Late Quaternary vegetation and climate dynamics in central-eastern 1 Brazil: insights from a ~35k cal a BP peat record in the Cerrado 2 biome 3 Short running title: Late Quaternary vegetation and climate in central-4 eastern Brazil 5 INGRID HORÁK-TERRA1*, ANTONIO MARTÍNEZ CORTIZAS², CYNTHIA FERNANDES 6 PINTO DA LUZ³, ALEXANDRE CHRISTÓFARO SILVA⁴, TIM MIGHALL⁵, PLÍNIO 7 BARBOSA DE CAMARGO⁶, CARLOS VICTOR MENDONCA-FILHO⁷, PAULO EDUARDO 8 DE OLIVEIRA⁸, FRANCISCO WILLIAN CRUZ⁸, PABLO VIDAL-TORRADO⁹ 9 10 ¹Instituto de Ciências Agrárias, Universidade Federal dos Vales do Jequitinhonha e Mucuri - ICA/UFVJM, BR 251 Av. 11 Universitária, 1000, Universitários, 38610000, Unaí, MG, Brazil; ingrid.horak@ufvjm.edu.br. 12 ²Eco-Past (GI-1553), Faculty of Biology, Universidade de Santiago de Compostela - USC, Santiago de Compostela, 15782, Spain; 13 antonio.martinez.cortizas@usc.es. 14 ³Núcleo de Pesquisa em Palinologia, Instituto de Botânica, Secretária de Infraestrutura e Meio Ambiente do Estado de São Paulo -15 IBt/SP, São Paulo, SP, 04301902, Brazil; cyluz@yahoo.com.br. 16 ⁴Departamento de Engenharia Florestal, Universidade Federal dos Vales do Jequitinhonha e Mucuri - UFVJM, Diamantina, MG, 17 39100000, Brazil; alexandre.christo@ufvjm.edu.br. 18 ⁵School of Geosciences, University of Aberdeen, Aberdeen, G22 St Mary's, UK; t.mighall@abdn.ac.uk. 19 ⁶Laboratório de Ecologia Isotópica, Centro de Energia Nuclear na Agricultura - CENA/USP, Piracicaba, SP, 13416-903, Brazil; 20 pcamargo@cena.usp.br. 21 ⁷Departamento de Ciências Biológicas, Universidade Federal dos Vales do Jequitinhonha e Mucuri - UFVJM, Diamantina, MG, 22 39100000, Brazil; cvmendonca@gmail.com. 23 ⁸Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências – IGc/USP, São Paulo, SP, 05508-080, Brazil; 24 paulo.deoliveira@usp.br; cbill@usp.br.

⁹Departamento de Ciência do Solo, Escola Superior de Agricultura "Luiz de Queiroz" – ESALQ/USP, Piracicaba, SP, 13418900,
Brazil; pvidal@usp.br.

27 *Corresponding author. Instituto de Ciências Agrárias, Universidade Federal dos Vales do Jequitinhonha e Mucuri – ICA/UFVJM,

28 BR 251 Av. Universitária, 1000, Universitários, 38610000, Unaí, MG, Brazil, E-mail addresses: ingrid.horak@ufvjm.edu.br,

29 ingridhorak@yahoo.com.br (I. Horák-Terra).

ABSTRACT: The late Quaternary evolution of central-eastern Brazil has been under-researched. 30 31 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. 32 We investigated the factors that influenced the expansion and contraction of the Cerrado and 33 Capões during the late Quaternary (last ~35 ka), using a multi-proxy approach: stable isotopes 34 $(\delta^{13}C, \delta^{15}N)$, geochemistry, pollen, and multivariate statistics derived from a peat core (Pinheiro 35 mire, Serra do Espinhaço Meridional). Five major shifts in precipitation, temperature, vegetation 36 and landscape stability occurred at different timescales. Our study revealed that changes in the 37 South Atlantic Convergence Zone (SACZ) seem to have been coeval with these shifts: from late 38 glacial maximum to mid-Holocene the SACZ remained stationed near (~29.6 to ~16.5k cal a BP) 39 and over (~16.5 to ~6.1k cal a BP) the study area, providing humidity to the region. This challenges 40 previous research which suggested that climate was drier for this time period. At present, the 41 Capões are likely to be a remnant of a more humid climate; meanwhile, the Cerrado biome seems to 42 have stablished in the late Holocene, after ~3.1k cal a BP. 43

44 KEYWORDS: Paleoclimatology; Stable isotopes; Pollen; Geochemistry; Peatlands.

45 Introduction

46 Central-eastern Brazil, with a sub-humid and seasonal climate and well-defined seasons (~4-47 5 months of dry season and mean winter temperature $\geq 15^{\circ}$ C), maintains the Cerrado biome, which 48 is a vast tropical savanna and part of the so-called "xeric vegetation" corridor (Bucher, 1982). This 49 tropical savanna is characterized by large diversity of phytophysiognomies and high levels of 50 endemism, and quite specific vegetation patterns are found in certain regions, such as the Serra do 51 Espinhaço Meridional (Minas Gerais state). Here small vegetation islands, called "Capões" (also 52 "florestas em mancha" by Rizzini, 1979), are characterized by tree and shrub species of semi-53 deciduous forest (with double climatic seasonality) and mountain forests (mean winter temperature 54 $< 10^{\circ}$ C; Ledru, 1993) dispersed among grassland formations.

The response of tropical biomes to climate change has been the focus of investigations 55 covering the last glacial maximum (LGM; peaked 21.5 ka) and mid-Holocene (MH; 5 ka) 56 57 (Colinvaux et al., 1996; Ledru et al., 2009; Bueno et al., 2016; Arruda et al., 2017; Pinaya et al., 2019). However, none of them were performed in the Cerrado biome, specifically in the Serra do 58 59 Espinhaço Meridional. Therefore, palaeorecords and Pleistocene reconstructions are absent from 60 this area and this is one of the main reasons for undertaking this study. Several earlier studies have challenged established hypotheses, such as Amazonian refugia (Haffer, 1969) and Pleistocene arc 61 hypotheses (Prado and Gibbs, 1993), which assert that aridity was prevalent in the Cerrado biome 62 during these periods. More recent research has questioned this interpretation, stating that the humid 63 forest of the Amazon region was already present in the LGM (Colinvaux et al., 1996; Haberle and 64 Maslin, 1999; Leite et al., 2016; Arruda et al., 2017). Additionally, the spatial distribution of 65 seasonal biomes was larger during the Holocene compared to the LGM, helped by improved recent 66 climatic conditions (Werneck et al., 2011; Horák-Terra et al., 2015). 67

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 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, since a vast dense forest should cover the approximately 2 million km² of the Brazilian territory if this idea was true. Similarly, there are other unsolved questions such as: are the present occurrence 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?; and was there a time when the area now occupied by the Cerrado served as 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), since it is bordered by almost all other biomes today. However, paleoclimate data of central-eastern Brazil are still 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.

86 Supported by the interhemispheric anti-phase behavior, the Younger Dryas (YD)-Heinrich (H) and the Dansgaard-Oeschger (D/O) events respectively expressed in South America as wet and 87 dry episodes (Cheng et al., 2013). The YD occurred by 12.9-11.7 ka, while the H and D/O were 88 characterized by a series of events (10 and 25 events respectively) during the last glacial period. 89 The abrupt increase in monsoon rainfall during the YD-H events was likely related to a southward 90 shift in the average position of the Intertropical Convergence Zone (ITCZ), a strengthening of the 91 asymmetry in Hadley circulation in response to an interhemispheric gradient of sea surface 92 temperature, and a possible influence of Antarctic climate changes (Wang et al., 2004, 2006; 93 Kanner et al., 2012; Cheng et al., 2013). Despite this coherent pattern of millennial-scale 94 variability, the spatial structure of precipitation is complex at orbital timescales (Wang et al., 2006). 95 96 For instance, it is known that northeastern Brazil experienced humid conditions during low summer insolation phases and aridity conditions when summer insolation was high, whereas the rest of 97 southern tropical South America showed an opposite behavior (Cheng et al., 2013). Thus, obtaining 98

99 accurate information about the past climate of central-eastern Brazil is important, mainly due to its 100 strategic location. This region is deeply influenced by the South Atlantic convergence zone (SACZ) 101 during the austral summer, resulting in increasing precipitation from November to March (Garreaud 102 *et al.*, 2009), when it extends into a southeastern direction from the interior of the continent to the 103 South Atlantic (Vera *et al.*, 2006).

