

Late Quaternary vegetation and climate dynamics in central-eastern Brazil: insights from a ~35k cal a BP peat record in the Cerrado biome

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ABSTRACT: The late Quaternary evolution of central-eastern Brazil has been under-researched. Questions remain as to the origin of the Cerrado, a highly endangered biome, and other types of vegetation, such as the Capões – small vegetation islands of semi-deciduous and mountain forests. We investigated the factors that influenced the expansion and contraction of the Cerrado and Capões during the late Quaternary (last ~35 ka), using a multi-proxy approach: stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), geochemistry, pollen and multivariate statistics derived from a peat core (Pinheiro mire, Serra do Espinhaço Meridional). Five major shifts in precipitation, temperature, vegetation and landscape stability occurred at different timescales. Our study revealed that changes in the South Atlantic Convergence Zone (SACZ) seem to have been coeval with these shifts: from the Late Glacial Maximum to mid-Holocene the SACZ remained near (~29.6 to ~16.5k cal a BP) and over (~16.5 to ~6.1 k cal a BP) the study area, providing humidity to the region. This challenges previous research which suggested that climate was drier for this time period. At present, the Capões are likely to be a remnant of a more humid climate; meanwhile, the Cerrado biome seems to have established in the late Holocene, after ~3.1 k cal a BP. Copyright © 2020 John Wiley & Sons, Ltd.

KEYWORDS: geochemistry; paleoclimatology; peatlands; pollen; stable isotopes

Introduction

Central-eastern Brazil, with a sub-humid and seasonal climate and well-defined seasons (~4–5 months of dry season and mean winter temperature $\geq 15^\circ\text{C}$), maintains the Cerrado biome, which is a vast tropical savanna and part of the so-called 'xeric vegetation' corridor (Bucher, 1982). This tropical savanna is characterized by a large diversity of phytophysognomies and high levels of endemism, and quite specific vegetation patterns are found in certain regions, such as the Serra do Espinhaço Meridional (Minas Gerais state). Here, small vegetation islands, called 'Capões' (also 'florestas em mancha' by Rizzini, 1979), are characterized by tree and shrub species of semi-deciduous forest (with double climatic seasonality) and mountain forests (mean winter temperature $< 10^\circ\text{C}$; Ledru *et al.*, 1998) dispersed among grassland formations.

The response of tropical biomes to climate change has been the focus of investigations covering the Last Glacial Maximum (LGM; peaked 21.5 ka) and mid-Holocene (5 ka)

(Colinvaux *et al.*, 1996; Ledru *et al.*, 2009; Bueno *et al.*, 2017; Arruda *et al.*, 2018; Pinaya *et al.*, 2019). However, none of them were performed in the Cerrado biome, specifically in the Serra do Espinhaço Meridional. Therefore, paleorecords and Pleistocene reconstructions are absent from this area and this was one of the main reasons for undertaking the present study. Several earlier studies have challenged established hypotheses, such as Amazonian refugia (Haffer, 1969) and Pleistocene arc hypotheses (Prado and Gibbs, 1993), which assert that aridity was prevalent in the Cerrado biome during these periods. More recent research has questioned this interpretation, stating that the humid forest of the Amazon region was already present at the LGM (Colinvaux *et al.*, 1996; Haberle and Maslin, 1999; Leite *et al.*, 2016; Arruda *et al.*, 2018). Additionally, the spatial distribution of seasonal biomes was larger during the Holocene compared to the LGM, helped by improved recent climatic conditions (Werneck *et al.*, 2011; Horák-Terra *et al.*, 2015).

It has been proposed that the advance of Quaternary glaciers in temperate regions (the last glacial period encompassed the period 115–11.7 ka) resulted in the development of xerophile vegetation, such as savannas in

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tropical and subtropical areas (Goldblatt, 1978; Pennington *et al.*, 2006), but it is not clear whether this is a typical vegetation response to changing climate. Currently, the distribution of these complex Neotropical plant communities – the actual Cerrado – contradicts this proposal, because a vast dense forest should cover the ~2 million km² of the Brazilian territory if this idea was true. Similarly, there are other unsolved questions such as: Are the present occurrences of Capões relicts of a more dense arboreal vegetation of former times? Was there a more arid climate in the past, and was its vegetational composition similar to the current one? Was there a time when the area now occupied by the Cerrado served as an ecotone of the wettest biomes?

Precise characterization of climate variability in the Cerrado biome on a wide range of timescales is necessary to understand its possible link to the establishment of tropical biomes in South America (Simon *et al.*, 2009; Werneck *et al.*, 2012), as it is bordered by almost all other biomes today. However, paleoclimate data of central-eastern Brazil remain scarce (Ferraz-Vicentini and Salgado-Labouriau, 1996; Barberi *et al.*, 2000; Stríkis *et al.*, 2011; Horák-Terra *et al.*, 2015). Therefore, it is unclear how millennial and orbital-scale climate variability manifested itself in this area and how it compares with adjacent regions.

Supported by the interhemispheric anti-phase behavior, the Younger Dryas (YD)–Heinrich (H) and the Dansgaard-Oeschger (D/O) events are respectively expressed in South America as wet and dry episodes (Cheng *et al.*, 2013). The YD occurred by 12.9–11.7 ka, while the H and D/O were characterized by a series of events (10 and 25 events, respectively) during the last glacial period. The abrupt increase in monsoon rainfall during the YD–H events was probably related to a southward shift in the average position of the Intertropical Convergence Zone (ITCZ), a strengthening of the asymmetry in Hadley circulation in response to an interhemispheric gradient of sea surface temperature, and a possible influence of Antarctic climate changes (Wang *et al.*, 2004, 2006; Kanner *et al.*, 2012; Cheng *et al.*, 2013). Despite this coherent pattern of millennial-scale variability, the spatial structure of precipitation is complex at orbital timescales (Wang *et al.*, 2006). For instance, it is known that north-eastern Brazil experienced humid conditions during low summer insolation phases and aridity conditions when summer insolation was high, whereas the rest of southern tropical South America showed an opposite behavior (Cheng *et al.*, 2013). Thus, obtaining accurate information about the past climate of central-eastern Brazil is important, mainly due to its strategic location. This region is deeply influenced by the South Atlantic convergence zone (SACZ) during the austral summer, resulting in increasing precipitation from November to March (Garreaud *et al.*, 2009), when it extends into a south-eastern direction from the interior of the continent to the South Atlantic (Vera *et al.*, 2006).

Tropical and subtropical peatlands are ideal archives for reconstructing climate changes from the late Pleistocene, i.e. from 126 ka (Weiss *et al.*, 2002; Muller *et al.*, 2008; Ledru *et al.*, 2009; Dommain *et al.*, 2011; Swindles *et al.*, 2018), because they are extremely sensitive to changes in hydrology. For example, Horák-Terra *et al.* (2015) investigated a peat core from Pau de Fruta mire, located in the Serra do Espinhaço Meridional (Brazil), using a combination of biotic (pollen) and abiotic (peat physical properties, elemental and isotopic composition) proxies to trace Holocene climate changes in the area. Morphological, physical, chemical and elemental properties were used to show that the peatland showed a complex evolution resulting from varying mineral fluxes from the catchment, regional dust deposition, changes in peat plant

communities and degree of peat decomposition (Horák-Terra *et al.*, 2014). Similarly, we present results from a core (PI, 130 cm deep) spanning the last ~35 k cal a BP, and taken from a tropical mountain peatland (Pinheiro mire) from Serra do Espinhaço Meridional. The same core was also investigated for mercury (Hg) (Pérez-Rodríguez *et al.*, 2015, 2016). This research showed that variations in Hg concentrations were probably driven by climate, either indirectly by enhancing the mineral matter fluxes from the mire's catchment (i.e. increased soil erosion) and regional dust deposition, or directly by long-term changes in atmospheric wet deposition (humid vs arid phases). So, this core presents a unique opportunity for a detailed investigation to reconstruct climate change in central-eastern Brazil since the late Pleistocene, considering the existence of autogenic changes in Pinheiro mire by multiple mechanisms as cited above.

We present inferences about past environmental conditions in central-eastern Brazil during the ~35 k cal a BP using multiproxy data including stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), geochemistry (major, minor and trace elements) and pollen records (pollen, spores and other non-pollen palynomorphs). From these data, reconstructions of changes in precipitation, temperature, vegetation and landscape stability occurring at different timescales allowed us to achieve our main aims: (i) to obtain accurate information about the past climate of central-eastern Brazil, and (ii) to reconstruct the vegetation history and the conditions culminating in the formation of the current biome. Our study is one of the most complete for central-eastern Brazil. The data can also be used to predict future conditions through climate models, as well as to compare with other paleoclimatic and paleoecological records from different regions in Brazil and globally. Furthermore, our research highlights the value of such data for conservation of tropical peatlands and the Cerrado biome, due to their environmental and ecological importance.

