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GEOSCIENCES

Late Quaternary hydroclimate and vegetation changes in an upland lake in southeastern Amazonia

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Abstract: An integrated approach considering facies, isotopic, and palynological analyses of lake sediments from the Serra Norte de Carajás, southeastern Amazonia, is presented in this work to refine paleoclimate and paleohydrological changes based on upland lake sediments during the late Quaternary. The sediments have a fining-upward deposition cycle typical of upland swamps/lakes. The origin of organic matter is autochthonous mainly related to C_3 terrestrial plants, macrophytes and algae. The pollen records of *Hedyosmum* during the Early Pleistocene suggest lower temperatures than those observed along Holocene. In the transitional period between the Pleistocene and the Holocene, rainfall decreased, causing the retraction of the flooded area, favoring the development of marshy conditions. The Late and Middle Holocene were marked by higher temperatures and lower humidity. Afterward, the increased pollen concentration from canga and forest vegetation, macrophytes, palms, and algae suggested increased humidity in the Early Holocene. The relative contribution of forest pollen along the records indicated that drier conditions were not strong enough for an extensive expansion of canga over forested areas.

Key words: Amazonia, Holocene, paleopalynology, paleovegetation, paleoclimate.

INTRODUCTION

The Amazon tropical forests play an important role as a C sink, although not completely understood, Nobre & Nobre (2002) suggest that the forest may be absorbing about of 0.5 gigatons of carbon per year, affecting actions to mitigate and control global emissions that seek to stabilize the concentration of greenhouse gases in the atmosphere. However, the mechanisms responsible for the functioning of the forest as a sink to offset emissions due to changes in land use are still unknown (Nobre & Nobre 2002).

The Amazon basin is an essential part of maintaining the hydrological system of South America, through the evapotranspiration process contributing to the formation of clouds and rain (Bush et al. 2011). Studies of past and present climatic dynamics in this region are essential, since climatic events play an important role in structuring the forest, and can affect human health and the region's economy.

The establishment of this climate pattern is related to the Andean orogeny during the Upper Cenozoic, when the paleoaltitudes of this mountain range became an orographic barrier, trapping moist air masses from the ocean (Vonhof & Kaandorp 2010). This climatic scenario favored an intense modeling of the landscape that culminated in the evolution of the Amazon lateritic profiles (Costa 1991), and the development of extensive doliniform features, including upland lakes. These lakes were the target of several studies, which demonstrated the paleoclimatic dynamics of the Amazon during the Late Quaternary (e.g., Absy et al. 1991, Birks et al. 2016, Bush et al. 2004, Colinvaux & De Oliveira 2000, Cheng et al. 2013, Cohen et al. 2014, Colinvaux et al. 1996, 2001, D'Apolito et al. 2013, Guimarães et al. 2016, 2017, Reis et al. 2017, Sifeddine et al. 2001, Van De Hammen & Absy 1994). However, these studies assumed that glacial-interglacial climate variations caused different responses in the forest composition. Some of them stated that in drier conditions, areas of open vegetation, such as savannas, advanced over forested areas (Absy et al. 1991, Sifeddine et al. 2001, Turcq et al. 2002, Cordeiro et al. 2008, Hermanowski et al. 2012, 2014, D'Apolito et al. 2017), in opposition to the hypothesis of forest stability (Colinvaux et al. 1996, Bush 2002, Guimarães et al. 2016, 2017, 2023a, Reis et al. 2017, 2022). However, Amazonian tree cover can be quite resilient to reduced precipitation (Kukla et al. 2021), questioning the widespread opening of forests during glacial times (Reis et al. 2022), or strengthening the occurrence of isolated dry corridors of precipitation (Bush 2017), or wider networks of gallery or riparian forests connecting different biomes (De Oliveira et al. 1999, Werneck et al. 2012). In addition, upland areas of this region may be more stable to climate change due to the orographic rainfall effect (e.g. Galán 1992).

The upland lakes of the Carajás Forest, in the southeast of the Amazonia, are important natural traps that hold valuable records for paleoclimatic and paleoenvironmental studies of the late Quaternary (Cordeiro et al. 2008, Costa et al. 2005, Guimarães et al. 2014, 2016, Reis et al. 2017, Sifeddine et al. 2001, Soubies et al. 1991). These lakes formed on lateritic crust (Sahoo et al. 2015), and can be hydrologically active or inactive/filled, with restricted drainage basins (Guimarães et al. 2017). Water levels are governed by natural processes, such as evaporation and precipitation (Sahoo et al. 2015). The analysis of these data is essential to understanding the dynamics of the climate and the forest throughout the late Quaternary.

Together with palynological analyses, C and N isotopes were very important to elucidate factors related to floristic composition, history of plant communities and sources of organic matter in Carajás lakes (Guimarães et al. 2023a). A detailed characterization of the organic matter components is a challenge, since it presents multiple sources, representing dynamic components of the sediments (Pereira et al. 2022). Facies analysis identifies the nature and scale of the physical processes that act in each sedimentary environment, with greater robustness in the interpretation of paleoenvironmental changes and in the distribution of vegetation in tropical forests during the Pleistocene-Holocene (Reis et al. 2017, Guimarães et al. 2021).

Therefore, climate changes recorded in lake sediments can provide information about how the climate and environment have changed in the past and describe the history of vegetation and biodiversity in the region. This information can be used to predict how the region may be affected by future climate changes and to develop strategies to adapt and mitigate losses in biodiversity, which is important for the conservation of local fauna and flora (Guimarães et al. 2016). This study aims to (I) describe the paleoclimatic changes that occurred in the late Pleistocene and in the Holocene. In addition, (II) analyze the impact of long periods of low rainfall on the structure of the forest landscape. Therefore, it presents an integrated approach based on depositional, carbon and nitrogen isotopes, and palynological analyses.

STUDY AREA

Geology and physiography

The study area is located in the Igarapé Geladinho sub-basin that is part of the Itacaiúnas River Watershed in the southeastern portion of the Amazon region (Figure 1). This sub-basin is inserted in the Carajás Basin, and locally are represented by the following geological units: 1) metavolcano-sedimentary sequences of the Igarapé Gigarra and Parauapebas formations (Macambira 2003, Martins et al. 2017), 2) banded-iron formations (BIFs) of the Carajás Formation (Beisiegel et al. 1973), 3) altered granodiorites and monzogranites of the Igarapé Gelado Metagranite (Barbosa 2004), and mature Fe-Al lateritic crusts located around 600-800 m altitude (Figure 1a, b).

Considering the lateritic crusts, the Cenozoic tropical paleoclimate favored extensive weathering events in the region, contributing to