Tropical and subtropical peatlands are ideal archives for reconstructing climate changes 104 from the late Pleistocene - i.e. from 126 ka (Weiss et al., 2002; Muller et al., 2008; Ledru et al., 105 106 2009; Dommain et al., 2011; Swindles et al., 2018), since they are extremely sensitive to changes in hydrology. For example, Horák-Terra et al. (2015) investigated a peat core from Pau de Fruta mire, 107 108 located in the Serra do Espinhaço Meridional (Brazil), using a combination of biotic (pollen) and 109 abiotic (peat physical properties, elemental and isotopic composition) proxies to trace Holocene 110 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 111 the catchment, regional dust deposition, changes in peat plant communities and degree of peat 112 decomposition (Horák-Terra et al., 2014). Similarly, we present results from a core (PI, 130 cm 113 deep) spanning the last ~35k cal a BP, and taken from a tropical mountain peatland (Pinheiro mire) 114 from Serra do Espinhaço Meridional. The same core was also investigated for mercury (Pérez-115 Rodríguez et al., 2015, 2016). This research showed that variations in Hg concentrations were most 116 likely driven by climate, either indirectly by enhancing the mineral matter fluxes from the mire's 117 catchment (i.e. increased soil erosion) and regional dust deposition, or directly by long-term 118 changes in atmospheric wet deposition (humid vs arid phases). So, this core presents a unique 119 opportunity for a detailed investigation to reconstruct climate change in central-eastern Brazil since 120 the late Pleistocene, taking into account the existence of autogenic changes in Pinheiro mire by 121 multiple mechanisms as cited above. 122

We present inferences about past environmental conditions in central-eastern Brazil during 123 the ~35k cal a BP using a multi-proxy data including stable isotopes (δ^{13} C, δ^{15} N), geochemistry 124 (major, minor, and trace elements), and pollen records (pollen, spores, and other non-pollen 125 palynomorphs). From these data, reconstructions of changes in precipitation, temperature, 126 vegetation, and landscape stability occurring at different timescales allowed us to achieve our main 127 aims: (1) to obtain accurate information about the past climate of central-eastern Brazil, and (2) to 128 reconstruct the vegetation history and the conditions culminating in the formation of the current 129 biome. Our study is one of the most complete for central-eastern Brazil. The data can also be used 130 to predict future conditions through climate models, as well as for comparing with other 131 paleoclimatic and paleoecological records from different regions in Brazil and globally. 132 Furthermore, our research highlights the value of such data for conservation of tropical peatlands 133 and Cerrado biome, due to their environmental and ecological importance. 134

135 Materials and methods

136 Regional setting

The PI core was collected from the Pinheiro mire (18°3'44.42" S 43°39'42.37" W), a 137 tropical mountain peatland located at ~1240 m a.s.l. in the Serra do Espinhaço Meridional, Minas 138 Gerais state (Brazil) (Fig. 1 and Figs. 2A and 2B). Pinheiro is an oligotrophic valley mire located in 139 a catchment with limited drainage. The catchment is narrow (0.1 to 0.6 km wide) and elongated 140 (~3.7 km long) in a SW-NE direction, and the mire covers the lower and flatter parts of the valley 141 overlaying quartzitic sediments. The Pinheiro mire is also a soligeneous peatland: it is affected by 142 water from external sources percolating through or over surface peat. Today, the peat is mostly 143 144 formed by graminoid species, among them grasses and sedges. The basal lithology is part of the Galho do Miguel formation, constituted by pure and thin quartzites (~90%), thin micaceous 145 quartzites and some gray or greenish metargilites (~5 a 10%; Knauer, 2007). 146

At present, the climate of the area is tropical montane with mean annual temperature of 18.7 At present, the climate of the area is tropical montane with mean annual temperature of 18.7 and mean annual precipitation about 1500 mm - period 1950 to 1990 (Alves 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 characterised by extensive, open grasslands (wet, dry, and rupicola-saxicolous), with a limited presence of trees and shrubs. However, it also contains the "Capões" (with semi-deciduous forest and mountain forest species), which appear as small, dispersed forest islands (Figs. 2A and 2B). Currently, the Pinheiro area is quite well preserved, since access for the locals living in the surrounding villages is difficult. However, there are reports of some natural bushfires during the driest times of the year.

157 Sampling and stratigraphic description

The core was sampled in 2010 using a vibracore (constructed according to Martin et al., 158 1995) to a depth 324 cm. However, as this paper mainly deals with changes in environment and 159 climate for the LGM - mid-Holocene, we have decided to only present the upper 130 cm, which 160 span the last ~35ka. The stratigraphy was described according to the Field Book for Describing and 161 Sampling Soils (Schoeneberger et al., 1998) and the Guidelines for Soil Description (FAO, 2006), 162 163 whereas the horizons were defined according to the Soil Taxonomy (Soil Survey Staff, 2010). The upper 130 cm is composed of 5 peat horizons (Oi, Oa, Oa2, Oa3, and Oa4), defined by the content 164 165 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, 166 differing only in fine roots content (greater in Oa4 than in Oa3); horizons Oa2 (58-20 cm) and Oa 167 (20-8 cm) are also similar, both with abundant fine roots and highly sticky; and the uppermost layer, 168 Oi (8-0 cm), is a fibric horizon of poorly decomposed peat. The core was sliced into continuous 2 169 cm-thick sections. 170

171 Age-depth model of the core

Seven peat samples (Supplementary Table S1) were radiocarbon dated by AMS in Beta 172 Analytic Inc. (Miami, USA); the analyses were done on the acid-alkaline-acid extraction of bulk 173 174 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) (Figure 3). The calibration curve was 175 SHCal13.14C (Hogg et al., 2013). Based on the hypothesis that Northern Hemisphere air masses 176 may have been the main source of humidity for the area in the late Quaternary, we also performed 177 the age model using the NH calibration data set (IntCal13; Supporting Fig. S1). Since the results 178 indicated that the models are in close agreement, with very close ages, we present the chronologies 179 with the model obtained with the Southern Hemisphere calibration curve here. The model was fitted 180 by assigning the year of sampling as age of the upper peat sample and no smoothing was applied. 181 182 All ages presented in the text are expressed as calibrated ages.

183 Elemental and isotopic composition

Carbon and nitrogen contents and isotopic composition - δ^{13} C and δ^{15} N - were determined in 184 dried, milled, and homogenized peat samples, using an elemental analyzer coupled to a mass 185 spectrometer hosted in the Laboratório de Ecologia Isotópica of the Centro de Energia Nuclear na 186 Agricultura - CENA/USP (Piracicaba, SP, Brazil). Major, minor and trace elements (P, S, Al, Si, 187 Fe, Ti, K, Ca, Ga, Rb, Sr, Y, Zr, Nb, Th, Cr, Mn, Ni, Cu, Zn, As, Pb, Cl, and Br) were determined 188 by X-ray fluorescence in the same samples using two energy dispersive XRF analyzers (Cheburkin 189 and Shotyk, 1996; Weiss et al., 1998) hosted in the RIAIDT facility (Infrastructure Network for the 190 Support of Research and Technological Development) of the Universidade de Santiago de 191 Compostela (Spain). 192

193 Instrument calibrations were performed for organic matrices using several reference 194 materials (NIST 1515, 1541, 1547, and 1575; BCR 60 and 62; and V-1). Detection limits were: 195 <100 μ g g⁻¹ for Al, Si, S, K, Ca, and Fe; 50 μ g g⁻¹ for P; 10 μ g g⁻¹ for Mn; 5 μ g g⁻¹ for Ti; 10 μ g g⁻¹ 196 for Cl; 1 μ g·g⁻¹ for Cr, Ni, Cu, Zn, Br, Ga, Rb, Sr, As, Y, Zr, Th, Pb, and Nb. One in every five 197 samples was analyzed in triplicate, and the measurements agreed within a 5% for most elements. 198 Values that did not agree within 10% were rejected (in this case, more replicates were done).