Materials and methods

Regional setting

The PI core was collected from the Pinheiro mire (18°3'44.42" S, 43°39'42.37" W), a tropical mountain peatland located at ~1240 m a.s.l. in the Serra do Espinhaço Meridional, Minas Gerais state (Brazil) (Figs 1 and 2A,B). Pinheiro is an oligotrophic valley mire located in a catchment with limited drainage. The catchment is narrow (0.1–0.6 km wide) and elongated (~3.7 km long) in a SW–NE direction, and the mire covers the lower and flatter parts of the valley overlying quartzitic sediments. The Pinheiro mire is also a soligeneous peatland: it is affected by water from external sources percolating through or over surface peat. Today, the peat is mostly formed by graminoid species, among them grasses and sedges. The basal lithology is part of the Galho do Miguel Formation, consisting of pure and thin quartzites (~90%), thin micaceous quartzites and some gray or greenish metargillites (~5–10%; Knauer, 2007).

At present, the climate of the area is tropical montane with mean annual temperature of 18.7 °C and mean annual precipitation of about 1500 mm for the period 1950–1990 (Alvares *et al.*, 2013), restricted by the South American Monsoon System (SAMS) activity and SACZ.

The vegetation is typical of the Cerrado biome (Brazilian savanna), one of the most endangered in the world (Klink and Machado, 2005). This is characterized by extensive, open grasslands (wet, dry and rupicola-saxicolous), with a limited presence of trees and shrubs. However, it also contains the

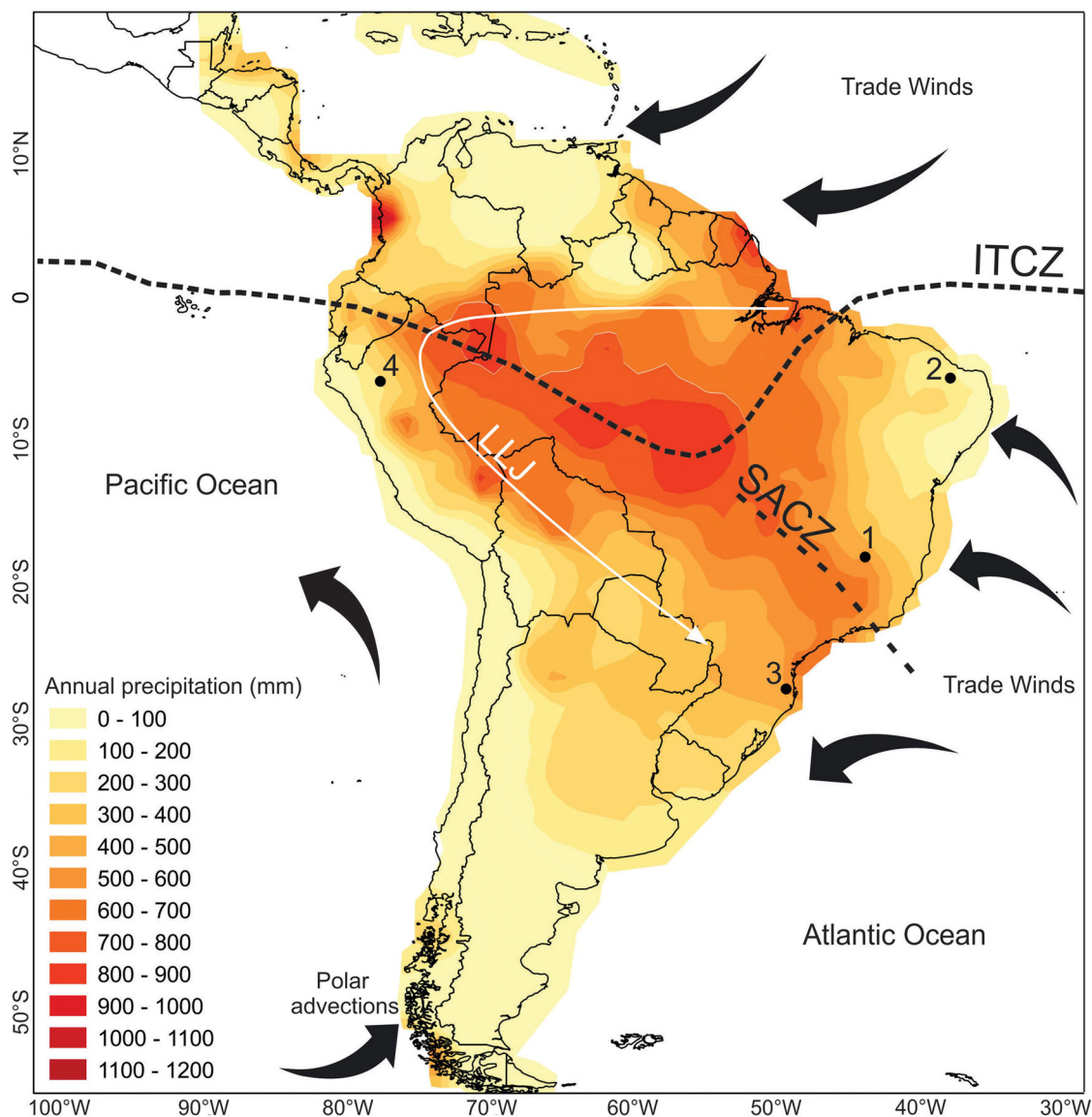


Figure 1. Long-term mean (AD 1979–2000) precipitation (mm) for December–February (DJF) from the Climate Prediction Center Merged Analysis of Precipitation. Numbers in the map indicate the study site and other climate records from South America: 1 – Pinheiro mire in Minas Gerais state, central-eastern Brazil; 2 – Rio Grande do Norte caves in Rio Grande do Norte state, north-eastern Brazil (Cruz *et al.*, 2009); 3 – Botuverá cave in Santa Catarina state, southern Brazil (Cruz *et al.*, 2005); and 4 – western Amazonia caves, northern Peru (Cheng *et al.*, 2013). ITCZ – Intertropical Convergence Zone; SACZ – South Atlantic Convergence Zone; LLJ – low-level jet. [Color figure can be viewed at wileyonlinelibrary.com]

‘Capões’ (with semi-deciduous forest and mountain forest species), which appear as small, dispersed forest islands (Fig. 2A,B). Currently, the Pinheiro area is quite well preserved, because access for locals living in the surrounding villages is difficult. However, there are reports of some natural bushfires during the driest times of the year.

Sampling and stratigraphic description

The core was sampled in 2010 using a vibracore (constructed according to Martin *et al.*, 1995) to a depth of 324 cm. However, as this paper mainly deals with changes in environment and climate for the LGM–mid-Holocene, we have decided to only present the upper 130 cm, which spans the last ~35 ka. The stratigraphy was described according to the Field Book for Describing and Sampling Soils (Schoeneberger *et al.*, 1998) and the Guidelines for Soil Description (FAO, 2006), whereas the horizons were defined according to the Soil Taxonomy (Soil Survey Staff, 2010). The upper 130 cm is composed of five peat horizons (Oi, Oa, Oa2, Oa3 and Oa4), defined by the content of mineral/organic matter, the degree of peat decomposition and

consistency (Fig. 2C): horizons Oa4 (130–98 cm) and Oa3 (98–58 cm) are slightly sticky and with low mineral matter content, differing only in fine roots content (greater in Oa4 than in Oa3); horizons Oa2 (58–20 cm) and Oa (20–8 cm) are also similar, being highly sticky and both with abundant fine roots; and the uppermost layer, Oi (8–0 cm), is a fibric horizon of poorly decomposed peat. The core was sliced into continuous 2-cm-thick sections.

Age–depth model of the core

Seven peat samples (Supporting Information Table S1) were radiocarbon dated by accelerator mass spectrometry (AMS) in Beta Analytic, Inc. (Miami, FL, USA); the analyses were done on the acid–alkaline–acid extraction of bulk organic matter. The age–depth model was fitted with a Bayesian statistical approach using the Bacon R package (v.2.3.5) (Blaauw and Christen, 2011) (Fig. 3). The calibration curve was SHCal13.14C (Hogg *et al.*, 2013). Based on the hypothesis that Northern Hemisphere air masses may have been the main source of humidity for the area in the late Quaternary, we also