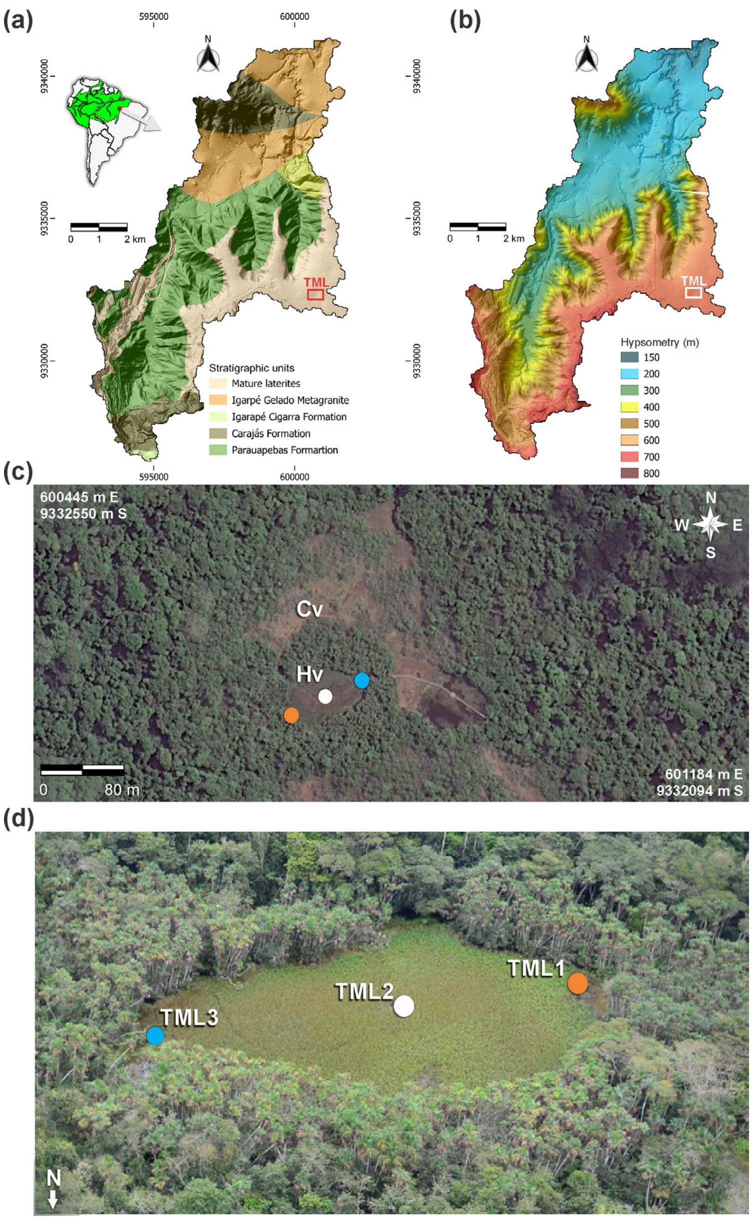

Figure 1. a) geological map of the drainage basin in which the Trilha da Mata Lake (TML) is inserted, with its b) hypsometric data; c) location of the Trilha da Mata Lake (TML) and related canga vegetation (Cv); d) Aerial photography showing different vegetation types of the TML area: rainforest, canga vegetation (Cv), and hydromorphic vegetation (Hv). Detail of the inactive lake showing the core collection points with colored circles.

the development of mature laterites, which were mainly derived from metavolcano-sedimentary rocks and BIFs (Vasconcelos et al. 1994, Maurity & Kotschoubey 1995). Upland lakes were formed according to neotectonic and weathering events that affected the lateritic crusts (Maurity & Kotschoubey 1995).

Vegetation and climate

Canga formations occur on the top of plateaus at an average altitude of 670 m over lateritic crusts (Secco & Mesquita 1983, Souza-Filho et al. 2019). Soil properties are the main factors affecting vegetation composition. Canga forest patches and rainforests share few species, a consequence of the different nutrient and water requirements between these vegetation structures (Mitre et al. 2018). Tropical forests are predominant in the slopes of the plateaus. The canga presents a rich mosaic of open and shrubby vegetation types that occurs on ferruginous crust, directly related to this substrate (Secco & Mesquita 1983, Viana et al. 2016).

Despite the similarity of the type of substrate the cangas that occur in the southeastern region (Quadrilátero Ferrífero, in Minas Gerais) and the center-west (Corumbá, in Mato Grosso do Sul) of Brazil, the phytogeographic played a determining role in the floristic identity of the Carajás cangas. These are areas with high species richness that have more than 1000 terrestrial species documented in about 120 km^2 and unique floristic composition, including several endemic species that frame the Carajás region as a key area of biodiversity and important for the conservation of the flora Amazonian (Giulietti et al. 2019, Mota et al. 2018, Zappi et al. 2019). The speciation of canga species is a result of their isolation imposed by the surrounding vegetation that reduces gene flow between mountain tops (Lanes et al. 2018, Moraes et al. 2012, Pereira et al. 2007). In the rupestrian fields of canga de Carajás 58 taxa were recognized as acknowledged endemics, including 53 angiosperms and five ferns and lycophytes. In the Carajás National Forest, nine taxa were considered highly restricted endemic: Araceae: *Philodendron carajasense* EG Gonç. & A.J. Arruda; Asteraceae: *Cavalcantia glomerata* (GMBarroso & RMKing) RMKing & H.Rob., *Lepidaploa paraenses* (H.Rob.) H.Rob.; Erythroxylaceae: *Erythroxylum carajasense* (Plowman) Costa-Lima, *E. nelson-rosae* Plowman; Gesneriaceae: *Sinningia minima* A.O.Araujo & Chautems; Picramniaceae: *Picramnia ferrea* Pirani & W.W.Thomas and Poaceae: *Bulbostylis cangae* CS Nunes & A. Gil, *Paspalum cangarum* CO Moura, PLViana & RC Oliveira (Giulietti et al. 2019).

The regional climate is tropical monsoon (Am), according to the Koppen classification system (Lopes et al. 2013). The rainfall regime is characterized by two seasons: a rainy season from November to May (1863-1545 mm^{-1} yr) and a dry season from November to April (321-159 mm^{-1} yr) (Lopes et al. 2013, Silva Júnior et al. 2017). The band of convective clouds in the Intertropical Convergence Zone is the main meteorological system that affects the rainfall regime during the rainy season. In the dry season, this regime is influenced by frontal systems, which are responsible for convective activity in eastern Amazonia (Souza et al. 2017). The mean temperature is 27.2 °C, with a minimum of 26.6 °C in January and a maximum of 28.1 °C in September (Tavares et al. 2018).

Sampling area

The study was conducted in the Serra Norte de Carajás, southeastern Pará state, at a site known as Trilha da Mata Lake (TML), which is located over a lateritic plateau colonized by canga vegetation at an area of 21,856 m^2 (Figure 1). Three cores were collected as follow: two on opposite lake margins, TML1 (100 cm depth;

6° 0’52.12”S/50° 17’50.24”W) and TML3 (75 cm depth; 6° 2’3.82”S/50° 16’48.66”W); and one core at the lake depocenter, TML2 (135 cm depth; 6° 1’50.99”S/50° 17’25.42”W) (Figure 1).

The lake has a high accumulation of organic sediments, which favors the colonization of macrophytes in its central portion, and *Mauritiella armata* (Mart.) Burret in its margins. To the north, there is grass vegetation with a strong herbaceous and shrubby component, and some restricted areas of open forests (Da Silva et al. 2020).

MATERIALS AND METHODS

Collection of cores

A peat sampler (Russian peat borer) was used for core collection. The cores were subjected to facies description, including the color, lithology, texture, and sedimentary structure (Walker 1992). The lacustrine sediment classification system of the Global Lake Drilling Program was used (Schnurrenberger et al. 2001, 2003).

^{14}C dating

Samples weighing approximately 2 g were collected every 10 cm for ^{14}C dating by accelerator mass spectrometry at the facilities of Beta Analytic (Miami, Florida, USA). The age-depth model was made based on Bayesian accumulation histories for lake and peat deposits-Bacon (Blaauw & Christen 2011) using R (R Development Core Team 2018) as an interface and Intcal20 calibration dataset (Reimer et al. 2020). A complete description of the age modelling process can be found in Guimarães et al. (2016).

Isotopic analysis

Sediment samples (6-50 mg) were taken at 5 cm intervals along the sedimentary facies cores. The natural abundance of C and N stable isotopes (δ^{13}C and δ^{15}N) were analyzed in an EA 1108 CHN elemental analyzer coupled to a Delta S mass spectrometer (Finnigan MAT, Thermo Scientific™, Waltham, Massachusetts, USA) at the Stable Isotope Center of the Biosciences Institute of UNESP, Botucatu, São Paulo. BRA. The ^{13}C/^{12}C and ^{15}N/^{14}N ratios are expressed as δ^{13} C and δ^{15} N relative to Pee Dee Belemnite and atmospheric N_2, respectively, using the conventional notation δ (‰). The analytical precision was ± 0.1% and ± 0.2‰, respectively. Total Sulphur (TS) and Total Organic Carbon (TOC) at the ALS Global, Vancouver, Canada, values were obtained for approximately 0.2 g air-dried ground samples using a LECO CS-300 combustion analyzer. The binary diagrams were based on (Deines 1980, Hamilton & Lewis 1992, Meyers 1997, Troxler & Richards 2009, Sahoo et al. 2015, 2016, 2017, Smith et al. 2012, Thornton & McManus 1994).