199 Pollen study

For the pollen study, 13 wet samples of 1 cm in thickness taken every 10 cm were obtained 200 from the center of the PI core. A modified version of the physico-chemical treatment (Ybert et al. 201 1992) extracted pollen, spores, and other non-pollen palynomorphs (NPP). Hydrofluoric acid was 202 added for the dissolution of silicates, hydrochloric acid for elimination of fluorosilicates, acetic acid 203 for dehydration and acetolysis mixture for dissolution of the organic matter and acetylation of the 204 exine. Ultrasound was used to separate large organic remains. The counting was undertaken at 400 205 X under microscope (Supplementary Table S2), obtaining an average total land pollen sum (TLP) 206 207 of 800 terrestrial pollen grains per sample. Hydro-hygrophytes and NPP were not included in the TLP, but they were expressed as percentages of it. The average sum of hydro-hygrophytes and NPP 208 was 560 palynomorphs. Identification was helped by the reference collection (modern pollen 209 deposition) of the Pau de Fruta mire (Horák, 2009; Horák et al., 2015; Luz et al., 2017), 210 identification keys, and atlases (van Geel, 1978; Tryon and Tryon, 1982; Roubik and Moreno, 211 1991). Taxa included in the TLP are considered indicators of regional vegetation, while hydro-212 hygrophytes and NPP are mainly considered to constitute a local signal. The NPP can be mostly 213 considered as local indicators since their dispersal is limited (Salgado-Labouriau, 2007); however, 214 the case of the hydro-hygrophyte taxa, e.g. Cyperaceae, is more complex, as they could also be part 215 of the regional communities (Horák-Terra et al., 2015). Pinheiro is a valley mire and variations in 216 the water table depth could be responsible for differences in the spatial distribution of local plant 217 218 communities. For this reason, we added the hydro-hygrophytes in the local signal. Pollen diagrams were obtained in the R software using Rioja package (Juggins, 2019). 219

Groups corresponding to the types of vegetation and environments were obtained (Fig. 5) 220 and based on the ecological preferences of the identified taxa (Figs. 6 and 7, Supporting Figs. S8, 221 S9, S10, and S11). The knowledge of each taxa is based on the detailed botanical survey of the 222 Pinheiro mire and of other peatlands from the region (all materials are cataloged in the DIAM 223 Herbarium of the Universidade Federal dos Vales do Jequitinhonha e Mucuri - UFVJM, Diamantina 224 city, Minas Gerais state, Brazil), but also used several other references when necessary (van Geel, 225 1978; Guy-Ohlson, 1992; Mendonça et al., 1998; Marchant et al., 2002; Luz et al., 2017). The 226 Supplementary Table S3 contains all identified taxa and their respective habit and coverage regional 227 or local information, as well as indicating their phytophysiognomy or preferred environmental 228 229 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 230 not be exclusive of one habitat and cannot be associated exclusively to one type of vegetation or 231 environment. We also take into account the concept of "non-analogous community" and, therefore 232 we assume that plant communities are not fixed through time (Williams and Jackson, 2007; Keith et 233 al., 2009), and that species respond individualistically to climate change. So, the floristic 234 composition of vegetation changed through time, probably occurring a certain dynamic (or, a 235 rearrangement) of the different taxa within each group. 236

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 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. And, finally, no dry season was considered for mountain forest (encompassing cold and humid forest).

243 Statistical analysis

Stratigraphically constrained cluster analysis (total sum of squares method; Grimm, 1987) 244 was applied to pollen and NPP/hydro-hygrophyte data to define regional and local palynological 245 zones, using the broken stick model to find the appropriate number of zones. For geochemical data, 246 principal component analysis (PCA) was performed on the data matrices (these data can be seen in 247 Supporting Figs. S3-S7) after log-transformation and standardization (as suggested for 248 compositional data, i.e., close data sets; Reimann et al., 2008) in correlation mode and applying a 249 varimax rotation to maximize the variable loadings in the components (Eriksson et al., 1999). PCA 250 was performed using SPSS 20.0 software. 251

252 Supporting studies

The δ^{18} O curve from a Greenland ice record (Grootes and Stuiver, 1997) was included in 253 this study, showing the typical sequence of stadial (YD + H1 to H3, at the top of the Fig. 4B) and 254 interstadial (D/O cycles, from 1 to 7 at the bottom of the Fig. 4B) periods. For comparison, δ^{18} O 255 records of speleothems from northeastern (Cruz et al., 2009; Fig. 4C) and southern Brazil (Cruz et 256 al., 2005; Fig. 4D) and western Amazonia (Cheng et al., 2013; Fig. 4E) are also included, as well as 257 the Austral summer insolation (ASI) curve (Berger, 1978; in red). The oxygen isotope ratios are 258 mainly interpreted as a function of the isotopic composition of rainfall, therefore as indicative of 259 past precipitation, where more negative δ^{18} O values are associated with intense SAMS regime 260 (Wang et al., 2004, 2006) or wet climate conditions (Cheng et al., 2013). The ASI can be used to 261 examine the impact of orbital forcing, defined as the combined effects of precession and 262 263 eccentricity (Berger, 1978) on central-eastern Brazilian climate. Changes in Earth's orbit around the sun cause quasi-periodic changes in insolation reaching the top of the atmosphere (Liu and Battisti, 264 2015). 265

266 **Results**

267 **Proxies: meaning and interpretation**

The age-depth model obtained for PI core provides a chronology for the last ~35k cal a BP of environmental changes in central eastern Brazil (Figure 3). We are aware of the limitation imposed by such a coarse dating resolution for the covered period, and the larger uncertainty introduced by extrapolating ages for the last 30 cm (older than ~26ka). This extrapolation is necessary because we have data for almost all proxies in this secction, 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., 2019; Rodríguez-Zorro et al., 2020).

We use a selection of proxies (Fig. 4), such as δ^{13} C, δ^{15} N, Cp2 (factor scores of the second 275 PCA component on geochemical properties - Supporting Fig. S2), and the Br/C ratio, as well as 276 277 information about distribution of the main taxa by type of vegetation and environment inferred by 278 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 Fig. 6 and Fig.7 respectively, while the 279 remaining taxa not included in these figures can be found in Supporting Figs. S8 and S9. Factor 280 281 loadings of the extracted components and the fractionation of communalities of the variables used in the PCA of the geochemical properties are provided in Supporting Fig. S3. Depth records of 282 physical properties and elemental-isotopic composition of C and N (Supporting Fig. S4), major and 283 minor elements (Supporting Fig. S5), trace lithogenic elements (Supporting Fig. S6), and trace 284 metallic elements and halogens (Supporting Fig. S7) also used in the PCA are in the Supporting 285 286 Information.

The δ^{13} C values can be used to identify carbon derived from different photosynthetic pathways, since the isotopic ratio does not change with time (Cerling *et al.*, 1989). This ratio also provides information about source vegetation and climate dynamics, because C₃ plants (most trees and some graminoids of wet grasslands and indicators of humid environments) have δ^{13} C values between -32 and -22‰, while C₄ 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 δ^{13} C, in agreement with the increase in ASI, and an "antiphase" when the increase in humidity is not directly related to the ASI.

The main factors affecting the δ^{15} 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 ¹⁵N (Schellekens *et al.*, 2014). In general, these processes occur during drier periods. In tropical soils, the values vary between +3.5 and +21.7‰, with much smaller variations in hydromorphic soils (between ≈+4 and +5‰) (Martinelli *et al.*, 2009).