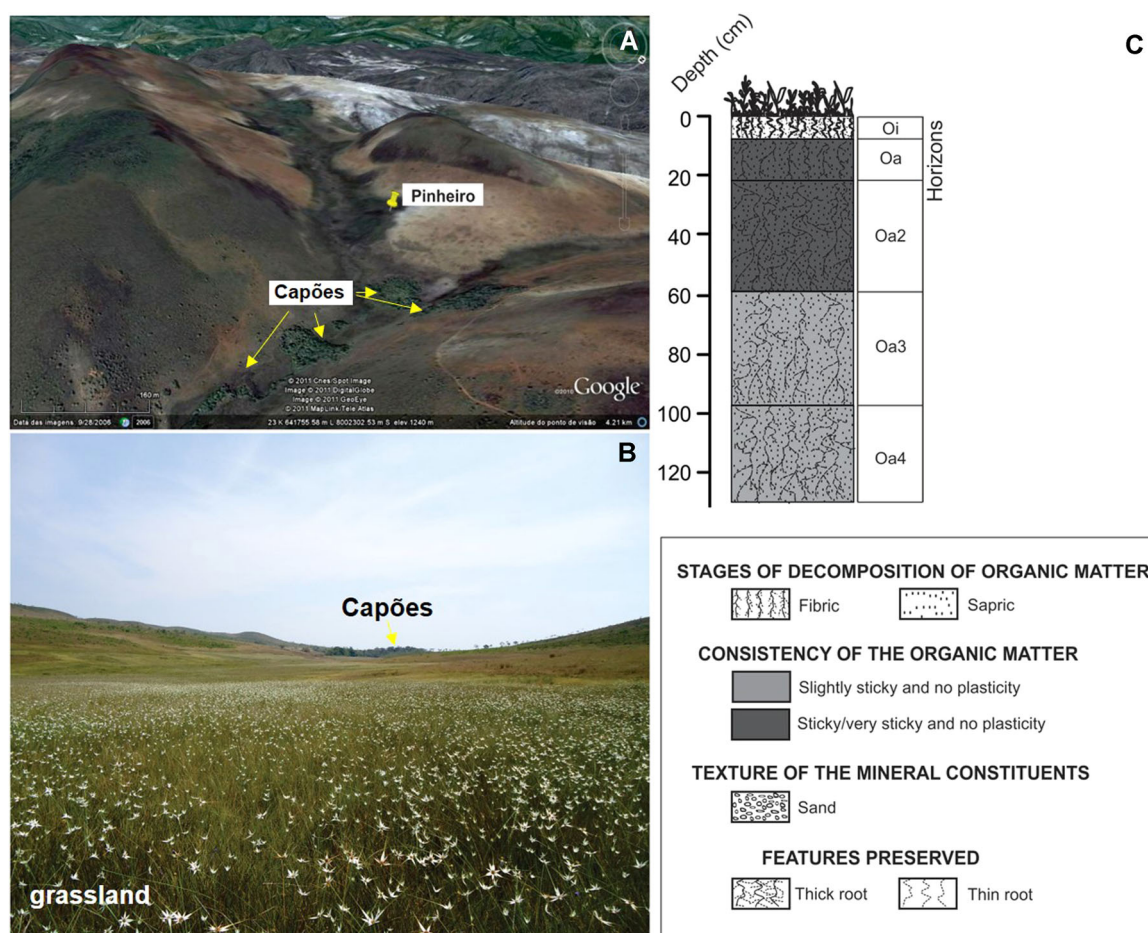


Figure 2. (A) Satellite image of the Pinheiro mire location (drains from SW to NE, situated between 1270 and 1230 m a.s.l.) obtained from Google Earth. (B) Photo of the sampling site – Pinheiro mire (valley mire and minerogenic under wet grassland). (C) Stratigraphy of the PI core. Oi and Oa are fibric and sapric peat layers, respectively; C are sediment layers. [Color figure can be viewed at wileyonlinelibrary.com]

performed the age model using the NH calibration data set (IntCal13; Fig. S1). Because the results indicated that the models are in close agreement, with very close ages, we present the chronologies with the model obtained with the

Southern Hemisphere calibration curve here. The model was fitted by assigning the year of sampling as age of the upper peat sample and no smoothing was applied. All ages presented in the text are expressed as calibrated ages.

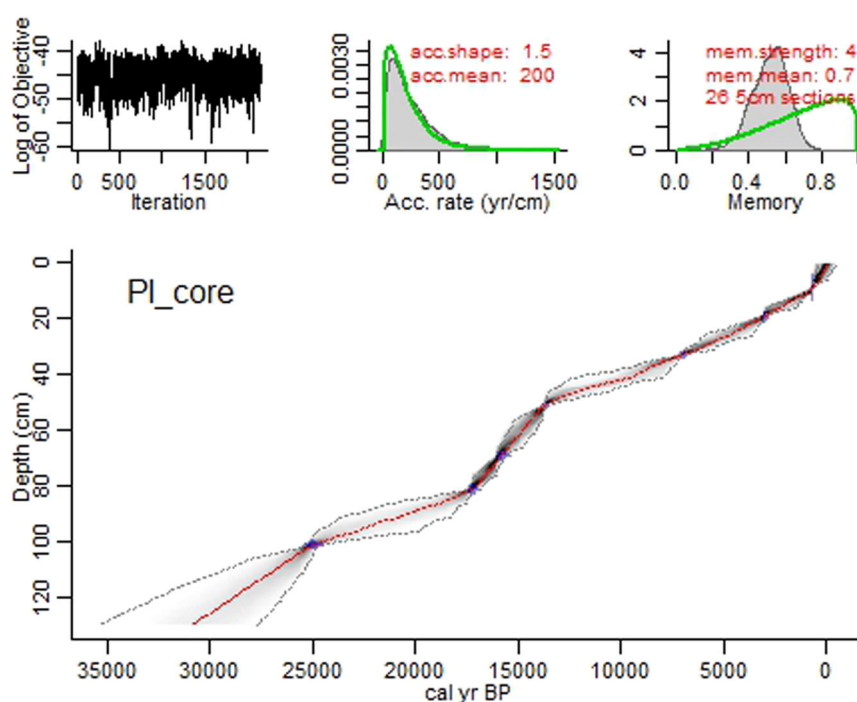


Figure 3. Age–depth model of the PI core fitted with Bacon (Blaauw and Christen, 2011) using the dating for the peat samples of the upper 1 m of the core (blue) and Southern Hemisphere calibration curve (SHCal13.14 C). [Color figure can be viewed at wileyonlinelibrary.com]

Elemental and isotopic composition

Carbon and nitrogen contents and isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were determined in dried, milled and homogenized peat samples, using an elemental analyzer coupled to a mass spectrometer hosted in the Laboratório de Ecologia Isotópica of the Centro de Energia Nuclear na Agricultura – CENA/USP (Piracicaba, SP, Brazil). Major, minor and trace elements (P, S, Al, Si, Fe, Ti, K, Ca, Ga, Rb, Sr, Y, Zr, Nb, Th, Cr, Mn, Ni, Cu, Zn, As, Pb, Cl and Br) were determined by X-ray fluorescence in the same samples using two energy-dispersive XRF analyzers (Cheburkin and Shotyky, 1996; Weiss *et al.*, 1998) hosted in the RIAIDT facility (Infrastructure Network for the Support of Research and Technological Development) of the Universidade de Santiago de Compostela (Spain).

Instrument calibrations were performed for organic matrices using several reference materials (NIST 1515, 1541, 1547 and 1575; BCR 60 and 62; and V-1). Detection limits were $<100\text{ }\mu\text{g g}^{-1}$ for Al, Si, S, K, Ca and Fe; $50\text{ }\mu\text{g g}^{-1}$ for P; $10\text{ }\mu\text{g g}^{-1}$ for Mn; $5\text{ }\mu\text{g g}^{-1}$ for Ti; $10\text{ }\mu\text{g g}^{-1}$ for Cl; and $1\text{ }\mu\text{g g}^{-1}$ for Cr, Ni, Cu, Zn, Br, Ga, Rb, Sr, As, Y, Zr, Th, Pb and Nb. One in every five samples was analyzed in triplicate, and the measurements agreed within 5% for most elements. Values that did not agree within 10% were rejected (in this case, more replicates were done).

Pollen study

For the pollen study, 13 wet samples of 1 cm in thickness taken every 10 cm were obtained from the center of the PI core. A modified version of the physico-chemical treatment (Ybert *et al.*, 1992) extracted pollen, spores and other non-pollen palynomorphs (NPPs). Hydrofluoric acid was added for the dissolution of silicates, hydrochloric acid for elimination of fluorosilicates, acetic acid for dehydration, and acetylation mixture for dissolution of the organic matter and acetylation of the exine. Ultrasound was used to separate large organic remains. Counting was undertaken at 400x under a microscope (Supporting Information Table S2), obtaining an average total land pollen sum (TLP) of 800 terrestrial pollen grains per sample. Hydro-hygrophites and NPP were not included in the TLP, but they were expressed as percentages of it. The average sum of hydro-hygrophites and NPP was 560 palynomorphs. Identification was helped by the reference collection (modern pollen deposition) of the Pau de Fruta mire (Horák, 2009; Horák-Terra *et al.*, 2015; da Luz *et al.*, 2017), identification keys and atlases (van Geel, 1978; Tryon and Tryon, 1982; Roubik and Moreno, 1991). Taxa included in the TLP are considered indicators of regional vegetation, while hydro-hygrophites and NPP are mainly considered to constitute a local signal. The NPP can be mostly considered as local indicators because their dispersal is limited (Salgado-Labouriau, 2007); however, the case of the hydro-hygrophite taxa (e.g. Cyperaceae) is more complex, as they could also be part of the regional communities (Horák-Terra *et al.*, 2015). Pinheiro is a valley mire and variations in the water-table depth could be responsible for differences in the spatial distribution of local plant communities. Therefore, we added the hydro-hygrophites in the local signal. Pollen diagrams were obtained in the R software using the Rioja package (Juggins, 2019).