Palynological analysis

From the TML2 core, 1-cm^3 samples were taken every 5 cm to prepare palynological slides using cold hydrofluoric acid and acetolysis (Faegri & Iversen 1989). A spore tablet of *Lycopodium clavatum* (20,848 ± 3,457 grains/tablet) was added to each sample to calculate the pollen concentration (Colinvaux et al. 1999). The palynomorphs were counted at 400x and 1000x magnification under a transmitted-light microscope (Scope.A1 with the program Zen 2.3 lite). A total of 300 pollen grains of terrestrial and aquatic taxa were counted in 27 slides (26 slides plus one to record the 133 cm of the LTM2 core). Tilia and Tilia Graph software programs were used to calculate and plot diagrams (Grimm 1990).

Palynological identification was made by comparison with the morphological characteristics found in specialized publications (Carreira et al. 1996, Colinvaux et al. 1999, Roubik & Moreno 1991) and based on the ITV/Gaban-Vale

(PaliITV Collection) and Museu Paraense Emílio Goeldi (MPEG) pollen databases. Information on the habitat of the pollen types was obtained in related literature (Hall & Gil 2016, Harley 2016, Guimarães et al. 2014, 2017, Mota et al. 2018, Nunes 2009, Pirani & Devecchi 2018, Reis et al. 2017, Da Silva et al. 2020).

The data from the pollen diagrams were grouped into canga vegetation, forest (forest patch and rainforest), macrophytes, palms, cold-adapted taxa, algae, and spores, except Poaceae and Fabaceae, given its wide dispersion across biomes. These data were statistically subdivided into pollen zones (palynozones) based on the square-root transformation of the percentage data and stratigraphically constrained cluster analysis using CONISS (constrained incremental sum of squares) (Grimm 1987).

Statistical methods

Modern pollen rain (MPR) (Da Silva et al. 2020) was used as a modern vegetation reference and as aid in the analysis of palynozones. Stats and vegan (Oksanen et al. 2019) R packages were used for statistical analyses. The concentration data of common pollen types between palynozones and MPR were considered.

The data, which included 55 common pollen types found between the modern pollen rain (Da Silva et al. 2020) and fossil pollen, were normalized for the Wilcoxon hypothesis test. To better understand the relationship between the composition of the pollen types of each palynozone and MPR, we ordered the samples using nonmetric multidimensional scaling (nMDS), which projects complex multivariate data onto a minimum number of axes. It is a nonparametric approach that uses ordered distances between samples (Bush et al. 1990, Hammer & Harper 2006, Legendre & Legendre 1998, Ter Braak 1995). It has been used in several palynoecological studies to efficiently portray the distances between samples (Absy et al. 2014, Burn et al. 2010, Bush & Brame 2010, Bush et al. 1990, Jardine et al. 2012, Schüler et al. 2014, Shi 1993). Data were double-standardization transformed and used in the meta-MDS function using the Bray-Curtis distance metric.

RESULTS

Geochronology and facies description

The sedimentation rates calculated for the TML1 and TML3 cores taken from the lake margins were 2.25-0.02 mm^{-1} yr, and for the TML2 core from the center of the lake, they were 0.30-0.02 mm^{-1} yr. The Bacon age modeling resulted in maximum deposition ages for the TML1 and TML3 cores and the TML2 core of ~11,560-7,110 cal yr BP and 17,680 cal yr BP, respectively. The 95% confidence intervals were lower in the upper part, at 2,431-2,182 years in TML1, 2,414-2,157 years in TML2, 727-586 years in TML3, and higher closer to the base, at 12,070-8,203 years in TML1, 10,130-5,131 years in TML2, 7,549-4,667 years in TML3, with a maximum and minimum in TML1, TML2, and TML3 of 72 and 48 cm, 85 cm and 56 cm, and 70 cm and 31 cm, respectively (Figure 2 and Table I).

Three sedimentary facies were described, representing a filling cycle with a fining-upwards pattern, standard of filled lakes (Figure 2; Table II). In the TML1 and TML2 cores, laminated mud (LM) occurred only at the base and in the TML3 core from the base to the middle portion. This facies was deposited from suspension with low energy flow alternating with increased energy, causing deposition of ferruginous clasts.

The LM facies were gradually superimposed by predominantly organic deposits. The organic deposits were related to granular (Pg) and herbaceous (Ph) peat. The Pg and Ph facies were present in all three cores, with plant tissue as the main source of the deposit. The contact between detritic and organic facies is gradational.

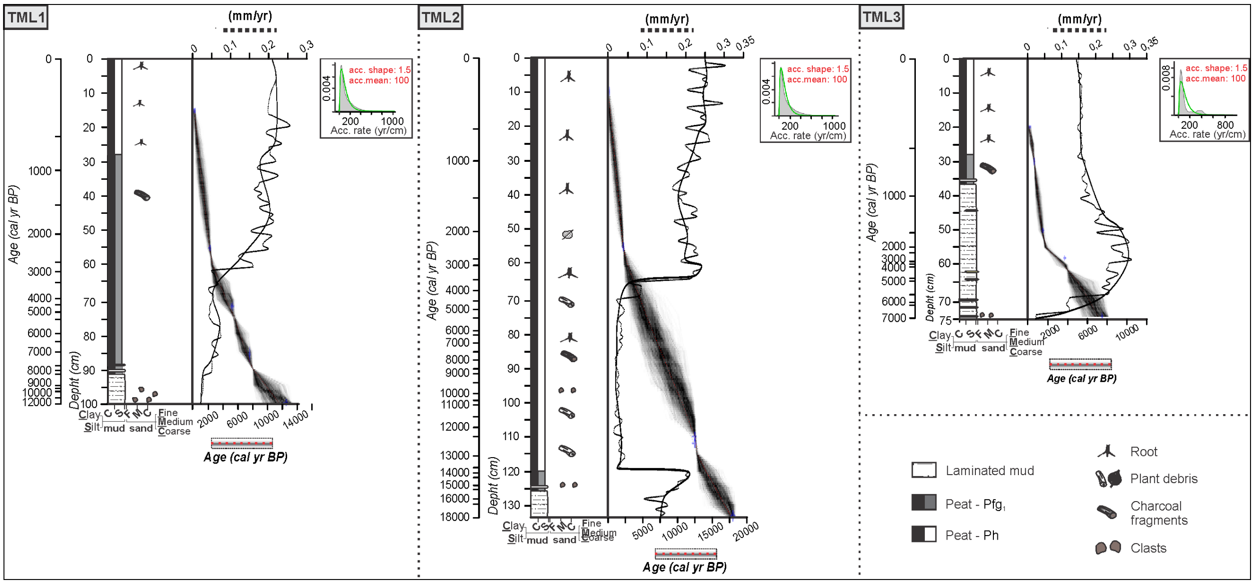

Figure 2. Graphic sedimentary record with facies characteristics and succession in TML1 (100 cm), TML2 (135 cm), and TML3 (75 cm) collected in Serra Norte de Carajás. The profiles include calibrated 14C dating, the age–depth model (the darkest shades of gray indicate probable ages), and sedimentation rates (mm/year) along the depth profile, considering the weighted mean for each depth. Each profile is accompanied by the age–depth model: the green curve is the accumulation rate (anterior), and the gray shading is the modeled accumulation rate (posterior).

Table I. Radiocarbon dates (AMS) of the samples from the Trilha da Mata Lake (TML).