301 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 302 303 loadings of Si, Cr, and K (lithogenic elements) (Supporting Fig. S2). Since the main geological 304 material of the catchment of the mire is quartzite, Si content is most probably related to the amount of quartz transported from the catchment soils into the mire. Thus, Cp2 likely reflects a local signal: 305 the mire accumulates organic matter (positive factor scores) under stable conditions in the 306 catchment, while larger amounts of coarse mineral matter (i.e. quartz from the quartzite) are 307 transported to the mire (negative factor scores) under unstable conditions (erosion episodes). 308

The oceans are the main source of Br, which reaches the peatland by wet deposition and accumulates as organo-halogenated compounds (Biester *et al.*, 2006). Given the inland location of the Pinheiro mire, Br deposition may have been linked to atmospheric circulations bringing seaspray 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.

315 The chronology of environmental changes

316 Marine Isotope Stage 3 (MIS 3)

Although our record only shows the end of the MIS 3, a cold phase in the Northern 317 Hemisphere, it is noteworthy that a change in the climate pattern occurs from the first half (~35.0 to 318 ~31.8k cal a BP) to the second half (~31.8 to ~29.6k cal a BP) and before the LGM. There was no 319 speleothem deposition (formation) in caves in northeastern Brazil during MIS 3 (Fig. 4C; Wang et 320 al., 2004; Cruz et al., 2009). The D/O 7, 6, and 5 cycles (~34.6, ~32.9, and ~31.7k cal a BP 321 respectively) correspond to high δ^{13} C values in our record, indicating that long dry seasons (5 or 322 more months) were particularly recurrent, as corroborated by high peat mineralization (high $\delta^{15}N$ 323 values; Fig. 4A2). High levels of erosion from catchment soils (negative Cp2 values; Fig. 4A3) 324 were probably triggered and facilitated by the reduction of seasonal forests (see for example 325 Cedrela, Celtis, Sorocea, Trema, Hyeronima, and Myrtaceae) and expansion of pioneer trees 326 327 (Cecropia) (Figs. 5 and 6), which reduced soil protection. Given these fluctuations, a dry climate is evident for the MIS 3 in central-eastern Brazil, much drier in the first phase. However, climate was 328 warm overall (Byrsonima and Smilax; representative of savanna) with some inter-dispersed cooling 329 events (Cedrela, Myrsine, Podocarpus, and Weinmannia taxa; all indicators of tropical coniferous 330 forest related to mountainous and cold conditions), which are synchronous with the milder climate -331 relative short increases in humidity (as seen by fluctuating of the already mentioned taxa of 332 seasonal forest), but still within a dry season (from 2 to 3 months, lasting less than 1,000 years). 333

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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 δ^{13} 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, most probably due to the denser tree-shrub vegetation cover (increasing trend of δ^{15} N values see-342 saw pattern suggesting a greater accumulation of organic material; Fig. 4A2). From ~29.6 to ~17.0k 343 cal a BP, the increased humidity is simultaneous with an increase in southern Brazil and a decrease 344 in northeastern from ~26 to ~17.0k cal a BP. From ~16.0 to ~7.1k cal a BP, after the abrupt event of 345 dry (Amaranthus, Borreria, and Gleichenia; indicators of dry grassland) and very cold (highest 346 percentage of Drimys and presence of Araucaria, both are tropical coniferous) conditions by ~16.4k 347 cal BP, humid conditions returned when humidity also increased in the northeast and decreased in 348 the south as well as in western Amazonia (Figs. 4C, D, E). The Bølling-Allerød interstadial is 349 coeval with the D/O 1 cycle and is registered as a slight reduction of precipitation by ~14.3k cal BP, 350 which coincides with an absence of speleothem deposition in northeastern Brazil (Fig. 4C) and wet 351 352 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 BP (Fig. 4A4) provide evidence of the probably wettest period 353 of the record, which is in agreement with records from northeastern Brazil (Fig. 4C). 354

355 Mid to Late Holocene

356 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. Up until ~3.1k cal a BP, seasonal, cold and 357 humid- and mountain- forests retracted as dry grassland expanded (for example, Amaranthus and 358 Borreria; Fig. 6) and point to a decrease in humidity, while an almost constant presence of wet 359 grassland (Drosera, Sagittaria, Utricullaria, HdV-18 van Geel; Fig. 7) suggests local (i.e. in the 360 361 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 362 shallow open water indicators, such as *Mougeotia* and *Zygnema*; Figs. 5 and 7), similar to a shallow 363 lake and populated with species of wet grassland (C3 plants; Fig. 4). An abrupt reduction of 364 oceanic-atmospheric activity suggested by the Br/C ratios (Fig. 4A4), like that observed during MIS 365 3, supports the interpretation of prevailing dry climatic conditions. In this period, humidity also 366

decreased in the northeast while an opposite trend is seen for southern Brazil and western Amazonia(Figs. 4C, D, E).

An abrupt change in δ^{13} C occurred again after ~3.1k cal a BP, reaching its maximum value 369 by AD ~740 (Fig. 4A1). The isotope ratios are comparable to those observed during MIS 3 and, 370 together with indications of a decline in wet grasslands (Araceae, Cyperaceae, Drosera, Typha, 371 Utricullaria, and diverse NPPs such as Meliola niessleana; Fig. 7), a slight increase in dry 372 grassland (Amaranthus, Borreria, Gleichenia, Gelasinospora, Pleospora; Figs. 6 and 7), and 373 374 increase in organic matter mineralization (Fig. 4A2), provide evidence of a decrease in local humidity. At regional scale, the small increase in the seasonal, mountain and pioneer trees - with 375 376 typical taxa of the conditions mentioned above (Fig. 6) – indicates a relative increase in humidity. 377 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). 378 Spiniferites (a dinoflagellate) is an indicator of warm waters (Price et al., 2013) and its presence is 379 380 consistent with a warmer climate (Fig. 7). The change into current conditions probably started during this time, with a strengthening of seasonality and a slight reduction of torrential rainfalls, 381 facilitating the establishment of the Cerrado biome (i.e. dry season with ~4-5 months). Semi-arid 382 conditions prevailed in the northeast, while southern Brazil and western Amazonia returned to 383 humid and very humid climates, respectively, typical of today (Aziz Ab'Sáber, 2003). 384

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 (*Amarathus*, and in general the Amaranthaceae family; Fig. 6).

389 **Discussion**

Our findings demonstrate that the climate in central-eastern Brazil underwent several 390 significant changes during the last ~35k cal a BP, mainly related to rainfall variability, but also, to 391 some extent, to temperature variations as inferred from vegetation dynamics. Consequently, these 392 changes are also reflected in different landscape conditions. Five main phases could be established: 393 (C I) between ~35.0 to ~29.6k cal a BP - the climate was dry and warm with cooling events and 394 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 395 - very wet, both very cold and with reduced landscape instability; (C IV) ~6.1 to ~3.1k cal a BP -396 very dry and warm with increasing catchment instability; and (C V) ≤ -3.1 k cal a BP – from dry 397 and warm to sub-humid climate (Fig. 8). 398

The low humidity during MIS 3 suggested by our data coincides with the expansion of sea-399 400 ice and very low temperatures in the northern hemisphere (Heinrich, 1988; Dansgaard et al., 1993; 401 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 402 403 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 404 405 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 406 from high summer insolation in certain periods, and apparently in phase with $\delta^{13}C$ and austral 407 408 summer insolation (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 415 alignment with the same trends in northeastern Brazil, including an antiphase with ASI (Fig. 8). 416 This means that the increased precipitation occurred during weak monsoon seasons when ASI was 417 low since ~16.9k cal a BP when precipitation was related to insolation. However, it is not yet clear 418 419 if orbital-scale variability is the dominant control on precipitation after H1 and YD events. In the northern hemisphere, abrupt temperature increases may have caused changes in the Atlantic 420 meridional overturning circulation and SACZ location, with the latter possibly shifted northward 421 providing more humidity to central-eastern Brazil. 422