Groups corresponding to the types of vegetation and environments were obtained (Fig. 5) and based on the ecological preferences of the identified taxa (Figs. 6 and 7; Supporting Information Figs. S8–S11). Knowledge of each taxon is based on the detailed botanical survey of the Pinheiro mire and of other peatlands from the region (all materials are cataloged in the DIAM Herbarium of the Universidade Federal

dos Vales do Jequitinhonha e Mucuri – UFVJM, Diamantina city, Minas Gerais state, Brazil), but we also used several other references when necessary (van Geel, 1978; Guy-Ohlson, 1992; Mendonça *et al.*, 1998; Marchant *et al.*, 2002; da Luz *et al.*, 2017). Table S3 provides details of all identified taxa and their respective habit and coverage regional or local information, as well as indicating their phytophysiognomy or preferred environmental conditions. We are aware that some taxa can only be identified at the family or genera level and may include plants from various habitats, and also that most taxa identified at the species level may not be exclusive of one habitat and cannot be associated exclusively with one type of vegetation or environment. We also take into account the concept of ‘non-analogous community’ and therefore we assume that plant communities are not fixed through time (Williams and Jackson, 2007; Keith *et al.*, 2009), and that species respond individualistically to climate change. So, the floristic composition of vegetation changed through time, probably due to a rearrangement of the different taxa within each group.

Information about the length of the dry season for the main vegetation types from south to north Brazil was obtained to support climate inferences (Ledru *et al.*, 1998). For vegetation typical of the drier climate (Cerrado encompassing savanna forest and dry grassland), 5–6 months of dry season was considered. For seasonal forests (mainly semi-deciduous forest), 2–3 months of dry season was considered. Finally, no dry season was considered for mountain forest (encompassing cold and humid forest).

Statistical analysis

Stratigraphically constrained cluster analysis (total sum of squares method; Grimm, 1987) was applied to pollen and NPP/hydro-hygrophite data to define regional and local palynological zones, using the broken stick model to find the appropriate number of zones. For geochemical data, principal component analysis (PCA) was performed on the data matrices (these data can be seen in Supporting Information Figs S3–S7) after log-transformation and standardization (as suggested for compositional data, i.e. close data sets; Reimann *et al.*, 2008) in correlation mode and applying a varimax rotation to maximize the variable loadings in the components (Eriksson *et al.*, 1999). PCA was performed using SPSS 20.0 software.

Supporting studies

The $\delta^{18}\text{O}$ curve from a Greenland ice record (Groote and Stuiver, 1997) was included in this study, showing the typical sequence of stadial (YD + H1–3, at the top of the Fig. 4B) and interstadial (D/O cycles, from 1 to 7 at the bottom of Fig. 4B) periods. For comparison, $\delta^{18}\text{O}$ records of speleothems from north-eastern (Cruz *et al.*, 2009; Fig. 4C) and southern Brazil (Cruz *et al.*, 2005; Fig. 4D) and western Amazonia (Cheng *et al.*, 2013; Fig. 4E) are also included, as well as the Austral summer insolation (ASI) curve (Berger, 1978; in red). The oxygen isotope ratios are mainly interpreted as a function of the isotopic composition of rainfall, and therefore as indicative of past precipitation, where more negative $\delta^{18}\text{O}$ values are associated with an intense SAMS regime (Wang *et al.*, 2004, 2006) or wet climate conditions (Cheng *et al.*, 2013). The ASI can be used to examine the impact of orbital forcing, defined as the combined effects of precession and eccentricity (Berger, 1978), on central-eastern Brazilian climate. Changes in the Earth’s orbit around the sun cause quasi-periodic changes in insolation reaching the top of the atmosphere (Liu and Battisti, 2015).

Results

Proxies: meaning and interpretation

The age–depth model obtained for the PI core provides a chronology for the last ~35k cal a BP of environmental changes in central-eastern Brazil (Fig. 3). We are aware of the limitation imposed by such a coarse dating resolution for the period covered, and the larger uncertainty introduced by extrapolating ages for the last 30 cm (older than ~26 ka). This extrapolation is necessary because we have data for almost all proxies in this section, so it seems recommendable to indicate the expected ages for the observed changes. We emphasize that this strategy is

widely used in Quaternary studies (De Oliveira *et al.*, 2020; Rodríguez-Zorro *et al.*, 2020).

We use a selection of proxies (Fig. 4), such as $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Cp2 (factor scores of the second PCA component on geochemical properties – Supporting Information Fig. S2), and the Br/C ratio, as well as information regarding the distribution of the main taxa by type of vegetation and environment inferred by pollen analysis (Fig. 5; we have not included those taxa considered as ubiquitous). Synthetic pollen diagrams for the regional and local taxa are shown in Figs 6 and 7, respectively, while the remaining taxa not included in these figures can be found in Figs S8 and S9.

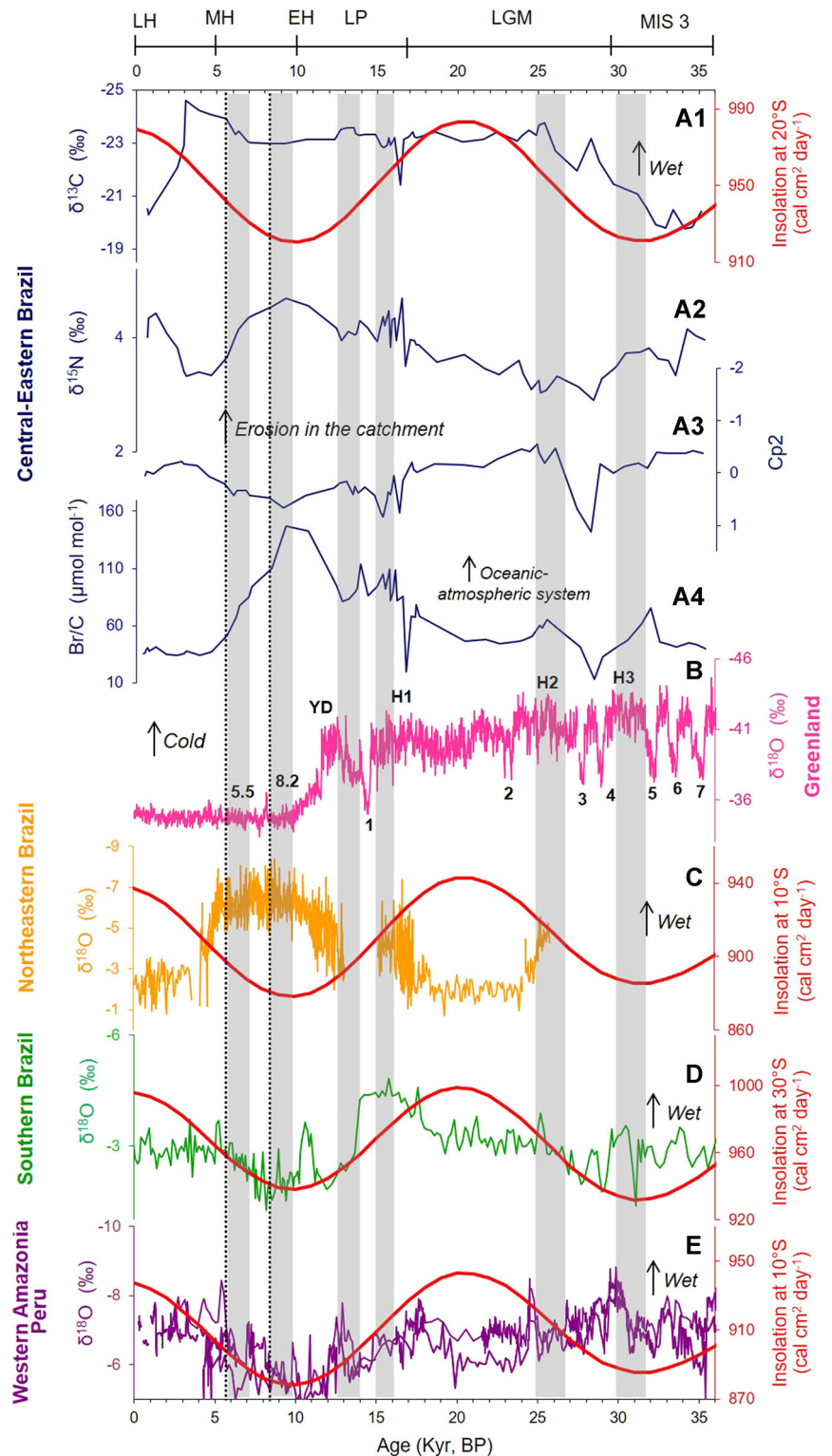


Figure 4. Comparison between South America records over the past 35 ka BP. (A1) $\delta^{13}\text{C}$; (A2) $\delta^{15}\text{N}$; (A3) Cp2; and (A4) Br/C ratio of the Pinheiro record, central-eastern Brazil. (B) Greenland ice (GISP2) $\delta^{18}\text{O}$ record (Grootes and Stuiver, 1997). (C) Rio Grande do Norte speleothem $\delta^{18}\text{O}$ record, north-eastern Brazil. (D) Botuverá speleothem $\delta^{18}\text{O}$ record, southern Brazil. (E) Western Amazonia speleothem $\delta^{18}\text{O}$ record, northern Peru. The red curves represent austral summer (DJF) insolation (ASI^{TM}) (Berger, 1978). Gray bars show periods of increased humidity in central-eastern Brazil. MIS 3 = Marine Isotope Stage 3; LGM = Last Glacial Maximum; LP = late Pleistocene; EH = early Holocene; MH = middle Holocene; and LH = late Holocene. [Color figure can be viewed at wileyonlinelibrary.com]