Sample	Pretreatment	^{13}C (%)	^{14}C age (cal yr BP)	Cal. age, 2σ-range (cal yr BP)
TML1-15	(Organic sediment): acid wash	-28.5	150 ± 30	168-232
TML1-55	(Organic sediment): acid wash	-29.8	2,190 ± 30	2,114-2,317
TML1-72	(Organic sediment): acid wash	-28.8	4,560 ± 30	5,052-5,189
TML1-86	(Organic sediment): acid wash	-27.2	6,720 ± 30	7,563-7,624
TML1-100	(Organic sediment): acid wash	-29.6	10,530 ± 30	12,479-12,626
TML2-10	(Organic sediment): acid wash	-29.9	127 ± 30	8-151
TML2-25	(Organic sediment): acid wash	-29.2	670 ± 30	628-672
TML2-55	(Organic sediment): acid wash	-29.5	790 ± 30	671-733
TML2-95	(Organic sediment): acid wash	-28.9	2,000 ± 30	1,867-1,998
TML2-110	(Organic sediment): acid wash	-28.8	2,010 ± 30	1,869 - 2,002
TML2-112	(Organic sediment): acid wash	-28.6	2,360 ± 30	2,335 - 2,468
TML2-133	(Organic sediment): acid wash	-29	14,780 ± 50	17,939 - 18,236
TML3-10	(Organic sediment): acid wash	-29.5	120,7 ± 0,4	modern
TML3-20	(Organic sediment): acid wash	-29.2	110 ± 30	11-149
TML3-30	(Organic sediment): acid wash	-29.2	650 ± 30	555 - 605
TML3-50	(Organic sediment): acid wash	-29.6	1,590 ± 30	1,403 - 1,532
TML3-58	(Organic sediment): acid wash	-29.6	3,430 ± 30	3,575-3,726
TML3-75	(Organic sediment): acid wash	-28	6,570 ± 30	7,426-7,511

Table II. Description of the facies and sedimentary processes of the Trilha da Mata Lake cores.

Facies	Description	Sedimentary process
Laminated mud (LM)	Light-olive-brown peat (2.5Y 5/4) to dark-brown mud (2.5Y 3/2). It wassometimes interlaminated with dark-gray (2.5Y 4/2) to dark-grayish (2.5Y 4/1) peat of approximately 2-5 mm in thickness and very fine sand lenses. Locally, ferruginous angular to subrounded clasts of ~1 cm are present.	Low energy flows with entry of suspended mud clouds or mud flows into the lake basin, followed by small stages of reduced conditions that allowed the preservation of organic matter. The fine sands wererelated to relatively higher energy flows in the basal portion of the suspended mud clouds or mud flows.
Fragmented granular peat (Pfg_1)	Dark-gray peat (2.5Y 4/1), very compact and decomposed but with little plant debris <0.3 mm. Locally, charcoal fragments between 3 and 1 cm werealso seen.	Stagnant and reduced water conditions, with plant tissues as the main source of the deposit. The charcoal fragments corresponded to the burning of woody plants.
Herbaceous peat (Ph)	Grayish-brown peat (2.5Y 5/2) with many herbaceous roots of approximately 7 cm in length, in a growing position.	Stagnant and reduced water conditions with plant tissues as the main source of the deposit. Development of herbaceous plants (macrophytes) during sediment deposition.

Isotopic data

The TML cores had $\delta^{13}C$ and $\delta^{15}N$ values ranging from -27.8 to -31‰ and 3.8 to 2.1‰, respectively, which suggests an organic matter derived mainly from C3 vascular plants and/or macrophytes, and algae with C3 grasses. The C/N values of 50.7 to 10.8 were indicative of the contribution of dissolved organic carbon (DOC), terrestrial C3 plants, and canga plants (Figure 3, Supplementary Material - Figure S1, available online).

The isotopic data corresponding to the Lm facies in the $\delta^{13}C$ and C/N diagram are more dispersed than those in the $\delta^{15}N$ and $\delta^{13}C$ diagrams due to higher C/N ratios (Figure 3). These higher ratios were due to C3 and canga plants, which reinforces the contribution of terrestrial organic matter (~18,000-15,500 cal yr BP), with a gradual change toward greater contributions from DOC, algae, and macrophytes (~3,500 cal yr BP to the present). The C/N ratio decreased in the Pg facies (Figure 3a), indicating an increase in DOC. The relationship between $\delta^{15}N$ and $\delta^{13}C$ indicates a diversified origin of the organic matter, including macrophytes, algae with grasses, Carajás marshes, and C3 plants (Figure 3b). The lowest DOC-related C/N ratios were found in the Ph facies, and the relationship between $\delta^{15}N$ and $\delta^{13}C$ reveals a contribution similar to that observed in the Pg facies, with an increased contribution of macrophytes.

Palynological data

The TML2 core, collected from the central portion of the lake, tended to best represent the local pollen signal, thus favoring the interpretation of its assemblage in relation to the MPR composition according to the previous modern pollen rain study in the same lake (Da Silva et al. 2020). In addition, the cores collected on the margins of the lake represented disturbed areas subject to overrepresentation of certain pollen types from lake shore plants (Colinvaux et al. 1999).

In general, 82 morphotypes were determined, distributed among canga vegetation (34 types,

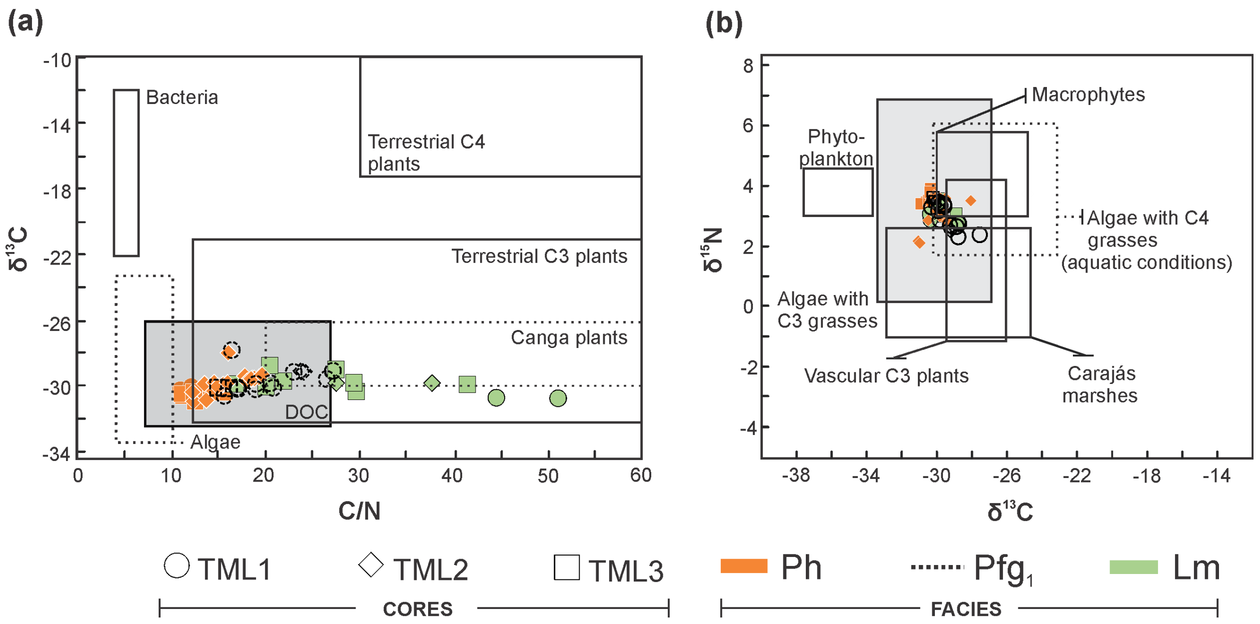

Figure 3. Binary diagrams of Trilha da Mata Lake. The cores are represented by geometric shapes; a) δ^{13}C and C/N; b) δ^{15}N and δ^{13}C (Fields based on Deines 1980, Hamilton & Lewis 1992, Thornton & McManus 1994, Meyers 1997, Troxler & Richards 2009, Smith et al. 2012, Sahoo et al. 2015, 2016, 2017, Guimarães et al. 2023a).

