

# An 8700-year record of the interplay of environmental and human drivers in the development of the southern Gran Sabana landscape, SE Venezuela

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T Ballesteros,<sup>1,2</sup> E Montoya,<sup>3</sup> T Vegas-Vilarrúbia,<sup>1</sup> S Giralt,<sup>4</sup> MB Abbott<sup>5</sup> and V Rull<sup>2</sup>

## Abstract

The vegetation of the southern Gran Sabana (SE Venezuela) consists primarily of a treeless savanna with *morichales* (*Mauritia flexuosa* palm stands), despite the prevailing climate being more favorable for the development of extensive rainforests. Here, we discuss the results of our 8700-year paleoecological reconstruction from Lake Encantada based on the analysis of pollen, algal remains, charcoal, and geochemical proxies. We use the findings to assess a number of hypotheses that seek to explain the dominance of savanna vegetation and consider the relative importance of factors such as climate, fire, and erosion on the landscape. The reconstruction of vegetation changes suggests the following trends: open savanna with scattered forest patches (8700–6700 yr BP), forest-savanna mosaic (6700–5400 yr BP), open savanna with forest patches (5400–1700 yr BP), and treeless savanna with *morichales* (1700 yr BP–the present). We conclude that the interplay between climate and fire and the positive feedback between the presence of grasses and increased fire frequency played a major role in the vegetation dynamics from the early to middle Holocene (8700–6700 yr BP). The synergistic action between reduced fires and wetter conditions appears to be a determinant in the development of rainforest around 6700 yr BP. Despite higher available moisture at ~5400 yr BP, the savanna expanded with the increased frequency of fire, potentially driven by human land-use practices. We also propose that the interplay between fire and erosion created forest instability during the middle and late Holocene. The current southern Gran Sabana landscape is the result of the complex interplay between climate, fire, erosion, and vegetation.

## Keywords

environmental drivers, feedbacks, land-use practices, Neotropics, savanna expansion, vegetation dynamics

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## Introduction

Savanna is one of the most extensive tropical ecosystems, covering approximately 20% of the Earth's land surface, and occurring over a broad range of climatic, edaphic, and topographic conditions. Fire frequency is high in Savanna ecosystems from both natural and anthropogenic causes. This biome occurs in areas showing annual precipitation values between 300 and 1800 mm; values above 600–820 mm/yr correspond to humid ecosystems (Accatino and De Michele, 2013). The presence of savanna in these high-rainfall areas suggests that climate alone is not responsible for the distribution of this biome (Murphy and Bowman, 2012). Instead, the interplay of environmental drivers such as climate, soil development, geomorphology, land use, and fire frequency are important factors that influence the presence of savanna in areas that could be covered by tropical rainforest. Despite an increased understanding of how these drivers influence the evolution of savanna (Jeltsch et al., 2000; Murphy and Bowman, 2012), the underlying ecological processes and interactions that maintain this ecosystem are not well understood. Probably multiple factors operate at different spatial and temporal scales (Jeltsch et al., 2000), and their feedbacks with vegetation and soils contribute to the establishment and maintenance of the savanna physiognomy (Beckage et al., 2009; Hoffmann et al., 2012a, 2012b). Savanna

areas have experienced remarkable expansions in the last millennia (Behling and Hooghiemstra, 1999; Breman et al., 2011; Montoya and Rull, 2011) largely caused by the increased occurrence of human-caused fires. In order to prevent further expansion, an improved understanding of the interplay between human and environmental drivers is needed.

The Venezuelan Gran Sabana (GS) region is an upland savanna located in southeastern Venezuela (Figure 1a) and is situated within the extensive Guayanan and Amazon rainforests (Barbosa and Campos, 2011). Even though the regional climate is suitable for the development of rainforest vegetation, the