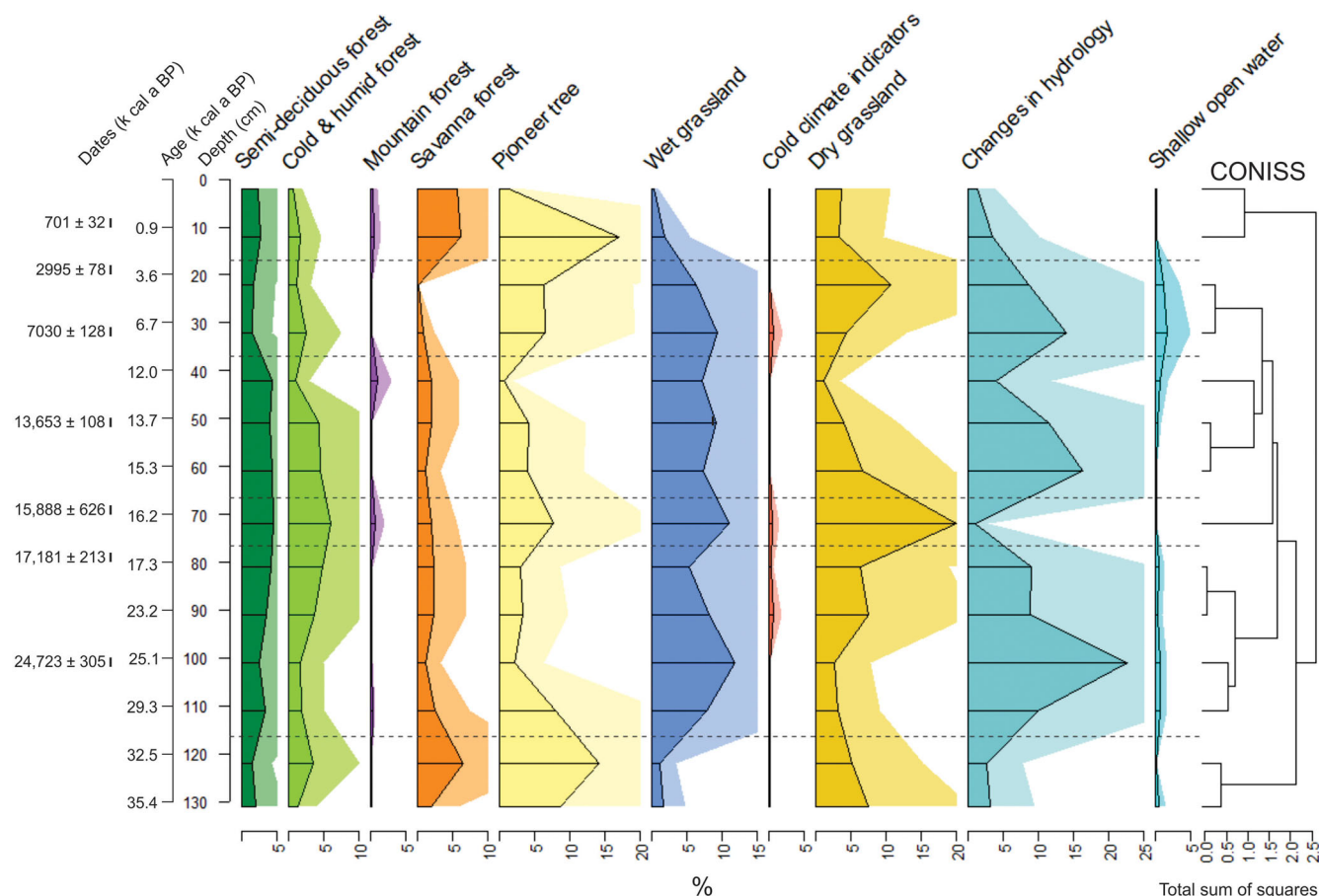


Figure 5. Distribution of the main taxa by type of vegetation or environment of the PI core. The silhouettes show the percentage curves, while shades show the 4x exaggeration curves. CONISS cluster analysis together with the Palynological Zones (separated by dashed lines) are plotted. Values are expressed as percentages of the total land pollen sum (TLP). [Color figure can be viewed at wileyonlinelibrary.com]

Factor loadings of the extracted components and the fractionation of communalities of the variables used in the PCA of the geochemical properties are provided in Fig. S3. Depth records of physical properties and elemental-isotopic composition of C and N (Fig. S4), major and minor elements (Supporting Information Fig. S5), trace lithogenic elements (Fig. S6), and trace metallic elements and halogens (Fig. S7) also used in the PCA.

The $\delta^{13}\text{C}$ values can be used to identify carbon derived from different photosynthetic pathways, because the isotopic ratio does not change with time (Cerling *et al.*, 1989). This ratio also provides information about source vegetation and climate dynamics, because C_3 plants (most trees and some graminoids of wet grasslands and indicators of humid environments) have $\delta^{13}\text{C}$ values between -32 and -22‰ , while C_4 plants (graminoids of dry environments) have ratios between -17 and -9‰ (O'Leary, 1988; Boutton, 1991). We might expect an 'in phase' trend when humidity increases, directly related by $\delta^{13}\text{C}$, in agreement with the increase in ASI, and an 'antiphase' when the increase in humidity is not directly related to ASI.

The main factors affecting the $\delta^{15}\text{N}$ ratio are: (i) the constant addition of organic matter from plants in the upper soil layers and (ii) transformations of organic-N to inorganic-N, and among inorganic-N forms. With increased mineralization, the remaining organic matter becomes enriched in ^{15}N (Schellekens *et al.*, 2014). In general, these processes occur during drier periods. In tropical soils, the values vary between $+3.5$ and $+21.7\text{‰}$, with much smaller variations in hydromorphic soils (between $\approx +4$ and $+5\text{‰}$) (Martinelli *et al.*, 2009).

The second PCA component (Cp2) based on geochemical properties is characterized by positive loadings of C, N, S (biophilic elements) and Br (organically bound element), and negative loadings of Si, Cr and K (lithogenic elements) (Supporting Information Fig. S2). Because the main geological material of the catchment of the mire is quartzite, the Si content is probably related to the amount of quartz transported from the catchment soils into the mire. Thus, Cp2 probably reflects a local signal: the mire accumulates organic matter (positive factor scores) under stable conditions in the catchment, while larger amounts of coarse mineral matter (i.e. quartz from the quartzite) are transported to the mire (negative factor scores) under unstable conditions (erosion episodes).

The oceans are the main source of Br, which reaches the peatland by wet deposition and accumulates as organohalogenated compounds (Biester *et al.*, 2006). Given the inland location of the Pinheiro mire, Br deposition may have been linked to atmospheric circulations bringing sea-spray and precipitation (Lalor, 1995). The Br/C ratio is used here to reflect the excess of Br that cannot be explained by a substrate effect (i.e. availability of organic matter for bromination) and thus infers changes in rainfall.

Chronology of environmental changes

Marine Isotope Stage 3 (MIS 3)

Although our record only shows the end of MIS 3, a cold phase in the Northern Hemisphere, it is noteworthy that a change in the climate pattern occurs from the first half (~ 35.0 to $\sim 31.8\text{ka}$)