2-53%; 10-16,854 grains/cm^3), forest (23 types, 5-68%; 37-13,449 grains/cm^3), macrophytes (8 types, 0-23%; 0-5,788 grains/cm^3), palms (five types, 0-11%; 0-6.299 grains/cm^3), cold-adapted taxa (one type, 0-8%; 0-2.213 grains/cm^3), algae (three types, 18-58%; 17-37.453 colonies /cm^3) and spores (six types, 0-4%; 0-1873 spores/cm^3), Poaceae undif. (0-41%; 0-21,791 grains/cm^3) and Fabaceae (0-9%; 0-170 grains/cm^3) The most representative canga vegetation types were Asteraceae (0-27%; 0-13,960 grains/cm^3) and *Borreria* (0-4%; 0-3,064 grains/cm^3). From the forest, the most representative were *Aparisthmium/Alchornea* (0-56%; 0-9,363 grains/cm^3), *Glycydendron* (0-5%; 0-1,192 grains/cm^3) and Anacardiaceae (0-7%; 0-170 grains/cm^3). Macrophytes were represented by Cyperaceae undif. (0-14%; 0-3,575 grains/cm^3) and *Echinodorus* (0-6%; 0-2,213 grains/cm^3); palms were represented by *Mauritiella armata* (0-7%; 0-5,958 grains/cm^3) and *Attalea maripa* (0-1.5%; 0-340 grains/cm^3); cold-adapted taxa were represented by *Hedyosmum* (0-6%; 0-2,213 grains/cm^3); algae were represented by *Zygnema* (0-34%; 17-24,344 colonies /cm^3); and spores were represented by Microgramma (0-3%; 0-1,872 spores/cm^3) (Figure 4 and Figure S2, available online).

The palynological assemblage was subdivided into five pollen zones. Zone 1 (14.000-18.000 cal yr BP) had the highest percentages and concentrations of *Hedyosmum* (1-6%; 170-2,213 grains/cm^3) and canga vegetation (2.5-53%; 10-16,854 grains/cm^3) and algae (13-45%; 6,809-37.453 grains/cm^3). It had a predominance of Poaceae undif. (20-41%; 4,639-21.791 grains/cm^3), Asteraceae (10-27%; 2,085-13.959 grains/cm^3), *Borreria* (3-4%; 808-3,064 grains/cm^3), *Cuphea* undif. (2-3%; 340-1,872 grains/cm^3), and *Zygnema* (6-32%; 1,702-24,344 grains/cm^3). Minor values were found for palms (0-0,3%; 0-340 grains/cm^3), macrophytes (2-1%; 85-851 grains/cm^3), and spores (0-2.5%; 0-1,872 grains/cm^3) (Figure 4 and Figure S2, available online).

Zone 2 (8.500-13.500 cal yr BP) showed decreased values of *Hedyosmum* (0-1%; 0-19

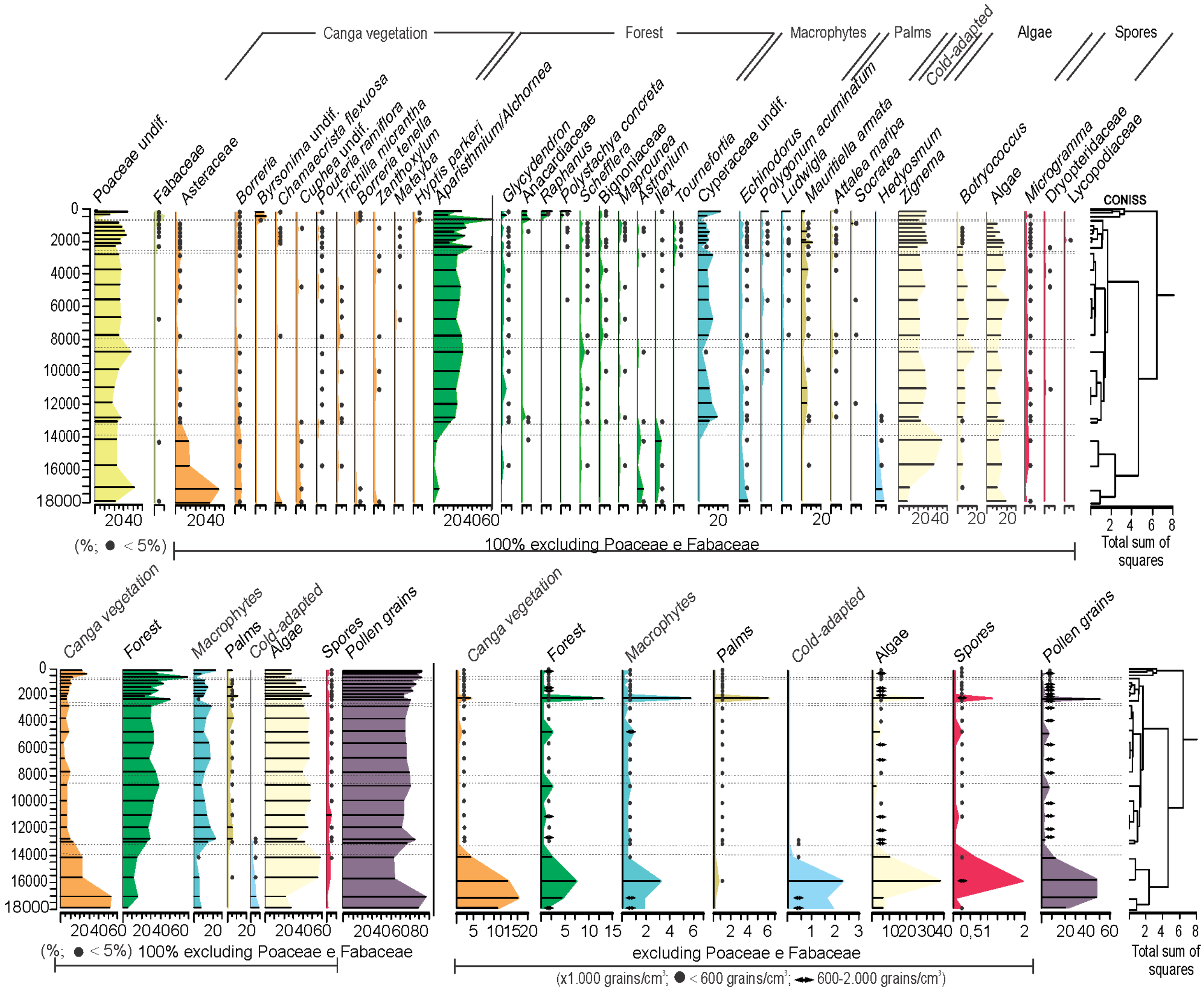

Figure 4. Percentage pollen diagram with the main pollen types obtained from sedimentary records of the TML2 core (lake depocenter) of Lagoa da Trilha da Mata, Serra Norte de Carajás, southeastern Pará state, Brazil. Pollen records of ~18000 cal BP are presented in five pollen zones, values lower than 5% are represented by a dot.

grains/cm^3) and canga vegetation (2.5-13%; 10-16,854 grains/cm^3) and increased values for forest vegetation (5-25%; 365-13,449 grains/cm^3) and macrophytes (2-17%; 112-526 grains/cm^3). Records of *Hedyosmum* extended up to ~12,500 cal yr BP. The main pollen types were *Aparisthmium/Alchornea* (forest, 13-20%; 304-1,668 grains/cm^3), *Glycydendron* (forest, 1-3,5%; 14-136 grains/cm3), and *Schefflera* (forest, 0-2,5%; 0-238 grains/cm^3). Macrophytes were represented by Cyperaceae undif. (1,5-13%; 76-417 grains/cm^3) and *Echinodorus* (1-2%; 10-204 grains/cm^3). Poaceae undif. remained over represented (17-37%; 365-3,472 grains/cm^3) (Figure 4 and Figure S2, available online).