<sup>1</sup>University of Barcelona, Spain

<sup>2</sup>Botanic Institute of Barcelona (IBB-CSIC-ICUB), Spain

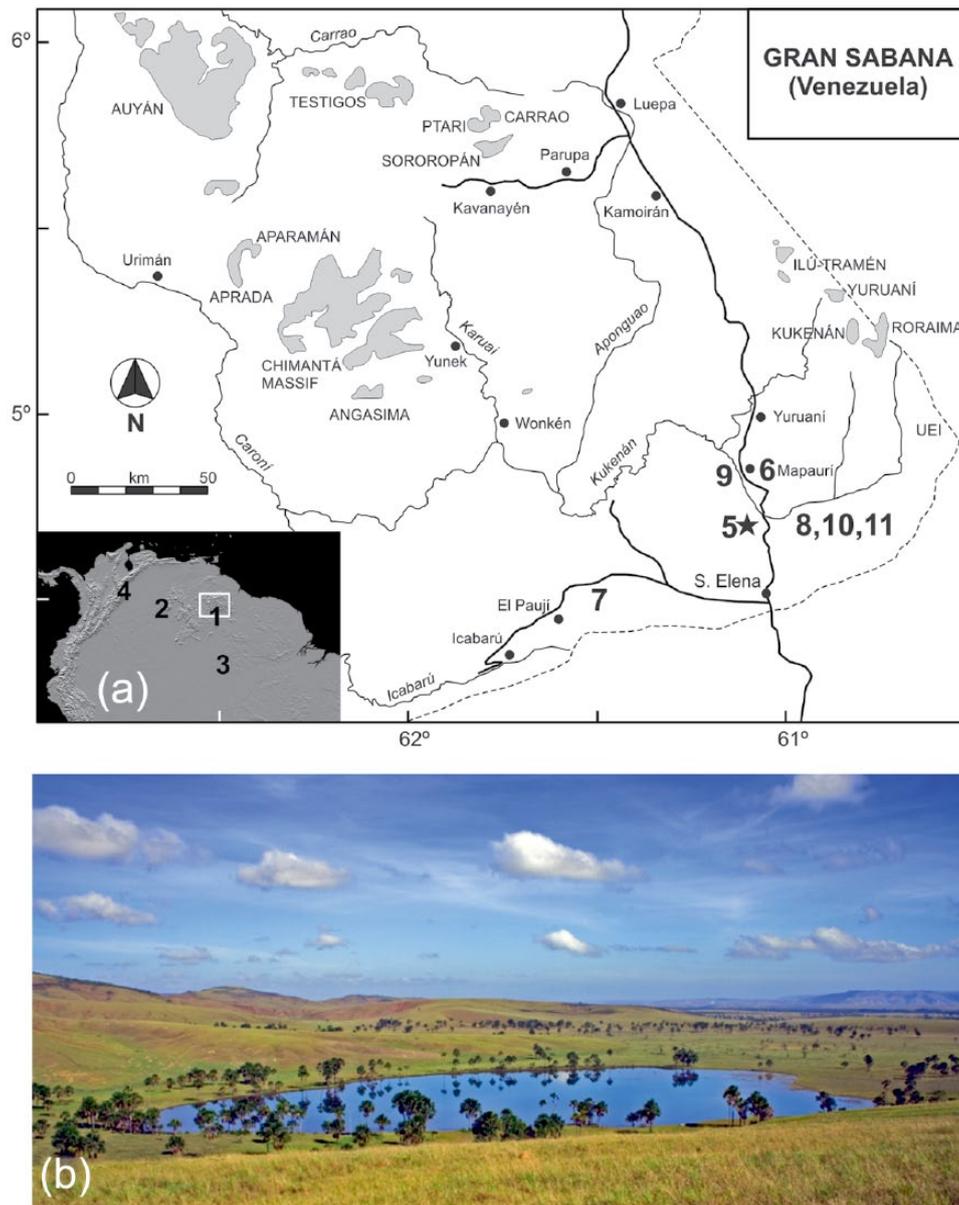
<sup>3</sup>The Open University, UK

<sup>4</sup>Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), Spain

<sup>5</sup>University of Pittsburgh, USA

## Corresponding author:

T Ballesteros, Department of Ecology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.  
Email: tmballesteros@gmail.com