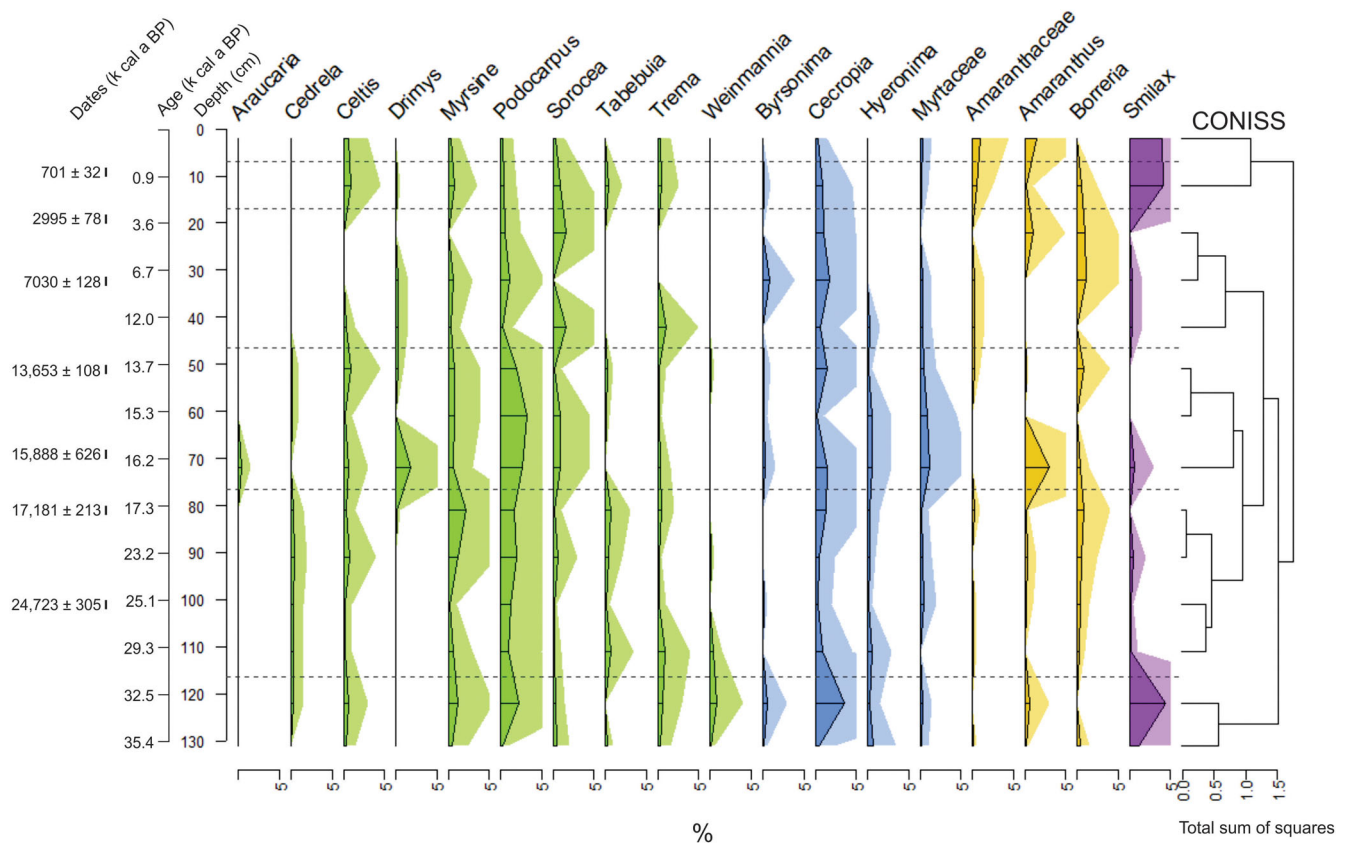


Figure 6. Synthetic regional (total land pollen sum) palynological diagram of the PI core. The silhouettes show the percentage curves of the taxa, while shades show the 4x exaggeration curves. CONISS cluster analysis together with the Regional Palynological Zones (RPZs; separated by dashed lines) are plotted. Values are expressed as percentages of the total land pollen sum (TLP). Green: trees; blue: trees/shrubs; yellow: herbs; and purple: lianas. [Color figure can be viewed at wileyonlinelibrary.com]

cal a BP) to the second half (~31.8 to ~29.6k cal a BP) and before the LGM. There was no speleothem deposition (formation) in caves in north-eastern Brazil during MIS 3 (Fig. 4C; Wang *et al.*, 2004; Cruz *et al.*, 2009). The D/O 7, 6 and 5 cycles (~34.6, ~32.9 and ~31.7k cal a BP, respectively) correspond to high $\delta^{13}\text{C}$ values in our record, indicating that long dry seasons (≥ 5 months) were particularly recurrent, as corroborated by high peat mineralization (high $\delta^{15}\text{N}$ values; Fig. 4A2). High levels of erosion from catchment soils (negative Cp2 values; Fig. 4A3) were probably triggered and facilitated by the reduction of seasonal forests (see for example *Cedrela*, *Celtis*, *Sorocea*, *Trema*, *Hyeronima* and *Myrtaceae*) and expansion of pioneer trees (*Cecropia*) (Figs 5 and 6), which reduced soil protection. Given these fluctuations, a dry climate is evident for MIS 3 in central-eastern Brazil, much drier in the first phase. However, climate was warm overall (*Byronima* and *Smilax*; representative of savanna) with some inter-dispersed cooling events (*Cedrela*, *Myrsine*, *Podocarpus* and *Weinmannia* taxa; all indicators of tropical coniferous forest related to mountainous and cold conditions), which are synchronous with the milder climate – relative short increases in humidity (as seen by fluctuations of the already mentioned taxa of seasonal forest), but still within a dry season (from 2 to 3 months, lasting <1000 years).

Last Glacial Maximum – mid-Holocene

With the onset of the LGM by ~29.6k cal a BP, a new pattern of climate conditions was established and remained until the early mid-Holocene (~6.1k cal a BP). Predominantly wet conditions are supported by the almost constant low $\delta^{13}\text{C}$ values (more negatives than in MIS 3; Fig. 4A1) and by the return of seasonal forest and expansion of cold and humid

forest (mainly represented by *Podocarpus*), as indicated by pollen data (Fig. 6) for H2, H1 and YD at ~25.3, ~15.8 and ~12.4k cal a BP, respectively, and beyond the ~8.2k cal a BP event. Catchment soil erosion increased with increasing humidity (Fig. 4A3), but it was relatively lower than during MIS 3, probably due to the denser tree–shrub vegetation cover (increasing trend of $\delta^{15}\text{N}$ values see-saw pattern suggesting a greater accumulation of organic material; Fig. 4A2). From ~29.6 to ~17.0k cal a BP, the increased humidity is simultaneous with an increase in southern Brazil and a decrease in north-eastern Brazil from ~26 to ~17.0k cal a BP. From ~16.0 to ~7.1k cal a BP, after the abrupt event of dry (*Amaranthus*, *Borreria* and *Gleichenia*; indicators of dry grassland) and very cold (highest percentage of *Drimys* and presence of *Araucaria*, both are tropical coniferous) conditions by ~16.4k cal a BP, humid conditions returned when humidity also increased in the north-east and decreased in the south as well as in western Amazonia (Fig. 4C,D,E). The Bølling–Allerød interstadial is coeval with the D/O 1 cycle and is registered as a slight reduction in precipitation by ~14.3k cal a BP, which coincides with an absence of speleothem deposition in north-eastern Brazil (Fig. 4C) and wet climate in the south (Fig. 4D). In that last phase, high oceanic–atmospheric activity with the highest Br/C ratios culminating by ~8.2k cal a BP (Fig. 4A4) provides evidence of the probably wettest period of the record, which agrees with records from north-eastern Brazil (Fig. 4C).

Mid- to Late Holocene

After ~6.1k cal a BP, periods of torrential rainfall probably started amid the driest (long dry season of ~6 months) and warm regional climate. Until ~3.1k cal a BP, seasonal, cold and