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 relation is in phase for our study area, or the effect of precession was likely significantly reduced at 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 timescales. During the last ~16.9k cal 428 a BP, the orbital-scale variability is the dominant control, or both millennial and orbital-scale act 429 together suggesting a common forcing. This mechanism is particularly important for tropical 430 precipitation, as during these times changes in the eccentricity of the Earth's orbit promoted the 431 modification to precessional forcing - hereafter defined as the "precessionally forced" or 432 "orbitally forced" changes in insolation –, with predominant periods at 19 ka and 23 ka (Liu and 433 434 Battisti, 2015). However, the millennial-scale is expressed through all the ~35k cal a BP record, to a greater or lesser extent, which allows to track the swings of the SACZ (Fig. 8): SACZ I - it shifted 435 to a southward position in MIS 3, very near to Botuverá cave in Santa Catarina state (number 3, Fig. 436 1); SACZ II - a northward shift during the LGM, with a northern limit probably located near or 437 within the location of the Pinheiro mire in Minas Gerais state (number 1, Fig. 1); SACZ III – a shift 438 further northward, remaining stable for all this time over the Pinheiro mire from LP to MH (until 439 18 440 ~6.1k cal a BP), with all the band within the central-eastern Brazil; and SACZ IV – a return to a 441 southward position. Today the SACZ is located between the central-eastern and southeastern 442 regions of Brazil ($20^{\circ}-40^{\circ}$ S and $50^{\circ}-20^{\circ}$ 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. Concerning the northeast, 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 449 to be relatively recent, probably established after ~3.1k cal a BP; although similar conditions may 450 451 have been present in MIS 3, mainly between ~35.0 to ~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 452 the Cerrado elements during the late Holocene, suggesting favourable conditions for this biome. 453 454 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. 455 Today, semi-deciduous (seasonal) and mountain (cold) forests, so-called Capões, are relicts of 456 wetter climates, indicating long-term climate variability during the Quaternary, since they were 457 much more developed in the past, especially between ~29.6 and ~6.1k cal a BP. During the Mid-458 Holocene, more humid climate was also prevalent in other current areas of Cerrado, as in Águas 459 Emendadas (Barberi et al., 2000) and Crominia palm swamp (Ferraz-Vicentini and Salgado-460 Labouriau, 1996; Barberi et al., 2000). This can be considered as key information on the origin of 461 tropical plant biodiversity. 462

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; Stríkis *et al.*, 2015), which is mainly due to its position being influenced by the constant
fluctuation and displacement of the SACZ.

467 **Conclusions**

The multi-proxy investigation of the Pinheiro mire (PI core) enhances our knowledge about the relationship between past climate and vegetation change in central-eastern Brazil. We show environmental and climate changes from late Pleistocene at millennial and orbital timescales and the displacements of the SACZ. Our work contributes to one of the current most controversial debates about the nature of climate during the Last Glacial Maximum (LGM) and mid-Holocene (MH) (between ~29.6 and ~6.1k cal a BP), which were not dry for the studied region. On the contrary, 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 in past periods. These taxa attest for 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 the Marine Isotope Stage 3, and even the modern forest islands – the Capões –, with typical taxa that resemble the forest of very wet climates occurred 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 a certain modification, mainly due to changes in climate.

482 Thus, the Pinheiro mire proved to be an insightful archive of past changes, showing its high483 scientific importance - a good reason for its preservation.

484 Figure legends

Figure 1. Long-term mean (A.D. 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, northeastern 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.

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.

496 Figure 3. Age-depth model of the PI core fitted with Bacon (Blaauw and Christen, 2011) using the 497 dating for the peat samples of the upper meter of the core (blue) and Southern Hemisphere 498 calibration curve (SHCal13.14C).

Figure 4. Comparison between South America records over the past 35 ka BP. (A1) δ^{13} C; (A2) 499 δ^{15} N; (A3) Cp2; and (A4) Br/C ratio of the Pinheiro record, central-eastern Brazil. (B) Greenland 500 ice (GISP2) δ^{18} O record (Grootes and Stuiver, 1997). (C) Rio Grande do Norte speleothem δ^{18} O 501 record, northeastern Brazil. (D) Botuverá speleothem δ^{18} O record, southern Brazil. (E) western 502 Amazonia speleothem δ^{18} O record, northern Peru. The red curves represent austral summer (DJF) 503 insolation (ASI) (Berger, 1978). Gray bars show periods of increased humidity in central-eastern 504 Brazil. MIS 3 = Marine Isotope Stage 3; LGM = Last Glacial Maximum; LP = late Pleistocene; EH 505 = early Holocene; MH = middle Holocene; and LH = late Holocene. 506

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

509 cluster analysis together with the Palynological Zones (separated by dashed lines) are plotted.510 Values are expressed as percentages of the total land pollen sum (TLP).

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 (RPZ; 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.

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 (LPZ) 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.

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 palinozones 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.

528 Supporting Information

Additional supporting information may be found online in the Supporting Information section at theend of the article.

Figure S1. Age-depth model of the PI core fitted with Bacon (Blaauw & Christen, 2011) using the dating for the peat samples of the upper meter 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. ¹Eigenv: eigenvalues; ²Var (%): percentage of explained variance; 3Var_ac: cumulative explained variance.

Figure S4. Contents (in %) of ash, fiber, C and N; BD (bulk density; in Mg m⁻³); and δ^{13} C and δ^{15} N (in ‰) of the PI core.

- **Figure S5.** Concentrations (in g kg⁻¹) of Si, Al, Fe, Ti, K, Ca, S, and P of the PI core.
- **Figure S6.** Concentrations (in μ g g⁻¹) of Ga, Rb, Sr, Zr, Y, and Nb of the PI core.

Figure S7. Concentrations (in $\mu g g^{-1}$) 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 the Figure 6. The silhouettes show the percentage curves of the taxa, while shades show 14x (Figure S8A) and 12x exaggeration curves (Figure 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 Figure S8A: Green: trees; blue:
trees/shrubs; and purple: shrubs. In Figure S8B: Yellow: herbs; light blue: lianas; and red: diverses.

Figure S9. Local (hydro-hygrophytes and NPP) palynological diagram of the PI record with taxa
not included in the Figure 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 Figure S9A: Blue: hydro-hygrophytes; light blue: bryophyte; and green:
pteridophytes. In Figure S9B: Purple: algae; red: fungi; and yellow: dinoflagellates.

Table S1. Results of ¹⁴C dating of the PI core, showing conventional age in a 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 PI core, their habit,
coverage, and phytophysiognomy belonging or probable environmental indicator.

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Figure 3.



Figure 4.



Figure 5.











1	Late Quaternary vegetation and climate dynamics in central-eastern
2	Brazil: insights from a ~35k cal a BP peat record in the Cerrado
3	biome
4	INGRID HORÁK-TERRA ^{1*} , ANTONIO MARTÍNEZ CORTIZAS ² , CYNTHIA FERNANDES
5	PINTO DA LUZ ³ , ALEXANDRE CHRISTÓFARO SILVA ⁴ , TIM MIGHALL ⁵ , PLÍNIO
6	BARBOSA DE CAMARGO ⁶ , CARLOS VICTOR MENDONÇA-FILHO ⁷ , PAULO EDUARDO
7	DE OLIVEIRA ⁸ , FRANCISCO WILLIAN CRUZ ⁸ , PABLO VIDAL-TORRADO ⁹
8	Supporting Information
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48 Figure S1. Age-depth model of the PI core fitted with Bacon (Blaauw and Christen, 2011) using the

49 dating for the peat samples of the upper meter of the core (blue) and Northern Hemisphere calibration

50 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.





¹ Eigenv	8.7	6.4	3.0
² Var (%)	33.5	24.5	11.6
³ Var ac	33.5	58.0	69.6

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; 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. ¹Eigenv: eigenvalues; ²Var (%):
percentage of explained variance; 3Var_ac: cumulative explained variance.





Figure S4. Contents (in %) of ash, fiber, C and N; BD (bulk density; in Mg m⁻³); and δ^{13} C and δ^{15} N (in **‰**) of the PI core.





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

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Figure S6. Concentrations (in $\mu g g^{-1}$) of Ga, Rb, Sr, Zr, Y, and Nb of the PI core.





Figure S7. Concentrations (in μ g 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 the Figure 6. The silhouettes show the percentage curves of the taxa, while shades show 14x (Figure S8A) and 12x exaggeration curves (Figure 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 Figure S8A: Green: trees; blue: trees/shrubs; and purple: shrubs. In Figure S8B: Yellow: herbs; light blue: lianas; and red: diverses.