**Figure 1.** (a) Location of the study area and its position within northern South America. The Gran Sabana is delimited by the white square. The coring site is indicated by a star. Numbers indicate the sites with paleoecological information mentioned in the text: 1 – Roraima savannas; 2 – Llanos (Llanos Orientales of Colombia and Venezuelan Orinoco llanos); 3 – Northern Amazonia; 4 – Encantada peat-bog; 6 – Mapauri; 7 – El Pauji; 8 – Lake Chonita; 9 – Urué; 10 – Divina Pastora; 11 – Santa Teresa. (b) Lake Encantada. *Morichales* bordering the lake shore. Regional open savanna landscape (photo: V. Rull, 2007).

vegetation of the GS is savanna and has persisted since the beginning of the Holocene (Montoya et al., 2011a; Rull, 2007). Three hypotheses have been proposed to explain the long-term presence of savanna vegetation in the GS. First, the climatic hypothesis suggests that the GS savannas are the relicts of larger savanna extensions that originated in drier and/or colder epochs (e.g. Last Glacial Maximum) (Eden, 1974). Second, the fire hypothesis presumes that frequent burning, potentially from anthropogenic sources, formed and maintained the savanna ecosystem. The more recent savanna expansion (~2000 yr BP—the present) appears to have been caused by human-induced forest clearing through burning (Montoya et al., 2011b, 2011c). The absence of archaeological studies to date in the GS currently limits our knowledge of the timing of human occupancy, as well as the associated land-use practices. Third, the edaphic hypothesis suggests that unfavorable soil conditions in the GS, such as low nutrient concentrations, low water retention, and a shallow soil profiles suppress forest growth resulting in Savanna

development (Dezzeo et al., 2004; Fölster et al., 2001). Modern short-term studies limited to the last several decades highlight the negative impacts of soil stress on vegetation and the landscape (Dezzeo et al., 2004; Fölster et al., 2001), although there are no studies to date that have focused on the influence of soil development on vegetation over longer timescales (centuries to millennia). A study of the long-term vegetation dynamics is required in order to assess these hypotheses and determine the interplay between climate, vegetation, fire ecology, soil-related factors, and the associated feedback processes.

In this work, we present a multiproxy investigation of a lacustrine sediment record recovered from a region in the southern GS covering the last 8700 years. We integrated pollen, spores, algal remains, charcoal, and geochemical analyses to generate a detailed reconstruction of the environmental changes in the region, with a specific focus on the interplay and synergies between the environmental drivers (climate and fire), soil erosion, and vegetation.

**Table 1.** AMS radiocarbon dates used for the age–depth model.

Laboratory number	Sample	Depth (cm)	Material	Age (yr <sup>14</sup> C BP)	Age (cal. yr BP) 2σ	Age (cal. yr BP) estimation <sup>a</sup>
UCI-43538	PATAM4C07_D1/40	40	Wood	2260 ± 60	2154–2272	2309
Beta-287338	PATAM4C07_D2/19	100	Pollen residue	5030 ± 40	5705–5896	5763
Beta-287340	PATAM4C07_D2/72	152	Pollen residue	7300 ± 40	8019–8180	8043
Beta-287339	PATAM4C07_D3/47	207	Pollen residue	8530 ± 50	9453–9556	9543

<sup>a</sup>Weighted average of the probability distribution function. This method is recommended as the best central point estimate.

## Present-day environmental setting

### Regional features

The GS is an extended region (~10,800 km<sup>2</sup>) located in the Venezuelan Guayana, in southeastern Venezuela (Bolívar state). This region lies in northeast of the Precambrian Guiana Shield and between the Orinoco and Amazon basins (4°36'–6°37'N and 61°4'–74°2'W) (Figure 1a). The climate of the GS has been described as submesothermic tropophilous, with annual average temperatures of approximately 18–22°C and precipitation of 1600–2000 mm/yr. The GS is a high, undulating erosion surface that forms an *Altiplano* inclined from north (1450 m a.s.l.) to south (750 m a.s.l.). The GS is situated on quartzite and sandstone bedrock, known as the Roraima group. These rocks have been subject to long weathering processes and produce iron- and aluminum-oxide-rich soils (Huber, 1995a), which have poor nutrient content, with low concentrations of phosphorous, calcium, and nitrogen (Huber, 1995a). The soil-chemical stress caused by the calcium deficiency and aluminum toxicity combined with the thin profile render the soils incapable of supporting certain types of vegetation, especially forests (Fölster et al., 2001). This reduces the capacity of the soil to withstand external and internal impacts such as burning and drought (Fölster et al., 2001; Schubert and Huber, 1989).