In zone 3 (3,000-8,000 cal yr BP), there was an increase in algae and a decrease in the concentrations of other groups. However, this zone was over represented by Poaceae undif. (23-26%; 315-567 grains/cm^3), Asteraceae (0-3.5%; 0-170 grains/cm^3), *Pouteria ramiflora* (0-1%; 0-106 grains/cm^3), *Aparisthmium/Alchornea* (forest, 16-22%; 195-1,893 grains/cm^3), *Glycydendron* (0.5-2%; 11-170 grains/cm^3), *Maprounea* (0-1.5%; 0-127 grains/cm^3), Cyperaceae undif. (6-10%; 70-617 grains/cm^3), *Polygonum acuminatum* (0-1.5%;

0-33 grains/cm3), *Mauritiella armata* (1,54%; 26-149 grains/cm^3), and *Zygnema* (14-20%; 205-1915 colonies /cm^3) (Figure 4 and Figure S2, available online).

In zone 4 (750-3,000 cal yr BP), the pollen concentrations of the groups increased. The main types were Poaceae undif. (21-33%; 260-21,791 grains/cm^3), Asteraceae (0.5-3%; 13-1,872 grains/cm^3), *Chamaecrista flexuosa* var. *flexuosa* (0-2%; 0-1,021 grains/cm^3), *Aparisthmium/Alchornea* (12-30%; 284-9,363 grains/cm^3), Bignoniaceae (0-2%; 0-1,364 grains/cm^3), Cyperaceae (1-7%; 9-3,575 grains/cm^3), *Mauritiella armata* (2-8%; 24-6,299 grains/cm^3), *Zygnema* (14-21%; 173-17,024 grains/cm^3), and Microgramma (0.5-1%; 7-1,021 spores/cm^3) (Figure 4 and Figure S2, available online).

In zone 5 (<750 cal yr BP), forest pollen was predominant (30-68%; 37-738 grains/cm^3). Lower pollen concentration rates were recorded here. The main taxa were *Aparisthmium/Alchornea* (11-55%; 52-522 grains/cm^3), Anacardiaceae (forest, 0-7.5%; 0-56 grains/cm^3), *Glycydendron* (0-5%; 0-34 grains/cm^3), Poaceae undif. (0-34%; 0-1,293 grains/cm^3), *Borreria tenella* (0-4%; 0-90 grains/cm^3), *Byrsonima* undif. (0-8%; 0-34 grains/cm^3), Cyperaceae undif. (0-14%; 0-533 grains/cm^3), *Polygonum acuminatum* (0-6%; 0-16 grains/cm^3), *Mauritiella armata* (0-2%; 0-68 grains/cm^3), *Zygnema* (17-20%; 17-669 colonies /cm^3), and Microgramma (0-2%; 0-6 spores/cm^3) (Figure 4 and Figure S2, available online).

Statistical analysis

When performing the Wilcoxon hypothesis, MPR pollen composition differed from palynozones 1 (W - 25, p = 2754e-09), 2 (W = 374, p = 5748e-05), 3 (W = 442, p = 0.001145), and 4 (W = 334, p = 1389e-05). Only palynozone 5 had simillar MPR composition (W = 759, p = 0.1192). Therefore, the null hypothesis was rejected, indicating a difference between the modern MPR and the pollen composition of zones 1, 2, 3, and 4. The p-value of MPR vs. zone 5 group does not allow the null hypothesis to be rejected; therefore, there was not a substantial difference between groups (Figure 5a). The NMDS plot (Figure 5a) shows that the distributions of zones 2, 3, and 4 are clustered. The proximity between the samples from zone 5 and MPR was also evident. Zone 1 samples showed little relationship with samples from the other zones (Figure 5b). This result was consistent with the results obtained in the Wilcoxon analysis, in which Zone 1 was isolated, Zone 5 and MPR showed similar groups, and there was proximity between the samples from zones 2, 3, and 4 (Figure 5a).

nMDS plot show zones 1 to 4 had negative values, whereas zone 5 and MPR had positive values nMDS1 axis (Figure 5a). The positions of the samples from zone 1 were influenced by Asteraceae, Ilex, *Cuphea* undiff., *Astronium*, and *Euphorbia*. Zones 2, 3, and 4 were mainly influenced by *Mauritiella armata*, Cyperaceae undif., Bignoniaceae, *Schefflera*, *Banisteriopsis malifolia*, *Trichilia micrantha* and *Fridericia*, and zone 5 with MPR was mainly influenced by *Sauvagesia, Serpocaulon*, Smilax, *Psychotria* and *Mimosa acutistipula*, *Protium pilosissimum*, *Byrsonima* undif., and *Hyptisparkeri* (Figure 5b).

DISCUSSION

History of lake filling and organic sources

Differences in confidence intervals of the age modelling of studied cores is probably due to the combined effects of greater calibration uncertainties, increased dispersion, and decreased sample density (e.g, Shanahan et al. 2012). The inversion of the ages at depths between 23 and 55 cm in TML2 core and 20 to 30 cm in TML3 core may be due to root penetration (Guimarães et al. 2016).

The sedimentation rates of the TML cores are in agreement with the value of 0.69-0.02

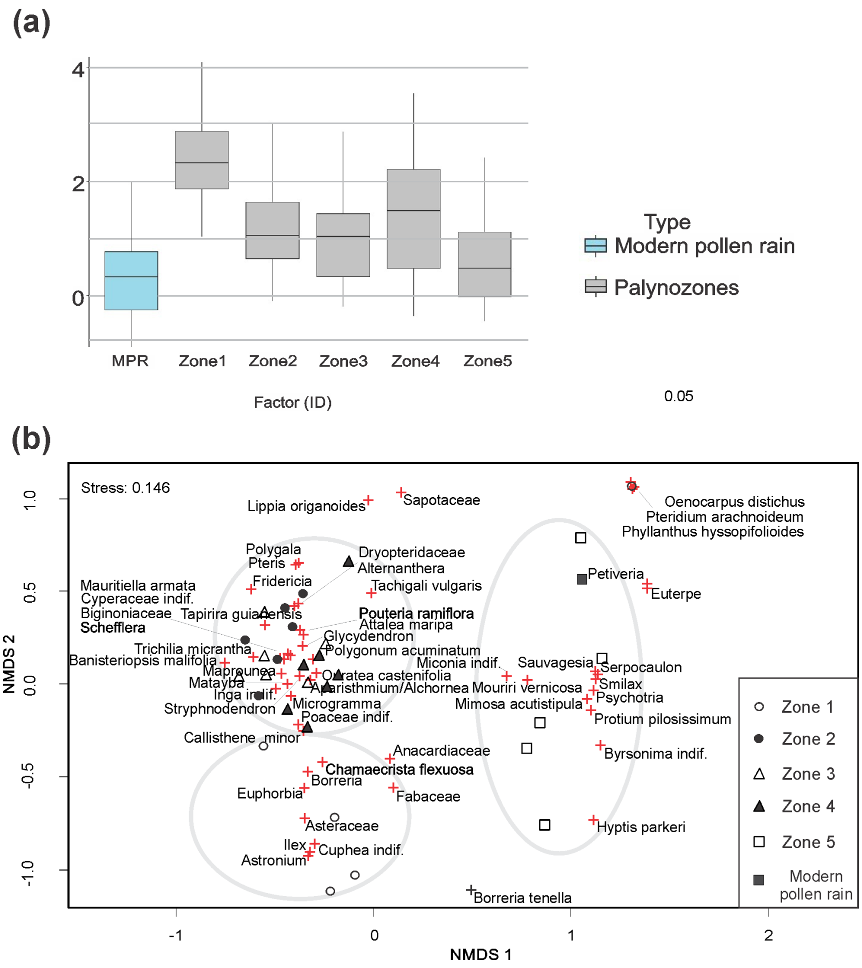

Figure 5. a) Boxplot of the palynozones of the TML2 core compared to modern pollen rain of Trilha da Mata lake obtained from Da Silva et al. (2020), Serra Norte de Carajás; b) NMDS analysis of the distribution of the pollen types of sedimentary samples and modern pollen rain in the Trilha da Mata Lake.

mm^{-1} yr found in previous paleoenvironmental studies (Guimarães et al. 2016, Hermanowski et al. 2012, Reis et al. 2017, Sifeddine et al. 2001) in Serra Sul de Carajás, and the value of 0.67-0.05 mm^{-1} yr found by (Cordeiro et al. 2008) in Serra Norte de Carajás.