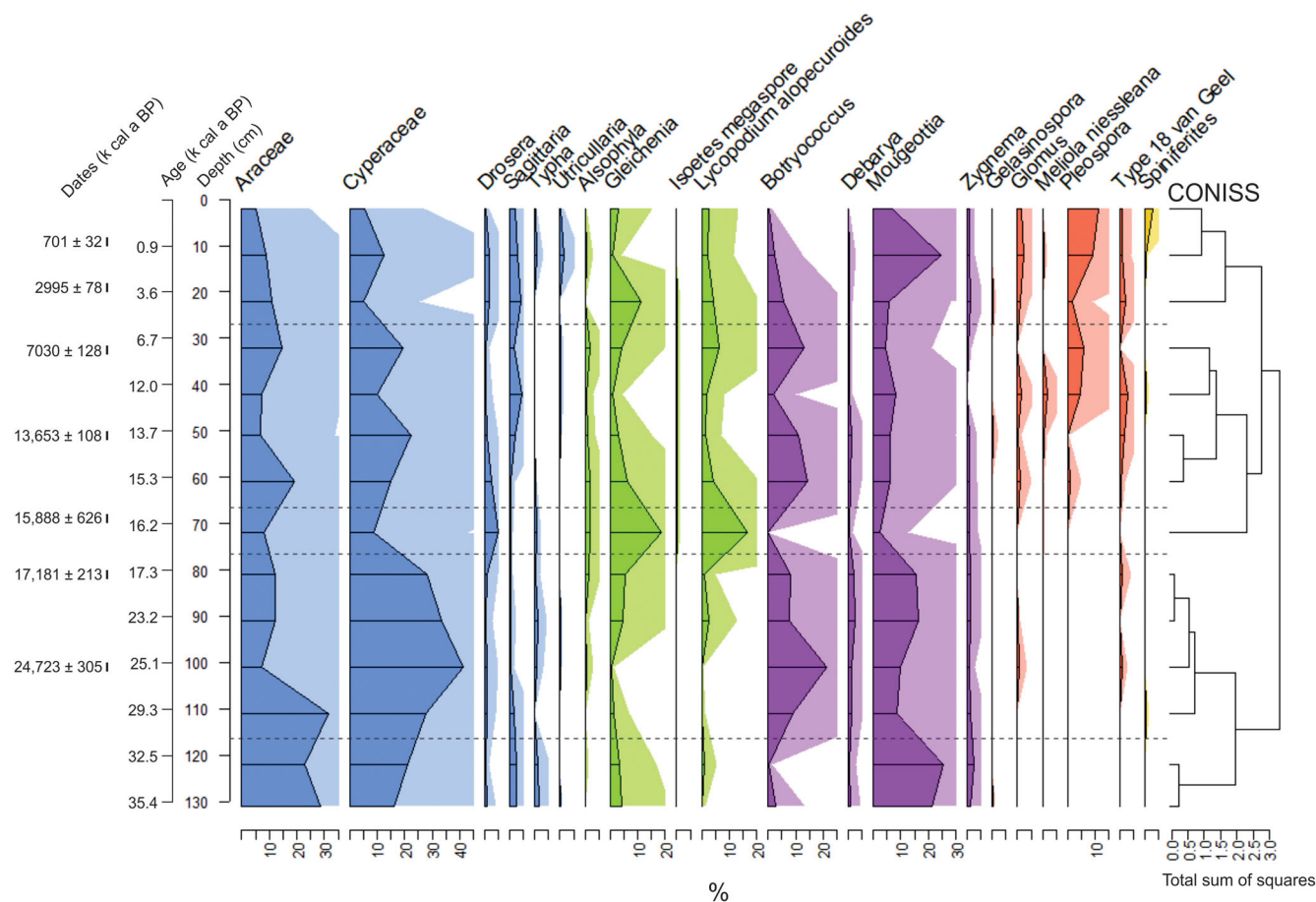


Figure 7. Synthetic local (hydro-hygrophytes and NPP) palynological diagram of the PI core. The silhouettes show the percentage curves of the taxa, while shades show the 4x exaggeration curves. CONISS cluster analysis together with the Local Palynological Zones (LPZs) are plotted. Values are expressed as percentages of the total land pollen sum (TLP). Blue: hydro-hygrophytes; green: pteridophytes; purple: algae; red: fungi; and yellow: dinoflagellates. [Color figure can be viewed at wileyonlinelibrary.com]

humid- and mountain-forests retracted as dry grassland expanded (e.g. *Amaranthus* and *Borreria*; Fig. 6) and point to a decrease in humidity, while an almost constant presence of wet grassland (*Drosera*, *Sagittaria*, *Utricularia*, HdV-18 van Geel; Fig. 7) suggests local (i.e. in the mire catchment) humid conditions. However, more seasonally distributed rainfall may have been abundant enough to create bodies of stagnant water on the Pinheiro mire (highest percentage of shallow open water indicators, such as *Mougeotia* and *Zygnema*; Figs 5 and 7), similar to a shallow lake and populated with species of wet grassland (C_3 plants; Fig. 4). An abrupt reduction of oceanic-atmospheric activity suggested by the Br/C ratios (Fig. 4A4), like that observed during MIS 3, supports the interpretation of prevailing dry climatic conditions. In this period, humidity also decreased in the north-east while an opposite trend is seen for southern Brazil and western Amazonia (Fig. 4C,D,E).

An abrupt change in $\delta^{13}C$ occurred again after ~ 3.1 k cal a BP, reaching its maximum value by AD ~ 740 (Fig. 4A1). The isotope ratios are comparable to those observed during MIS 3 and, together with indications of a decline in wet grasslands (Araceae, Cyperaceae, *Drosera*, *Typha*, *Utricularia*, and diverse NPPs such as *Meliola niessleana*; Fig. 7), a slight increase in dry grassland (*Amaranthus*, *Borreria*, *Gleichenia*, *Gelasinospora*, *Pleospora*; Figs 6 and 7) and increase in organic matter mineralization (Fig. 4A2), provide evidence of a decrease in local humidity. At the regional scale, the small increase in the seasonal, mountain and pioneer trees – with typical taxa of the conditions mentioned above (Fig. 6) – indicates a relative increase in humidity. However, this

period was probably warmer, as suggested by the expansion and stabilization of the savanna forest (Fig. 5), represented mainly by *Byrsonima*, *Tabebuia* and *Smilax* (Fig. 6). *Spinerites* (a dinoflagellate) is an indicator of warm waters (Price *et al.*, 2013) and its presence is consistent with a warmer climate (Fig. 7). The change to current conditions probably started during this time, with a strengthening of seasonality and a slight reduction of torrential rainfall events, facilitating the establishment of the Cerrado biome (i.e. dry season of ~ 4 – 5 months). Semi-arid conditions prevailed in the north-east, while southern Brazil and western Amazonia returned to humid and very humid climates, respectively, typical of today (Aziz Ab'Sáber, 2003).

The last ~ 740 years exhibit very minor variations suggesting no significant changes in climate. However, all pollen taxa representative of the range of vegetation communities gradually decrease, except for the dry grassland (*Amaranthus*, and in general the family *Amaranthaceae*; Fig. 6).

Discussion

Our findings demonstrate that the climate in central-eastern Brazil has undergone several significant changes during the last ~ 35 k cal a BP, mainly related to rainfall variability, but also, to some extent, to temperature variations as inferred from vegetation dynamics. Consequently, these changes are also reflected in different landscape conditions. Five main phases could be established: (C I) ~ 35.0 to ~ 29.6 k cal a BP – the climate was dry and warm with cooling events and some

landscape instability; (C II) ~29.6 to ~16.9k cal a BP – wet and (C III) ~16.9 to ~6.1k cal a BP – very wet, both very cold and with reduced landscape instability; (C IV) ~6.1 to ~3.1k cal a BP – very dry and warm with increasing catchment instability; and (C V) < ~3.1k cal a BP – from dry and warm to sub-humid climate (Fig. 8).

The low humidity during MIS 3 suggested by our data coincides with the expansion of sea-ice and very low temperatures in the northern hemisphere (Heinrich, 1988; Dansgaard *et al.*, 1993; Grootes and Stuiver, 1997; Fig. 4B). These conditions may have resulted in the displacement of the ITCZ and, consequently, also the SACZ to a southward position (Fig. 8), leading to an increase in monsoon rainfall activity mainly in the south (Wang *et al.*, 2004). The northern limit of the SACZ was probably located south of our study area, more than several hundred kilometers away from its present northern limit (Fig. 1). Millennial-scale rainfall variability is the dominant control during MIS 3, but increased rainfall is also possibly related to the strengthening of the SAMS resulting from high summer insolation in certain periods, and apparently in phase with $\delta^{13}\text{C}$ and ASI (Fig. 4A1).

During the last precession cycle (the last ~17 ka) strong convective activity and upward motion resulted in enhanced condensational heating over the western Amazon Basin when ASI was high, which in turn intensified the upper-tropospheric Nordeste low and resulted in large-scale subsidence and humidity reduction over eastern equatorial South America (Cheng *et al.*, 2013). According to these authors, this is the east–west dipole-like pattern of precipitation changes, also called the South American precipitation dipole (SAPD). It is also seen in our record from the beginning of the late Pleistocene to the

present, particularly after the ~16.9k cal a BP event, in alignment with the same trends in north-eastern Brazil, including an antiphase with ASI (Fig. 8). This means that the increased precipitation occurred during weak monsoon seasons when ASI was low after ~16.9k cal a BP when precipitation was related to insolation. However, it is not yet clear if orbital-scale variability is the dominant control on precipitation after the H1 and YD events. In the northern hemisphere, abrupt temperature increases may have caused changes in the Atlantic meridional overturning circulation and SACZ location, with the latter possibly shifted northward providing more humidity to central-eastern Brazil.

The SAPD can be probably applied to the LGM with some consistency as seen in records from other regions (Cheng *et al.*, 2013). However, the relationship is in phase for our study area, or the effect of precession was probably significantly reduced at the millennial scale, in periods when temperatures in the northern hemisphere began to slightly increase and SACZ was starting to shift northward.

Our study shows climate forcing operating at different time-scales. During the last ~16.9k cal a BP, orbital-scale variability is the dominant control, or both millennial- and orbital-scale variability act together suggesting a common forcing. This mechanism is particularly important for tropical precipitation, as during these times changes in the eccentricity of the Earth's orbit promoted the modification to precessional forcing – hereafter defined as the 'precessionally forced' or 'orbitally forced' changes in insolation – with predominant periods at 19 and 23 ka (Liu and Battisti, 2015). However, the millennial-scale variability is expressed through all the ~35k cal a BP record, to a greater or lesser extent, which allows us to track the swings of the SACZ (Fig. 8): SACZ I – it shifted to a southward position in MIS 3, very