In the Venezuelan Guayana region, the principal vegetation types are evergreen montane and gallery forest, but the majority of the GS is covered by savanna. Three primary types of savanna occur in this area (Huber, 1995b): (1) open treeless savannas, (2) shrubs savannas, and (3) open savannas with *morichales*, which are mostly monospecific dense stands of the Arecaceae *Mauritia flexuosa* (locally known as *moriche*). The stands of *morichales* grow along river courses and around lakes on poorly drained soils with high clay content (Rull, 1999). This type of gallery forest is an important vegetation component occurring in the central and southern regions of the GS at elevations lower than 1000 m a.s.l. (Huber, 1995b). Other vegetation types in the GS landscape that form patchy mosaics in the savanna (Huber, 1986) are montane rainforests (800–1500 m a.s.l.; Huber, 1995b; Hernández, 1999), shrublands, secondary woody communities, and *helechales* (dense fern communities). Generally, *helechales* establish after repeated burning, as part of successional trend (Huber, 1986). A more detailed description of the vegetation composition is provided in previous studies (Huber 1995b). For the main taxa, refer to Supplementary material (available online).

Fire currently plays a significant role in the landscape dynamics of the GS, with a fire frequency between 5000 and 10,000 fires per year (Gómez et al., 2000). Nearly 70% of detected fires start in savanna areas, but some fires cross the savanna–forest boundary (Bilbao et al., 2010), causing forest degradation (Dezzeo et al., 2004; Fölster, 1986; Fölster et al., 2001). The vast majority of these fires are of anthropogenic origin (Bilbao et al., 2010). Fire is a key element of the *Pemón* culture. This indigenous group currently inhabits the GS and belongs to the Carib-speaking ethnic group. They use fire daily to burn wide extensions of treeless open savanna (Kingsbury, 2001). Fires in savanna–forest borders are

scarcely controlled and cause concern about further savanna expansion. The anthropogenic fires have caused an impoverishment of tree species, a drastic reduction of biomass in terms of basal area, a strong change in the floristic composition and the loss of the organic-rich soil surface layer, which negatively impacts on soil fertility (Dezzeo et al., 2004). Therefore, the forest recovery may be strongly impaired by fire. To prevent further land degradation, studies and strategies for fire management in the GS are currently under investigation (Bilbao et al., 2009, 2010).

### Study site

Lake Encantada (4°42'37.44"N–61°05'03.29"W; 857 m a.s.l.; Figure 1a) is located near the town of Santa Elena de Uairén on a private farm named 'Hato Santa Teresa'. Lake Encantada is shallow with a maximum water depth of 2.6 m (measured in January 2007). The lake surface is <1 km<sup>2</sup>, and its watershed is also small, both of which suggest that the sediment record contains a local vegetation history (Mayle and Iriarte, 2012). Treeless savanna and scattered *morichales* patches currently surround Lake Encantada (Figure 1b). Therefore, pollen signal of *M. flexuosa* may indicate the local occurrence of *morichales* around the shores of the lake. However, wind-transported pollen taxa (e.g. *Urticales* pollen grains) might have been sourced extra-locally from neighboring forests (Jones et al., 2011).