Filling of the lake was started by the deposition of detrital sediments ~ 18,000 cal yr BP, which changed to organic sediments around 15,000 cal BP in the lake depocenter and around 8,000 cal yr BP and 1,000 cal yr BP in the western and eastern margins, respectively. The eastern margin represents an active drainage inflow of the lake with high sediment mobility and transport. The organic matter was derived from aquatic environments, with contributions by algae with C3 and C4 grasses, macrophytes, and marsh plants. However, the low δ^{13}C values represented vascular C3 forest plants, and the canga vegetation presented more enriched δ^{13}C values for having adapted to periods of water scarcity (Mitre et al. 2018). The lowest values of δ^{13}C, which are close to -31‰, most likely represent the forest signal. Organic matter in the Carajás lakes can originate from the vegetation cover of the drainage or from primary or secondary productivity (Sahoo et al. 2017), which may vary over time. *In situ* organic production of DOC, algae, and macrophytes indicated a strong contribution of the aquatic environment, but the isotopic data indicates that the canga vegetation and forest are important sources for lake sediments. The continuous record of algae without other physical and geochemical indicators indicates that even the dry periods were not intense enough to cause subaerial exposure of the lake.

Paleovegetation dynamics and the relationship with the paleoclimate

~14,000-18,000 cal yr BP – Early Pleistocene

The catchment area of the lake was weathered, with mud flows from the drainage basin deposited by suspension in the depocenter. Small stages of reduced energy preserved the organic matter and high pollen concentration and recorded the allochthonous signal of the canga vegetation and the forest C3 plants up to ~15,000 cal yr BP. Between 14,000 and 15,500 cal yr BP, the high humidity favored the production of DOC, followed by a constant contribution of the aquatic environment with DOC and algae on C3 grass (Figure S3).

Hedyosmum indicated low temperature, but it was not sufficient for the expansion of other cold-adapted populations limited by higher-altitude temperatures (Colinvaux et al. 2000). In the Early Pleistocene in Carajás, several cold-climate taxa have been described such as *Hedyosmum*, *Myrsine*, *Podocarpus*, *Styrax* and *Alnus* (Absy et al. 1991, Hermanowski et al. 2012, 2014, Reis et al. 2017).

The canga, algae, and forest pollen types are dominant, range from 21-53% and 3,532-16,854 grains/cm^3, 21-58% and 6,128-37,453 colonies/cm^3 and 5-15% e 1,191-7,490 grains/cm^3, respectively. The dominance of canga pollen in relation to the forest demonstrates its expansion. However, the good representation of the forest pollen types demonstrates that the expansion of the canga presented a certain limitation.

The canga and forest vegetation showed a well-developed mosaic with Asteraceae, *Aparisthmium/Alchornea, Ilex*, *Byrsonima*, *Borreria*, and *Cuphea*, used as indicators of dry climate and expansion of areas of canga vegetation, in addition Poaceae (Absy et al. 1991, D'Apolito et al. 2017, Van De Hammen & Absy 1994).

Pollen types in the Asteraceae, *Borreria*, *Cuphea*, and Poaceae have numerous species that colonize marshes and lakesides (Cavalcanti et al. 2016, Colinvaux et al. 2000, Cruz et al. 2016, Viana et al. 2019, Zappi et al. 2017). Thus, it is not possible that they represent dry-climate vegetation. Furthermore, the high sedimentation rate and algal concentration indicate that the conditions were humid. In addition, *Ilex* would not withstand dry conditions (Reis et al. 2017). A humid climate has also been described for the Bolivian Altiplano (Baker et al. 2001) and for Serra Sul de Carajás (Reis et al. 2017).

~8,500-13,500 cal yr BP – Transition between Early Pleistocene and Holocene

This period was marked by increased temperatures, as indicated by the records of *Hedyosmum* occurring up to ~12,500 cal yr BP. The sedimentation process occurred with reduced and stagnant water and low sedimentation rates. However, the diversity and concentration of macrophytes and palm trees increased. Decreased rainfall exposed flooded areas and established a swampy environment (Figure S3). Increased frequency and richness of macrophytes and palm trees was also observed in Serra Sul de Carajás (Reis et al. 2017). The dominance of pollen types of canga vegetation observed in the previous period was changed to dominance of pollen types of forest, especially *Aparisthimium/Alchornea*, thus maintaining sufficient moisture content to sustain forest species. Geochemical evidence in Serra Sul de Carajás reinforces this interpretation (Guimarães et al. 2021).

~4,500 to 8,000 cal yr BP – Middle Holocene

From ~4,000-8,500 cal yr BP, marsh vegetation and *Mauritiella armata* were established in the southwestern margin, and around 4,000 cal yr BP (Figure S3), the margins showed isotope signals corresponding to macrophytes (-30 to -25 δ^{13}C, 3.0 to 5.8 δ^{15}N; Guimarães et al. 2021). Taxa associated with environments with water stress were recorded, including *Chamaecrista flexuosa*, *Matayba*, and *Mouriri vernicosa* (Barbosa et al. 2018, Mattos et al. 2018, Rocha et al. 2017). The period of 4,500-9,000 cal yr BP recorded the highest concentration of *Botryococcus*, a genus represented by species adapted to shallow waters or ephemeral lakes (Cordeiro et al. 2008). Despite the increase in precipitation rates, the dry periods were significant, causing greater fluctuations in the lake's water level. The positive relationship between canga and forest does not indicate an intense retraction of the forest or expansion of the canga, but revealing local changes in floristic composition.

Charcoal fragments are local evidence of the occurrence of fires between 7,500 and 8,000 cal yr BP. In Serra Norte de Carajás, (Cordeiro et al. 2008) highlighted these events at 4,750-7,450 cal yr BP associated with the dry climate (Absy et al. 1991, Bush et al. 2007, Cordeiro et al. 1997, Moreira et al. 2013a, Moreira et al. 2013b, Sifeddine et al. 1994, Vidotto et al. 2007) suggest a dry phase in the Amazon region during the Mid-Holocene. In addition, the decrease in the flow of the Amazon River has been associated with drier periods (Guimarães et al. 2012). In the Carajás region, the rainfall levels dropped from the Late to the Middle Holocene (Absy et al. 1991, Cordeiro et al. 2008, Hermanowski et al. 2012, Turcq et al. 1998, Reis et al. 2017, Guimarães et al. 2021, 2023a, b).

~3,000 to 4,000 cal yr BP – Early Holocene

From 3,000-4,000 cal BP, conditions became humid, as indicated by the increased sedimentation rate (0.07-0.24 mm^{-1} yr). Increased moisture favored algal diversity, intensifying competition among these organisms and decreasing the concentration of *Botryococcus*. The occurrence of Dryopteridaceae reinforces the humid climate. The species that occur in Carajás are associated with the presence of water bodies (Moura & Salino 2016).

~750-3,000 cal yr BP – Early Holocene

Hot and humid environmental conditions were maintained. This interpretation is supported by the high sedimentation rates (0.17-0.24 mm^{-1} yr) and the increased pollen concentration. High abundance of forest elements such as *Aparisthmium/Alchornea*, *Mauritiella armata* palm, Zygnema colonies, Microgramma ferns support wet conditions during this period. Pollen data from eastern Bolivia indicate a 2,790-year cal yr BP increase in moisture, in agreement with our interpretation. The authors attribute the observed precipitation increases during this period to a southward shift of the Intertropical Convergence Zone (Mayle et al. 2000). The increase in canga vegetation, mainly those more adapted elements, was influenced by the flooded area due to increased rainfall, as shown by Mayle et al. (2000), and specially by Da Silva et al. (2020) for the studied area. The expansion of macrophytes and palms also exerted a strong influence on the high sedimentation rates of autochthonous organic sedimentation. This finding corroborates Cordeiro et al. (2008) and the results from other lakes in Amazonia (Bush et al. 2004, Cohen et al. 2014, Reis et al. 2017, Guimarães et al. 2012, Souza et al. 2021, Burbridge et al. 2004).