96 Figure S9. Local (hydro-hygrophytes and NPP) palynological diagram of the PI record with taxa not included in the Figure 7. The silhouettes show the

- 97 percentage curves of the taxa, while shades show 10x exaggeration curves. CONISS cluster analysis together with the Local Palynological Zones
- 98 (LPZ; separated by dashed lines) are plotted. Values are expressed as percentages of the total land pollen sum (TLP). In Figure S9A: Blue: hydro-
- 99 hygrophytes; light blue: bryophyte; and green: pteridophytes. In Figure S9B: Purple: algae; red: fungi; and yellow: dinoflagellates.

- **Table S1.** Results of ¹⁴C dating of the PI core, showing conventional age in a BP and calibrated ages
- 101 (2 σ) in cal a BP.

	Depth (cm)	¹ Lab. code	Conventional age (a BP)	Calibrated age 2ð (cal a BP)
	8-10	Beta - 330480	770 ± 30	701 ± 32
	18-20	Beta - 330481	2860 ± 30	2995 ± 78
	32-34	Beta - 330482	6120±40	7030 ± 128
	50-52	Beta - 532630	11,860±40	$13,\!653\pm108$
	68-70	Beta - 330483	13,140±60	$15,888 \pm 626$
	80-82	Beta - 532631	14,150±40	$17,181 \pm 213$
	100-102	Beta - 330484	20,730±100	$24,723 \pm 305$
¹ Beta: Be	ta Analytic Inc			

120 **Table S2.** The maximum number of total land pollen (TLP) and hydro-hygrophytes and non-pollen

121 palynomorphs (NPP) of the PI core.

Depth (cm)	2	12	22	32	42	51	61	72	81	91	101	111	122
TLP	323	1107	191	362	308	1282	931	329	1188	1134	1703	1184	360
hydro- hygrophytes and NPP	674	529	342	301	350	769	698	630	486	647	720	789	352

Table S3. Pollen and other non-pollen palynomorphs (NPP) observed in PI core, their habit, coverage, and phytophysiognomy belonging or probable 141 environmental indicator. 142

Pollen, spore	Pollen, spores and other NPP		Habit	Coverage*	Phytophysiognomy or
Genus/Species	Family	_ type			environmental indicator**
Acnistus	Solanaceae	Pollen	Shrubs	R	Semi-deciduous forest
Anadenanthera	Fabaceae	Pollen	Trees	R	Semi-deciduous forest
Apuleia	Fabaceae	Pollen	Trees	R	Semi-deciduous forest
	Aristolochiaceae	Pollen	Lianas/Herbs	R	Semi-deciduous forest
Bathysa	Rubiaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Cedrela	Meliaceae	Pollen	Trees	R	Semi-deciduous forest
Cissus	Vitaceae	Pollen	Lianas/Herbs	R	Semi-deciduous forest
Dennstaedtia	Dennstaedtiaceae	Spore	Arborescent	L	Semi-deciduous forest
Eugenia	Myrtaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Cryptocaria	Lauraceae	Pollen	Trees	R	Semi-deciduous forest
Gaylussacia	Ericaceae	Pollen	Shrubs	R	Semi-deciduous forest
Hedyosmum	Chloranthaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Hyeronima	Euphorbiaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest

Ilex	Aquifoliaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Jacaranda	Bignoniaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Laplacea	Theaceae	Pollen	Trees	R	Semi-deciduous forest
Lindsaea	Dennstaedtiaceae	Spore	Herbs	L	Semi-deciduous forest
Machaerium	Fabaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Micrograma	Polypodiaceae	Spore	Lianas/Herbs	L	Semi-deciduous forest
Mimosa bimucronata	Fabaceae	Pollen	Trees	R	Semi-deciduous forest
Mikania	Asteraceae	Pollen	Lianas/Herbs	R	Semi-deciduous forest
	Myrtaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Ormosia	Fabaceae	Pollen	Trees	R	Semi-deciduous forest
Paullinia	Sapindaceae	Pollen	Lianas	R	Semi-deciduous forest
Piptadenia	Fabaceae	Pollen	Trees	R	Semi-deciduous forest
Protium	Burseraceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
	Salicaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Siphoneugena	Myrtaceae	Pollen	Trees/Shrubs	R	Semi-deciduous forest
Sloanea	Elaeocarpaceae	Pollen	Herbs	R	Semi-deciduous forest
Sorocea	Moraceae	Pollen	Trees	R	Semi-deciduous forest

Spathiphyllum	Araceae	Pollen	Herbs	L	Semi-deciduous forest
Alnus	Betulaceae	Pollen	Trees	R	Cold and humid forest
Alsophila	Geometridae	Spore	Arborescent	L	Cold and humid forest
Araucaria	Araucariaceae	Pollen	Trees	R	Cold and humid forest
Dicksonia	Dicksoniaceae	Spore	Arborescent	L	Cold and humid forest
Drimys	Winteraceae	Pollen	Trees	R	Cold and humid forest
Hypolepis	Dennstaedtiaceae	Spore	Herbs/Shrubs	L	Cold and humid forest
Lophosoria	Dicksoniacea	Spore	Arborescent	L	Cold and humid forest
Myrsine	Myrsinaceae	Pollen	Trees	R	Cold and humid forest
Podocarpus	Podocarpaceae	Pollen	Trees	R	Cold and humid forest
Rhamnus	Rhamnaceae	Pollen	Trees/Shrubs	R	Cold and humid forest
Trichilia	Meliaceae	Pollen	Trees	R	Cold and humid forest
Clethra	Clethraceae	Pollen	Trees/Shrubs	R	Mountain forest
Galium	Rubiaceae	Pollen	Herbs	R	Mountain forest
Huperzia	Lycopodiaceae	Spore	Herbs	L	Mountain forest
Lamanonia	Cunnoniaceae	Pollen	Trees/Shrubs	R	Mountain forest
Marattia	Marattiaceae	Spore	Arborescent	R	Mountain forest

Mimosa scabrella	Fabaceae	Pollen	Trees	R	Mountain forest
Acacia	Fabaceae	Pollen	Diverses	R	Savanna forest
Aegiphila	Verbenaceae	Pollen	Trees/Shrubs	R	Savanna forest
	Anacardiaceae	Pollen	Trees/Shrubs	R	Savanna forest
Cabralea	Meliaceae	Pollen	Trees/Shrubs	R	Savanna forest
Casearia	Fabaceae	Pollen	Trees/Shrubs	R	Savanna forest
Chrysophyllum	Sapotaceae	Pollen	Trees	R	Savanna forest
Copaifera	Fabaceae	Pollen	Trees/Shrubs	R	Savanna forest
Luehea	Tiliaceae	Pollen	Trees	R	Savanna forest
Matayba	Sapindaceae	Pollen	Trees/Shrubs	R	Savanna forest
	Ochnaceae	Pollen	Trees/Shrubs	R	Savanna forest
Prestonia	Apocynaceae	Pollen	Lianas/Herbs	R	Savanna forest
	Sapotaceae	Pollen	Trees/Shrubs	R	Savanna forest
Schinus	Anacardiaceae	Pollen	Trees/Shrubs	R	Savanna forest
Senna	Fabaceae	Pollen	Trees/Shrubs	R	Savanna forest
Smilax	Smilacaceae	Pollen	Lianas	R	Savanna forest
Struthanthus	Loranthaceae	Pollen	Lianas/Herbs	R	Savanna forest