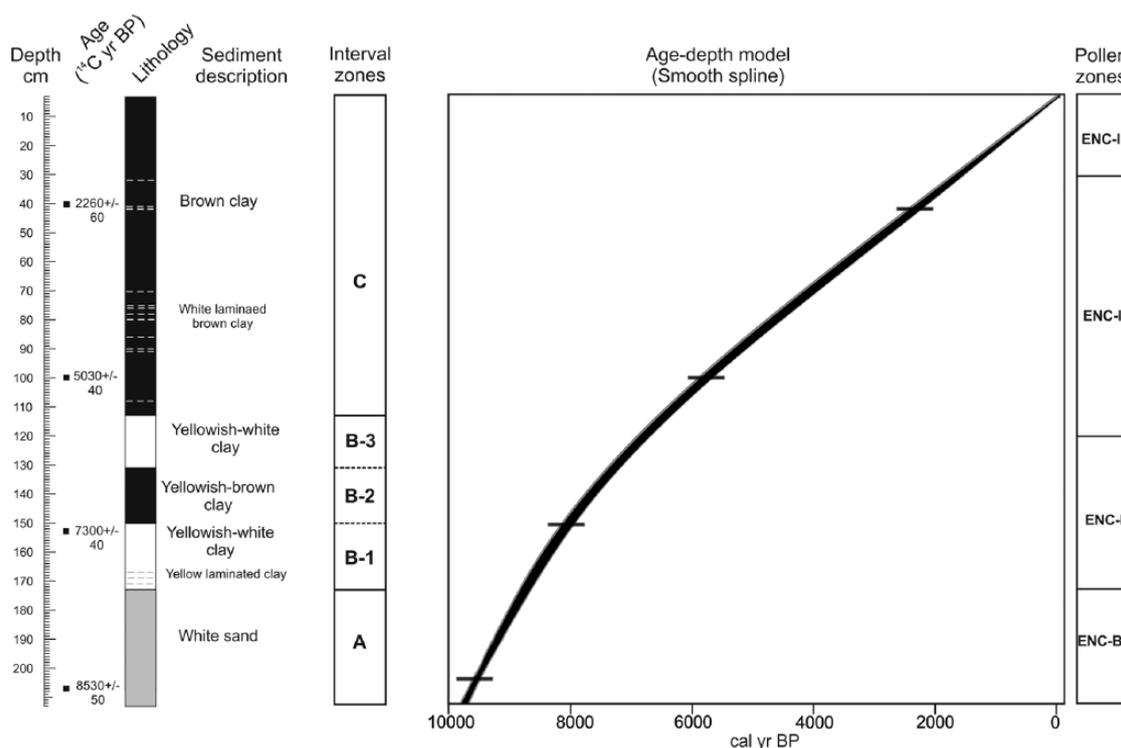
## Methodology

### Core recovery and radiocarbon dating

The core discussed here (PATAM4 C-07; 2.13 m long) was obtained in January 2007 and was taken from the deepest part of the lake using a modified Livingstone squared-rod piston (Wright et al., 1984). Four samples were taken along the core for AMS radiocarbon dating, which was carried out at the Radiocarbon Laboratory of the University of California, Irvine (UCI) and Beta Analytic (Beta). Three samples were produced from a pollen residue (Table 1) because of the absence/insufficiency of suitable macrofossil material. These samples were processed using a simplification of standard palynological techniques (KOH, HCl, and HF digestions). The radiocarbon dates were calibrated with the CALIB 6.0.1 and the IntCal09.14c database (<http://calib.qub.ac.uk/calib/>, accessed on October 2012). The age–depth model was produced with the Clam R statistical package (Blaauw, 2010).

### Magnetic, physical, and chemical analyses

Magnetic susceptibility (MS) was measured on half-core sections at 5 mm intervals with a Bartington Susceptibility Meter. Bulk density (BD) was measured on 1-cm<sup>3</sup> samples that were taken every 5 cm down the core and dried at 60°C for 24 h. The organic matter and inorganic carbon content of the sediments were determined for each sample by loss on ignition (LOI) at 550°C and 1000°C, respectively (Bengtsson and Enell, 1986; Heiri et al., 2001). Elemental determinations were performed with an ITRAX x-ray fluorescence (XRF) core scanner at the Large Lakes Observatory of the University of Minnesota, Duluth. Measurements were made at



**Figure 2.** Core stratigraphy with radiocarbon ages, sediment description, age–depth model of the sequence, pollen, and lithological zones.