<750 cal yr BP – Early Holocene to the present

Intensification of the expansion of macrophyte and palm populations accelerated the filling process (Figure S3), with colonization by

Cyperaceae, *Polygonum acuminatum* and *Mauritiela armata* pollen, as observed by Da Silva et al. (2020) based on modern pollen traps in the studied area.

Seasonal floods became frequent following lake filling, as suggested by the presence of *Hyptis parkeri*, which stays submerged part of the year and blooms only when the soil is dry (Harley 2016). Hydrological dynamics, in which the lake surroundings flood for a short time followed by months of dry soil, is described by Da Silva et al. (2020), who stated that this process influences the composition of the pollen assemblage, as confirmed by the nMDS analysis, which showed similarity between the samples from zone 5 (<750 cal yr BP) and the MPR Da Silva et al. (2020).

Despite the observed trend of increased humidity for the Late Holocene, episodic drought events may have occurred (Souza et al. 2021). Transition regions close to the limits of the Amazonia rainforest exhibit a more seasonal climate, characterized by periods of high precipitation with periods of drought (McMichael et al. 2012). In Carajás, the increase in the record of sponge species, adapted to lower lake levels and the increase in charcoal accumulation rates between 1.300 and 70 cal yr BP suggest periods of short drier events (Cordeiro et al. 2008). Drier conditions favor the spread of fires, whereas wetter periods can prevent the spread of these events (Souza et al. 2021).

Interpretation of the Poaceae pollen concentration

Some studies have already called attention to the ambiguous behavior of Poaceae in tropical forests (Colinvaux & De Oliveira 2000, Guimarães et al. 2014, 2016, Absy et al. 2014, Bush 2002, Reis et al., 2017, 2022). However, some studies have associated the increased concentrations to a dry climate and environment, as well as the expansion of areas with open vegetation (Absy et al. 1991, Behling et al. 2001, D’Apolito et al. 2017, Hermanowski et al. 2014, Hooghiemstra & Van der Hammen 1998, Van De Hammen & Absy 1994).

Poaceae undif. occur in the nMDS between the group formed by a wet period, zone 1 (14,000-18,000 cal yr BP), and those formed by zones 2, 3, and 4 (750-13,500 cal yr BP), which are considered to be relatively dry, relatively stable percentage and concentration, mean of 23% and 3,160 grains/cm^3, respectively. Furthermore, as demonstrated by Da Silva et al. (2020), the influx of Poaceae pollen grains can increase even in periods of high humidity, as observed in the pollen assembly of inorganic sedimentary facies. Species from temporary and swampy lakes, canga vegetation and forest have already been reported in the studied area by Da Silva et al. (2020), making evident the ecological range of this family.

Paleoenvironmental dynamics and future perspectives

Guimaraes et al. (2023a) based on a multiproxy approach in 11 lacustrine cores covering different plateaus of the Carajás region demonstrated that active upland lakes never dried up during the last 50 ka cal yr BP. In contrast, subaerial exposure occurred in some inactive lakes (swamps) during the Last Glacial Maximum (LGM) and the Holocene, as well as extensive siderite precipitation and some local expansion of C4 plants related to dry paleoclimate conditions. However, even these drier conditions were not sufficient to produce extensive replacement of humid evergreen tropical forests by savannah on the Carajás plateau in this period. It depends on the geomorphology and lithological properties of lake basins, which are quite variable in these plateaus (Da Silva et al. 2018). Indeed, based on the analysis of paleovegetation with modern pollen rain, the isotopic and palyonological data in this study demonstrate that the climatic variations were not intense enough to define significant changes to the forest area in order to reduce its area. The pollen concentrations of canga and forest vegetation showed similar increasing and decreasing trends. The frequency of *Microgramma*, common in rainforest (Almeida et al. 2017), reinforced the continuous representation of the forest. Thus, the paleoclimatic variations did not determine the expansion of canga vegetation into areas of tropical forest, as discussed in some studies (Absy et al. 1991, Van De Hammen & Absy 1994, Sifeddine et al. 2001, Hermanowski et al. 2014, D'Apolito et al. 2017, Turcq et al. 2002).

The analyses relating paleovegetation and modern pollen rain show that the climatic dynamics caused changes in the association of the pre-existing species, with the expansion of populations of the most adapted species and the retraction of the most sensitive species to new environmental conditions. In periods of greater humidity: Fabaceae, Asteraceae, *Cuphea*, *Chamaecrista flexuosa*, *Borreria tenella, Hyptis parkeri, Aparisthmium/Alchornea, Raphanus, Ilex* and *Tournefortia*. In relatively drier periods: *Trichilia micrantha, Zanthoxylum,* Bignoniaceae, Cyperaceae and *Socratea*.

The data showed that these changes intensified when the lake became inactive, causing significant changes in the dynamics of the water balance and thus determining an intense selection of species adapted to the new ecological dynamics of the area. Climatic variations influenced changes in the species composition, since differences in the pollen assembly of the Early Pleistocene were confirmed, in comparison to the Late and Middle Holocene and the Early Holocene. However, the similarity between the assembly registered in the last 750 cal yr BP with modern pollen rain and its distance from the assemblies from other periods, indicates besides the changes in the lake water balance also the anthropic action that accelerates the process of climate change. Although it is recent, the anthropic action was intense compared to natural processes and may has played a major role in the composition of species in more recent periods of the Early Holocene, as pointed out by (Esquivel-Muelbert et al. 2017, Harrison et al. 2015, Van der Sande et al. 2016, Van der Sande et al. 2019).

Suppression on a landscape at the expense of the expansion of savannah in tropical forests would only be possible with the convergence of factors such as decreased rainfall, increased temperatures, and the relatively constant incidence of fires, the latter being the greatest threat to the maintenance of tropical forests (Bush 2017). However, the combined occurrence of these factors, even with occasional records, resulted in a decrease in the pollen representation of all vegetation types and a rearrangement of the most representative species, demonstrating the resilience of the forest landscape even with the combination of adverse conditions.

Bush (2017) showed that in the future, it is very likely that climatic conditions will be unstable and that the frequency and intensity of extreme drought and flood events will increase, which may decide the future of the region. Our results, as well as those obtained by Wang et al. (2017), suggest that the Amazonia rainforest is resilient in a lower rainfall scenario. However, changes in land use, deforestation and large-scale burning can result in trends similar to savannization in the Amazonian rainforest (Bush 2017, Nobre & Nobre 2002). Therefore, in order to preserve the Amazonian Forest and maintain its ecosystem services, it is necessary to reduce deforestation rates and, mainly, to promote land use that excludes fire, otherwise destabilized climates will quickly lead to the degradation of this habitat (Bush 2017).

CONCLUSIONS

The organic matter of TML has a local origin. The organic components indicate changes in the paleoclimate and in the contribution of the paleovegetation, i.e., from wet conditions followed by long periods of peat deposition with a strong DOC contribution, which signal relatively dry conditions until the beginning of the Early Holocene.

The results indicate that drought was not intense enough to cause subaerial exposure of the lake. However, the signs of variations in temperature and humidity are clear. The record of cold-climate taxa during the Early Pleistocene indicates lower temperatures than in the Holocene.

In the transition from the Pleistocene to the Holocene, rainfall reduced the flooded area and established a marsh environment. However, the decreased rainfall was not enough to dry the lake. Temperatures were higher during the Holocene. In the Late and Middle Holocene, the humidity was relatively low, different from the Early Holocene.

The change from an active to an inactive lake condition directly affected the pollen concentration of the taxa most sensitive to seasonal floods. Thus, the most recent pollen rain, especially of canga vegetation, represents the selection of species adapted to flood events followed by periods with completely dry soil.

The occurrence of forest pollen types does not support the hypothesis of forest fragmentation, but changes in plant associations were observed throughout the events. Our data reinforce the hypothesis of forest stability in the face of climate change.

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SUPPLEMENTARY MATERIAL

Figure S1-S2.

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