Tabebuia rosea	Bignoniaceae	Pollen	Trees	R	Savanna forest
Tabebuia	Bignoniaceae	Pollen	Trees	R	Savanna forest
Vitex	Verbenaceae	Pollen	Trees/Shrubs	R	Savanna forest
Zanthoxylum	Rutaceae	Pollen	Trees	R	Savanna forest
	Arecaceae	Pollen	Trees/Shrubs	R	Humid savanna
Alchornea	Euphorbiaceae	Pollen	Trees	R	Humid savanna
Astronium	Anacardiaceae	Pollen	Trees	R	Humid savanna
Calyptranthes	Myrtaceae	Pollen	Trees	R	Humid savanna
Chelonanthus	Gentianaceae	Pollen	Shrubs	R	Humid savanna
Davilla	Dilleniaceae	Pollen	Lianas	R	Humid savanna
Diodia	Rubiaceae	Pollen	Herbs/Shrubs	R	Humid savanna
Euterpe	Arecaceae	Pollen	Trees	R	Humid savanna
Ferdinandusa	Rubiaceae	Pollen	Trees	R	Humid savanna
Genipa	Rubiaceae	Pollen	Trees	R	Humid savanna
Mascagnia	Malpighiaceae	Pollen	Lianas	R	Humid savanna
Mauritia flexuosa	Arecaceae	Pollen	Trees	R	Humid savanna
	Menispermaceae	Pollen	Lianas	R	Humid savanna

Myrcia	Myrtaceae	Pollen	Trees/Shrubs	R	Humid savanna
Platymiscium	Fabaceae	Pollen	Trees	R	Humid savanna
Schefflera	Araliaceae	Pollen	Trees	R	Humid savanna
Styrax	Styracaceae	Pollen	Trees	R	Humid savanna
Symplocos	Symplocaceae	Pollen	Trees	R	Humid savanna
Trixis	Asteraceae	Pollen	Herbs/Shrubs	R	Humid savanna
Andira	Fabaceae	Pollen	Trees/Shrubs	R	Dry savanna
Byrsonima	Malpighiaceae	Pollen	Trees/Shrubs	R	Dry savanna
Cassia	Fabaceae	Pollen	Diverses	R	Dry savanna
Croton	Euphorbiaceae	Pollen	Herbs/Shrubs	R	Dry savanna
Hortia	Rutaceae	Pollen	Shrubs	R	Dry savanna
Mimosa	Fabaceae	Pollen	Diverses	R	Dry savanna
	Proteaceae	Pollen	Trees/Shrubs	R	Dry savanna
Roupala	Proteaceae	Pollen	Trees/Shrubs	R	Dry savanna
Serjania	Sapindaceae	Pollen	Lianas	R	Dry savanna
Banara	Salicaceae	Pollen	Shrubs	R	Pioneer of secondary forest
Cecropia	Urticaceae	Pollen	Trees/Shrubs	R	Pioneer of secondary forest

Doliocarpus	Dilleniaceae	Pollen	Lianas	R	Pioneer of secondary forest
Erythroxylum	Erythroxylaceae	Pollen	Trees/Shrubs	R	Pioneer of secondary forest
Inga	Fabaceae	Pollen	Trees	R	Pioneer of secondary forest
Piper	Piperaceae	Pollen	Shrubs	R	Pioneer of secondary forest
Tapirira	Anacardiaceae	Pollen	Trees/Shrubs	R	Pioneer of secondary forest
Cestrum	Solanaceae	Pollen	Shrubs	R	Savanna abroad sense
Chamaecrista	Fabaceae	Pollen	Diverses	R	Savanna abroad sense
Clitoria	Fabaceae	Pollen	Diverses	R	Savanna abroad sense
Cordia	Boraginaceae	Pollen	Trees/Shrubs	R	Savanna abroad sense
Cupania	Sapindaceae	Pollen	Trees/Shrubs	R	Savanna abroad sense
Dasyphyllum	Asteraceae	Pollen	Trees/Shrubs	R	Savanna abroad sense
Eupatorium	Asteraceae	Pollen	Herbs/Shrubs	R	Savanna abroad sense
Guettarda	Rubiaceae	Pollen	Trees/Shrubs	R	Savanna abroad sense
Hyptis	Lamiaceae	Pollen	Herbs/Shrubs	R	Savanna abroad sense
Laetia	Salicaceae	Pollen	Shrubs	R	Savanna abroad sense
Lantana	Verbenaceae	Pollen	Herbs/Shrubs	R	Savanna abroad sense
Merremia	Convolvulaceae	Pollen	Lianas	R	Savanna abroad sense

Peixotoa	Malpighiaceae	Pollen	Shrubs	R	Savanna abroad sense
Periandra	Fabaceae	Pollen	Lianas	R	Savanna abroad sense
Psidium	Myrtaceae	Pollen	Trees/Shrubs	R	Savanna abroad sense
Rudgea	Rubiaceae	Pollen	Diverses	R	Savanna abroad sense
Sebastiania	Euphorbiaceae	Pollen	Diverses	R	Savanna abroad sense
Solanum	Solanaceae	Pollen	Diverses	R	Savanna abroad sense
Strychnos	Loganiaceae	Pollen	Diverses	R	Savanna abroad sense
Tetrapterys	Malpighiaceae	Pollen	Diverses	R	Savanna abroad sense
	Verbenaceae	Pollen	Diverses	R	Savanna abroad sense
Agalinis	Orobanchaceae	Pollen	Herbs	L	Wet grassland
Baccharis	Asteraceae	Pollen	Herbs/Shrubs	R	Wet grassland
Bacopa	Orobanchaceae	Pollen	Herbs	L	Wet grassland
Begonia	Begoniaceae	Pollen	Herbs	R	Wet grassland
Bidens	Asteraceae	Pollen	Herbs/Shrubs	R	Wet grassland
Campylopodium	Dicranaceae	Moss	Herbs	L	Wet grassland
Campylopus	Dicranaceae	Moss	Herbs	L	Wet grassland
Dicranella	Dicranaceae	Moss	Herbs	L	Wet grassland

Drosera	Droseraceae	Pollen	Herbs	L	Wet grassland
Eryngium	Apiaceae	Pollen	Herbs	R	Wet grassland
Genlisea	Lentibulariaceae	Pollen	Herbs	L	Wet grassland
Gnaphalium	Asteraceae	Pollen	Herbs	R	Wet grassland
Heliotropium	Boraginaceae	Pollen	Herbs	R	Wet grassland
Hydrocotyle	Apiaceae	Pollen	Herbs	L	Wet grassland
Ichthyothere/Aspilia	Asteraceae	Pollen	Herbs/Shrubs	R	Wet grassland
Myriophyllum	Haloragaceae	Pollen	Herbs	L	Wet grassland
	Nymphaeaceae/Pontederiaceae	Pollen	Herbs	L	Wet grassland
Nymphoides	Menyanthaceae	Pollen	Herbs	L	Wet grassland
	Orobanchaceae	Pollen	Herbs/Shrubs	R	Wet grassland
Phaeoceros	Anthocerotaceae	Moss	Herbs	L	Wet grassland
Sagittaria	Alismataceae	Pollen	Herbs	L	Wet grassland
Sphagnum recurvum	Sphagnaceae	Moss	Herbs	L	Wet grassland
Typha	Typhaceae	Pollen	Herbs	L	Wet grassland
Utricularia	Lentibulariaceae	Pollen	Herbs	L	Wet grassland
Acalypha	Euphorbiaceae	Pollen	Herbs/Shrubs	R	Dry grassland

Achyrocline	Asteraceae	Pollen	Herbs	L	Dry grassland
Amaranthus	Amaranthaceae	Pollen	Herbs	R	Dry grassland
Anemia	Schizaeaceae	Spore	Herbs	L	Dry grassland
Borreria	Rubiaceae	Pollen	Herbs	R	Dry grassland
Camarea	Maplpighiaceae	Pollen	Herbs/Shrubs	R	Dry grassland
Cleome	Capparaceae	Pollen	Herbs/Shrubs	R	Dry grassland
Chamaesyce	Euphorbiaceae	Pollen	Herbs	R	Dry grassland
Ephedra	Ephedraceae	Pollen	Schrubs	R	Dry grassland
Eremanthus	Asteraceae	Pollen	Diverses	R	Dry grassland
Euphorbia	Euphorbiaceae	Pollen	Herbs	R	Dry grassland
Galactia	Fabaceae	Pollen	Herbs	R	Dry grassland
Gleichenia 1	Gleicheniaceae	Spore	Shrubs	L	Dry grassland
Gleichenia 2	Gleicheniaceae	Spore	Shrubs	L	Dry grassland
Phytolacca	Phytolaccaceae	Pollen	Herbs	R	Dry grassland
	Polygalaceae	Pollen	Diverses	R	Dry grassland
Scoparia	Orobanchaceae	Pollen	Herbs	R	Dry grassland
Senecio	Asteraceae	Pollen	Herbs/Shrubs	R	Dry grassland