1 cm intervals during 60 s of exposure time. The elements are expressed as counts per second (cps), and those over 1500 cps were selected (Si, K, Ti, Mn, Fe, Co, Ni, Zn, As, Se, Br, Rb, Sr, and Zr) because they are usually considered to be statistically significant. Excluding Fe, Co, and Br, the remaining elements are considered a terrigenous-sourced group. Total organic carbon (TOC) and nitrogen (TN) and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured after acid pre-treatment using an elemental analyzer coupled with a Finnigan Delta-plus mass spectrometer. The isotope sample reproducibility was  $\pm 0.2\%$ . Carbon and nitrogen isotope ratios are reported in  $\delta$ -notation, with  $\delta = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$  and  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ . The isotopes are expressed per mil (‰) relative to the following international standards: Vienna Pee Dee Belemnite (VPDB) for carbon and air (VAIR) for nitrogen.

### Pollen analysis

Forty-three volumetric samples ( $2\text{ cm}^3$ ) were taken at 5 cm intervals. The samples were processed using standard palynological techniques (KOH, HCl, acetolysis, HF digestion, and dehydration). *Lycopodium* tablets were added as exotic markers (batch 177745, average of  $18584 \pm 1853$  spores/tablet). The slides were mounted in silicone oil without sealing and stored in the same mounting medium. Counts were conducted until a minimum of 300 terrestrial pollen grains was attained. Pollen count was performed until diversity saturation was reached (Rull, 1987). Identified pollen and pteridophyte spores were classified according to the vegetation types previously described for the region (Huber, 1995b). The pollen sum included pollen from trees, shrubs, and herbs and excluded pollen from aquatic (e.g. *Utricularia*, *Ludwigia*) and semi-aquatic plants (e.g. Cyperaceae, *Sagittaria*). The identification of pollen and spores was based on Burn and Mayle (2008), Colinvaux et al. (1999), Herrera and Urrego (1996), Leal et al. (2011), Roubik and Moreno (1991), and Rull (2003). Pollen diagrams were plotted with *PSIMPOLL 4.26*. The zonation for the pollen diagrams was performed using the optimal splitting by information content (OSIC) method, and the number of significant zones was determined by the broken-stick model test (Bennett,

1996). Only pollen types exceeding 1% abundance were used for zonation. Sample PATAM4C 07\_D3/50 at 213 cm was excluded because of methodological problems, so pollen diagrams up to 208 cm were created. Algal remains (e.g. *Botryococcus*, *Spirogyra*, *Mougeotia*) were counted on pollen slides and, together with aquatic plants, were plotted in terms of percentages based on pollen sum. The identification of the assemblages was based on comparison with modern pollen samples from previous studies (Leal et al., 2013; Rull, 1999) and the known autoecology of the taxa (Burn et al., 2010; Burn and Mayle, 2008; Marchant et al., 2002). Charcoal counts were carried out using the same pollen slides and were classified according to the two size classes defined by Rull (1999) for this study area: Type I (smaller microcharcoal particles of 5–100  $\mu\text{m}$ ) consists of windborne charcoal dispersed over long distances and represents regional fire events (Clark et al., 1998; Blackford, 2000), and Type II (larger microcharcoal particles  $> 100\ \mu\text{m}$ ) is indicative of local fire events because it is not transported far from the fire source (Clark et al., 1998).

Influx values ( $\text{cm}^2/\text{yr}$ ) were obtained using concentration values ( $\text{cm}^{-3}$ ) and accumulation rates ( $\text{cm}/\text{yr}$ ) for charcoal particles and main taxa. Additionally, we measured the woody:non-woody ratio after classifying the taxa into woody (trees and shrubs) and non-woody (herbs and sedges) types. This ratio is indicative of the vegetation cover (Bhagwat et al., 2012) and can be used to differentiate between forested and savanna vegetation.

### Silicobiolith analysis

Diatoms and sponge spicules were considered as silicobioliths, which are sediment from the remains of living organisms formed by amorphous silica. Forty-three samples taken at 5 cm intervals ( $1\text{ cm}^3$ ) were digested according to their organic matter content with either a mixture of sulfuric acid and potassium dichromate or hydrogen peroxide. Most samples were barren of silicobioliths. In the remaining samples, because of the extremely low number of valves and spicules in different stages of preservation (e.g. 0.2 valves/field on average), counting was stopped after approximately 500 fields and the results were expressed as ‘traces’. Diatoms were

identified using specialized literature (Krammer and Lange-Bertalot, 1986–1991). The identified spicules correspond to adult oxas type, so their taxonomic identification was not possible (Frost, 2001).

