 2018) and corresponds to the initial wet interval at ~1700 cal yr BP in our record, did not lead to permanent Araucaria Forest expansion at Matematico or in analogous records (Behling, 1997; Behling et al., 2004; Jeske-Pieruschka and Behling, 2011; Jeske-Pieruschka et al., 2013; Rodrigues et al., 2016). During that time, despite increased rainfall, the pollen data indicate that grasslands remained dominant and forest cover did not broaden beyond sheltered valleys. Even an exceptionally wet climate alone failed to overcome the ecological inertia keeping Campos intact. It appears that wetter climatic conditions were necessary but not sufficient for large-scale forest spread. The fire history of the site further complicates a purely climate-driven explanation. If a wetter climate were the sole driver, one would expect fire activity to decrease (since higher moisture generally suppresses natural fire ignition and spread). Yet at Matematico, we see the opposite: fires became more frequent or intense at ~500 cal yr BP precisely as conditions grew wetter and forests expanded. This suggests that fire was not simply a byproduct of aridity, but potentially a tool used by humans to influence the vegetation.

In sum, wetter climates alone cannot account for the pronounced Araucaria Forest expansion ~500 cal yr BP in the Southern Brazilian highlands, which seems to be tied to the peak of Southern Jê groups of the Taquara/Itararé Tradition occurrence around the study site (Fig. 6) (Riris and De Souza, 2021). These communities intensively exploited and managed the Araucaria Forests, as the pine nuts (pinhão) of *Araucaria angustifolia* were a dependable, nutrient-rich staple that supported permanent village settlement and social complexity (Iriarte and Behling, 2007). Archaeological excavations in the nearby Matemático cave, located approximately 30 km from our study site, revealed charred *Araucaria* seeds alongside maize cobs, ceramics, and human remains, indicating that Southern Jê communities in the region actively consumed *Araucaria angustifolia* as part of their subsistence strategy (Copé, 2006; Lazzarotto et al., 1971). Notably, *Araucaria*'s heavy seeds rely on animals or people for long-distance dispersal, so human gathering and redistribution would have significantly aided its spread beyond what climate alone could achieve (Bitencourt and Krauspenhar, 2006; Robinson et al., 2018). The timing and magnitude of the ~500 cal yr BP Araucaria Forest expansion, concurrent with peak Southern Jê activity and a marked shift in fire regime, strongly suggest that anthropogenic impact was a decisive driver of forest expansion, synergizing with wetter conditions but ultimately pushing the forest beyond its climate-determined limits.

The palaeoecological findings from the Matematico core can offer critical insights for conservation strategies in Southern Brazil. The long-term existence of Campos grasslands, documented through thousands of years of pollen records, challenges the narrative that portray these ecosystems as merely degraded forests or anthropogenic relics. Despite their antiquity and biodiversity, Campos remains drastically underrepresented in Brazil's conservation agenda (Overbeck et al., 2007). Our record shows that Campos has persisted through Holocene climate fluctuations and phases of forest expansion, albeit with changing internal composition, highlighting both their resilience and their sensitivity to management. Current reforestation and land-management policies often prioritize afforestation, frequently with exotic species like Pinus or Eucalyptus, which may further threaten the existence of these biodiverse grasslands. Moreover, the Araucaria Forest–Campos mosaic itself appears to have been historically dynamic, shaped by both climatic variability and human impact. Conservation approaches should therefore embrace the mosaic nature of these ecosystems, including their grassland components. Future strategies should integrate palaeoecological perspectives to better understand ecosystem baselines, natural variability, and the cultural dimensions of landscape change.

5. Conclusions

The Matematico multi-proxy record demonstrates that Southern Brazil's Araucaria Forest-Campos mosaic has been shaped by a complex interplay of climate variability and human activity throughout the late Holocene. While increased moisture availability facilitated Araucaria Forest expansion, climate alone could not account for the timing or magnitude of vegetation change. The pronounced forest expansion at ~500 cal yr BP is best explained by a synergy of wetter conditions and intensified land use by Southern Jê communities, whose practices, such as fire management and *Araucaria* nut harvesting, might have actively influenced forest distribution. Equally significant is the long-term persistence of Campos grasslands, a biodiverse ecosystem, which has existed for millennia rather than as degraded or purely anthropogenic landscapes. Their underrepresentation in current conservation policy, coupled with threats from agriculture, forestry, and afforestation with exotic species, underscores the urgent need to protect both grasslands and forests as integral components of the Araucaria-Campos mosaic. By integrating palynology, charcoal, and compound-specific isotope analyses, this study provides a high-resolution perspective on the ecological and cultural processes that shaped one of the world's most threatened biodiversity hotspots. Future research should expand this multi-proxy approach, particularly the combined use of palynology and compound-specific isotope analysis, across a broader range of sites within the region. High-resolution palaeoecological records paired with archaeological datasets would be crucial to further disentangle regional patterns of human–environment interaction. These deep-time insights are hopefully going to help anticipate ecosystem responses to future climate and land-use changes and are therefore essential for informed conservation measures.

Declaration of generative AI in scientific writing

During the preparation of this work, the author used ChatGPT (OpenAI) in order to improve readability and language of the manuscript. After using this tool, the author reviewed and edited the content as needed and takes full responsibility for the content of the published article.

CRediT authorship contribution statement

Antonia Lena Reinhardt: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Philip Riris:** Writing – review & editing, Project administration, Funding acquisition. **Barnabas Harris:** Writing – review & editing, Formal analysis. **Deepak Kumar Jha:** Writing – review & editing, Investigation. **Gisele Leite de Lima Primam:** Resources, Data curation. **Soraia Girardi Bauermann:** Resources, Data curation. **Kasun**

Gayantha: Writing – review & editing, Investigation. **Rachel Rudd:** Writing – review & editing, Investigation. **Patrick Roberts:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Hermann Behling:** Writing – review & editing, Supervision, Resources, Funding acquisition, Data curation, Conceptualization.

Funding

This project was supported by a joint grant from the AHRC and DFG (Project number: AH/X002217/1) awarded to PR, HB, and PR, as well as the Deutsche Forschungsgemeinschaft (DFG) (Project number: 657 0077) awarded to HB. PR would like to thank the Max Planck Society for funding.

Declaration of competing interest

Acknowledgements

We would like to thank Vivian Jeske- Pieruschka and colleagues for their valuable support in during field work. Furthermore, we would like to thank Uta Nüsse-Hahne and Sarah J. Veith (University of Göttingen) for their assistance and help in the laboratory.

Data availability

The palynological and geochemical data generated during this study will be submitted to the Neotoma Paleoecology Database (https://www.neotomadb.org) upon publication of the article. The data will be openly accessible and formatted according to Neotoma standards to ensure long-term preservation and reusability.

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