Zornia	Fabaceae	Pollen	Diverses	R	Dry grassland
	Bromeliaceae	Pollen	Herbs	R	Rupicola-saxicolous grassland
Coccocypselum/Declieuxia	Rubiaceae	Pollen	Herbs/Shrubs	R	Rupicola-saxicolous grassland
Cuphea	Lythraceae	Pollen	Herbs/Shrubs	R	Rupicola-saxicolous grassland
	Eriocaulaceae	Pollen	Herbs	R	Rupicola-saxicolous grassland
Xyris	Xyridaceae	Pollen	Herbs	R	Rupicola-saxicolous grassland
Alternanthera	Amaranthaceae	Pollen	Herbs	R	Grassland
	Araceae	Pollen	Herbs	L	Grassland
Buchnera	Orobanchaceae	Pollen	Herbs	R	Grassland
	Campanulaceae	Pollen	Herbs/Shrubs	R	Grassland
Cassytha	Lauraceae	Pollen	Herbs	R	Grassland
Crotalaria	Fabaceae	Pollen	Herbs/Shrubs	R	Grassland
	Cyperaceae	Pollen	Herbs	L	Grassland
Gomphrena	Amaranthaceae	Pollen	Herbs	R	Grassland
	Iridaceae	Pollen	Herbs	R	Grassland
	Monocotiledonea	Pollen	Herbs	R	Grassland
	Poaceae	Pollen	Herbs	R	Grassland

Thesium	Santalaceae	Pollen	Herbs	R	Grassland
	Apocynaceae	Pollen	Diverses	R	Diverse
	Bignoniaceae	Pollen	Diverses	R	Diverse
	Euphorbiaceae	Pollen	Diverses	R	Diverse
	Fabaceae	Pollen	Diverses	R	Diverse
Justicia	Acanthaceae	Pollen	Herbs/Shrubs	R	Diverse
	Lauraceae	Pollen	Diverses	R	Diverse
	Lythraceae	Pollen	Diverses	R	Diverse
	Malpighiaceae	Pollen	Diverses	R	Diverse
	Malvaceae	Pollen	Herbs/Shrubs	R	Diverse
	Melastomataceae	Pollen	Diverses	R	Diverse
Phyllanthus	Euphorbiaceae	Pollen	Herbs/Shrubs	R	Diverse
Polypodium	Polypodiaceae	Spore	Herbs	R	Diverse
Psychotria	Rubiaceae	Pollen	Diverses	R	Diverse
	Rubiaceae	Pollen	Diverses	R	Diverse
	Solanaceae	Pollen	Diverses	R	Diverse
Schizaea	Schizaeaceae	Spore	Herbs	L	Diverse

Selaginella	Selaginellaceae	Spore	Lianas/Herbs	L	Diverse
	Tiliaceae	Pollen	Diverses	R	Diverse
Vernonia	Asteraceae	Pollen	Herbs/Shrubs	R	Diverse
Vigna	Fabaceae	Pollen	Lianas	R	Diverse
Equisetum	Equisetaceae	Spore	Herbs/Shrubs	L	Humid forest and wet grassland
Lycopodiella alopecuroides	Lycopodiaceae	Spore	Herbs	L	Humid forest and wet grassland
Lycopodiella cernua	Lycopodiaceae	Spore	Herbs	L	Humid forest and wet grassland
Lycopodium contextum	Lycopodiaceae	Spore	Herbs	L	Humid forest and wet grassland
Lycopodium rufescens	Lycopodiaceae	Spore	Herbs	L	Humid forest and wet grassland
Osmunda	Osmundaceae	Spore	Herbs	L	Humid forest and wet grassland
Ophioglossum	Ophioglossaceae	Spore	Herbs	L	Humid forest and wet grassland
Adiantum	Pteridaceae	Spore	Herbs	L	Forest
	Moraceae	Pollen	Diverses	R	Forest
Pleopeltis	Polypodiaceae	Spore	Herbs	L	Forest

Thunbergia	Acanthaceae	Pollen	Lianas	R	Forest
Blechnum imperiale	Blechnaceae	Spore	Herbs	L	Soil erosion
Blechnum	Blechnaceae	Spore	Herbs	L	Soil erosion
Glomus	Glomeraceae	Fungi		L	Soil erosion
Pseudoschizaea		Algae		L	Soil erosion
Achomosphaera	Hystrichosphaeraceae	Pyrrophyta		L	Warm waters
	Dinophyceae	Pyrrophyta		L	Warm waters
Lingulodinium	Gonyaulacaceae	Pyrrophyta		L	Warm waters
Spiniferites	Gonyaulacaceae	Pyrrophyta		L	Warm waters
Delitschia	Delitschiaceae	Fungi		L	Coprophilous fungi
	Sordariaceae	Fungi		L	Coprophilous fungi
Type 19 van Geel		Fungi		L	Coprophilous fungi
Dryopteris	Dryopteridaceae	Spore	Lianas/Shrubs	L	Landscape disturbance
Hystrichosphaeres	Dinophyceae	Pyrrophyta		L	Landscape disturbance
	Lycopodiaceae	Spore	Herbs/Shrubs	L	Landscape disturbance
Pteridium	Dennstaedtiaceae	Spore	Herbs	L	Landscape disturbance
Coelastrum	Scenedesmaceae	Algae		L	Water quality

Euastrum	Desmidiaceae	Algae	L	Water quality
Penium	Peniaceae	Algae	L	Water quality
Sphaerocystis 1	Palmellaceae	Algae	L	Water quality
Sphaerocystis 2	Palmellaceae	Algae	L	Water quality
Botryococcus	Dictyosphaeriaceae	Algae	L	Changes in hydrology
Spyrogira	Zygnemataceae	Algae	L	Changes in hydrology
Type 718 van Geel		Palynomorph	L	Changes in hydrology
Type 726 van Geel		Palynomorph	L	Changes in hydrology
Assulina	Euglyphidae	Fungi	L	Wet conditions
Meliola niessleana	Melanconidaceae	Fungi	L	Wet conditions
Type 18 van Geel		Fungi	L	Wet conditions
Type 140 van Geel		Fungi	L	Wet conditions
Type 731 van Geel		Palynomorph	L	Wet conditions
Gelasinospora	Sordariaceae	Fungi	L	Dry conditions
Pleospora	Pleosporaceae	Fungi	L	Dry conditions
Type 20 van Geel		Fungi	L	Dry conditions
Type 37 van Geel		Rotifers	L	Dry conditions

Isoetes Megaspore	Isoetaceae	Spore Herb	os L	Permanent flooding
Type 121 van Geel		Fungi	L	Permanent flooding
Mougeotia	Zygnemataceae	Algae	L	Shallow open water
Zygnema	Zygnemataceae	Algae	L	Shallow open water
Debarya	Zygnemataceae	Algae	L	Airbone/lower temperature
Athelia	Corticiaceae	Fungi	L	Parasite on woody substrates
Dictyosporites sp.	Dictyosporae	Fungi	L	Parasite on woody substrates
Type 12 van Geel		Fungi	L	Cellulose decomposed
Peridinium	Podolampaceae	Pyrrophyta	L	Bloom's collapse post
Protoperidinium	Podolampaceae	Pyrrophyta	L	Paleoproductivity
Type 719 van Geel		Palynomorph	L	Moss samples

*L: Local; R: Regional. **References: Ellis and van Geel (1978); Guy-Ohlson (1992); Kołaczek et al. (2012); Marchant et al. (2002); Mendonça et al.
(1998); Nobel (1978); Sánchez-González et al. (2010); Sehnem (1970); van Geel (1976); van Geel (1978); van Geel and Aptroot (2006); van Geel et al.
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