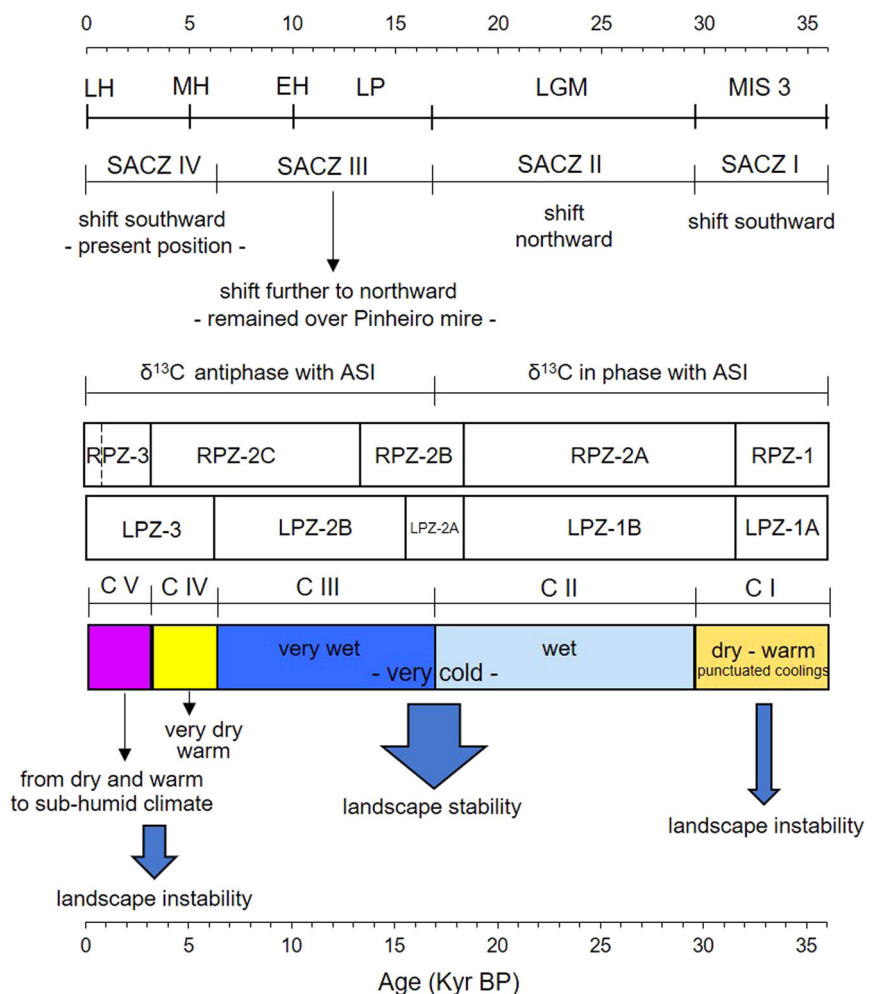


Figure 8. Chronology of Pleistocene environmental changes recorded in the PI core. MIS 3 = Marine Isotope Stage 3; LGM = Last Glacial Maximum; LP = late Pleistocene; EH = early Holocene; MH = middle Holocene; and LH = late Holocene. ASI = austral summer insolation. SACZ I to SACZ IV: swings of the South Atlantic convergence zone (SACZ). RPZ and LPZ are palynozones of regional and local vegetation, respectively. C I to C V: phases of environmental change. Orange: dry; yellow: very dry; light blue: wet; dark blue: very wet; and purple: sub-humid climatic. [Color figure can be viewed at wileyonlinelibrary.com]

near to Botuverá cave in Santa Catarina state (number 3, Fig. 1); SACZ II – a northward shift during the LGM, with a northern limit probably located near or within the location of the Pinheiro mire in Minas Gerais state (number 1, Fig. 1); SACZ III – a shift further northward, remaining stable for all this time over the Pinheiro mire from LP to MH (until ~6.1k cal a BP), with all the band within the central-eastern Brazil; and SACZ IV – a return to a southward position. Today, the SACZ is located between the central-eastern and south-eastern regions of Brazil (20–40°S and 50–20°W) (Barreiro *et al.*, 2002).

The precipitation pattern for central-eastern Brazil reconstructed in this study is out of phase with western Amazonia and, apparently, with southern Brazil (Cheng *et al.*, 2013). For southern Brazil, some periods of increased humidity appear to coincide with those found in our record. For the north-east, our record is in phase from ~35 to ~26k cal a BP (considering the absence of speleothem deposition), out of phase from ~26 to ~16.9k cal a BP, and in phase again after ~16.9k cal a BP.

The current sub-humid climatic conditions and predominant Cerrado biome vegetation seem to be relatively recent, probably established after ~3.1k cal a BP, although similar conditions may have been present in MIS 3, mainly between ~35.0 and ~29.6k cal a BP. Pollen records from Lagoa de Serra Negra (De Oliveira, 1992) and Lagoa Santa (Parizzi, 1993) also showed the expansion of the Cerrado elements during the late Holocene, suggesting favorable conditions for this biome. Similarly, Werneck *et al.* (2012) also verified the expansion of the Cerrado in this period by investigating the historical distribution of the Cerrado across Quaternary climatic fluctuations. Today, semi-deciduous (seasonal) and mountain (cold) forests, so-called Capões, are relicts of wetter climates, indicating long-term climate variability during the Quaternary, as they were much more developed in the past, especially between ~29.6 and ~6.1k cal a BP. During the mid-Holocene, a more humid climate was also prevalent in other current areas of the Cerrado, as in Águas Emendadas (Barberi *et al.*, 2000) and Crominia palm swamp (Ferraz-Vicentini and Salgado-Labouriau 1996; Barberi *et al.*, 2000). This can be considered as key information on the origin of tropical plant biodiversity.

Pinheiro mire certainly contains a sensitive record of climate variability when compared to other records (mires, speleothems, lake and marine sediments) from previous studies (Fritz *et al.*, 2007; Strikis *et al.*, 2015), which is mainly due to its position being influenced by the constant fluctuation and displacement of the SACZ.

Conclusions

Our multi-proxy investigation of the Pinheiro mire (PI core) enhances knowledge of the relationship between past climate and vegetation change in central-eastern Brazil. We show environmental and climate changes from the late Pleistocene at millennial and orbital timescales and the displacements of the SACZ. Our work contributes to the controversial debate about the nature of climate during the LGM and mid-Holocene (between ~29.6 and ~6.1k cal a BP), which were not dry for the studied region. By contrast, we suggest that these periods were the most humid of the last ~35k cal a BP.

The current vegetation on the Pinheiro mire has taxa that were part of the vegetation of past periods. These taxa attest to past climatic conditions, such as the presence of trees and shrubs with thick bark and tortuous trunks typical of savanna in more drier periods, as seen almost constantly during MIS 3, and even the modern forest islands – the Capões – with typical taxa that resemble the forest of very wet climates were present

since the LGM up until the mid-Holocene. However, it is important to note that the taxa were rearranged during the Quaternary and the communities readjusted by undergoing some modification, mainly due to changes in climate.

Thus, the Pinheiro mire proved to be an insightful archive of past changes, showing its high scientific importance – a good reason for its preservation.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1. Age–depth model of the PI core fitted with Bacon (Blaauw and Christen, 2011) using the dating for the peat samples of the upper 1 m of the core (blue) and Northern Hemisphere calibration curve (IntCal13).

Figure S2. Records of factor scores of the three components of PCA (Cp1, Cp2, and Cp3) for the geochemical composition of the PI core.

Figure S3. Factor loadings for the three components and fractionation of communalities of the variables used in the PCA of geochemical properties of the PI core. The communality of each variable (i.e. the proportion of its variance explained by each component) corresponds to the total length of the bar, and the sections of the bars represent the proportion of variance in each component. The variables are ordered by the component with the largest share of variance. ¹Eigen: eigenvalues; ²Var (%): percentage of explained variance; ³Var_ac: cumulative explained variance.

Figure S4. Contents (%) of ash, fiber, C and N; BD (bulk density; mg m⁻³); and δ¹³C and δ¹⁵N (‰) of the PI core.

Figure S5. Concentrations (g kg⁻¹) of Si, Al, Fe, Ti, K, Ca, S and P of the PI core.

Figure S6. Concentrations (µg g⁻¹) of Ga, Rb, Sr, Zr, Y and Nb of the PI core.

Figure S7. Concentrations (µg g⁻¹) of Mn, Th, Cr, Pb, Cl and Br of the PI core.

Figure S8. Regional (total land pollen sum) palynological diagram of the PI record with taxa not included in Fig. 6. The silhouettes show the percentage curves of the taxa, while shades show 14x (Fig. S8A) and 12x exaggeration curves (Fig. S8B). CONISS cluster analysis together with the Regional Palynological Zones (RPZ; separated by dashed lines) are plotted. Values are expressed as percentages of the total land pollen sum (TLP). In A: green: trees; blue: trees/shrubs; and purple: shrubs. In B: yellow: herbs; light blue: lianas; and red: diversives.

Figure S9. Local (hydro-hygrophytes and NPP) palynological diagram of the PI record with taxa not included in Fig. 7. The silhouettes show the percentage curves of the taxa, while shades show 10x exaggeration curves. CONISS cluster analysis together with the local palynological zones (LPZ; separated by dashed lines) are plotted. Values are expressed as percentages of the total land pollen sum (TLP). In A: blue: hydro-hygrophytes; light blue: bryophytes; and green: pteridophytes. In B: purple: algae; red: fungi; and yellow: dinoflagellates.

Table S1. Results of ¹⁴C dating of the PI core, showing conventional age in BP and calibrated ages (2σ) in cal a BP.

Table S2. The maximum number of total land pollen (TLP) and hydro-hygrophytes and non-pollen palynomorphs (NPP) of the PI core.

Table S3. Pollen and other non-pollen palynomorphs (NPP) observed in the PI core, their habit, coverage and belonging phytophysiognomy, or probable environmental indicator.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Abbreviations. ASI, Austral summer insolation; ITCZ, Intertropical Convergence Zone; LGM, Last Glacial Maximum; MIS, Marine Isotope Stage; NPP, non-pollen palynomorphs; PCA, principal component analysis; SACZ, South Atlantic Convergence Zone; SAMS, South American Monsoon System; SAPD, South American precipitation dipole; TLP, total land pollen; YD, Younger Dryas.

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