### Statistical analysis

Canonical correspondence analysis (CCA) was performed with the Multivariate Statistical Package (MVSP) v.3.13 software using all physico-chemical data and the influx of charcoal and algae as environmental variables. All data were root-square transformed, and rare pollen taxa were down weighted. Six samples (3, 123, 128, 138, 143, and 173 cm) were excluded because of a lack of physico-chemical data. The interval 213–173 cm was also excluded because it is barren of biological proxies. Additionally, correlation analysis was carried out between the environmental variables and the main pollen taxa by using influx values calculated according to the Pearson product–moment correlation coefficient ( $r$ ) and its corresponding significance ( $p$ -value).

## Results

### Stratigraphy and chronology

The Encantada lacustrine sequence was characterized by three lithological units from bottom to top (Figure 2). The first unit is from 213 to 173 cm and is characterized by homogeneous, well-sorted, and fine white sands. The second unit is from 173 to 113 cm and is made up of homogeneous, yellowish-white clays, but between 150 and 131 cm, a yellowish-brown clay layer is present. The third lithological unit is present from 113 cm to the top and consists of massive, brown clay sediments.

The results of AMS radiocarbon dating (Table 1) were used to build the age–depth model for the sequence. The best fit was obtained with a smooth-spline model (Blaauw, 2010) (Figure 2). Sedimentation rates fluctuated between 0.04 and 0.02 cm/yr and progressively decreased from the bottom to the top. The sequence encompassed most of the Holocene (*c.* 9700 cal. yr BP–the present), and the time interval between consecutive samples ranged from approximately 100 to 300 years (centennial to multi-centennial resolution). We focused on the last 8700 years for the paleoecological analysis because of the absence of biological proxies prior this time (see section ‘ENC-BZ (208–173 cm, eight samples)’).

### Geochemical proxies

Figure 3 shows the results of the geochemical analyses. According to variations along the entire sequence, three intervals (listed below) were identified that coincide with those based on the sediment description.

**Interval A (213–173 cm).** This interval corresponds to the oldest described lithological unit. All geochemical elements had values that were low to very low and roughly constant, except Si (up to 8330 cps) and BD (ranging between 1.3 and 1.5 g/cm<sup>3</sup>), which exhibited the highest values of the entire record.

**Interval B (173–113 cm).** Most physico-chemical proxies displayed high variability related to the lithological changes present in this interval, which allowed three sub-intervals to be defined: B-1, B-2, and B-3. B-1 and B-3 coincided with the yellowish-white clay layers, whereas B-2 corresponded to the intermediate yellowish-brown clays of lithological unit 2 (Figure 3). B-1 and B-3 were characterized by a high cps of K, Ti, Mn, Se, Sr, and Zr; these chemical elements abruptly dropped in B-2, whereas Fe ( $22.9 \times 10^5$  cps) and Co ( $13.6 \times 10^3$  cps) were found at their

maximum values. MS (up to  $240 \times 10^{-6}$  S.I),  $\delta^{13}\text{C}$  (1.3‰), C/N (191), and TOC (*c.* 10%) peaked in B-2.  $\delta^{15}\text{N}$  reached minimum values in B-2 (up to 1‰).

**Interval C (113–0 cm).** Most of the elements showed medium to low values in Interval C in comparison with values from two previous intervals, but Br displayed the highest ones (up to 1737 cps) of the entire record. TOC (from 8% to 31%), TN (ranging between 0.5% and 2.1%) progressively increased upward, and  $\delta^{15}\text{N}$  decreased (varying from 0.8‰ to –1.3‰).

### Biological proxies

The stratigraphic variations of pollen assemblages allowed us to subdivide the pollen diagram into four zones. Because silicobio-liths were only found in trace amounts, they could not be plotted in a taxa percentage diagram; however, these results were included in the diagram of aquatics and expressed qualitatively.

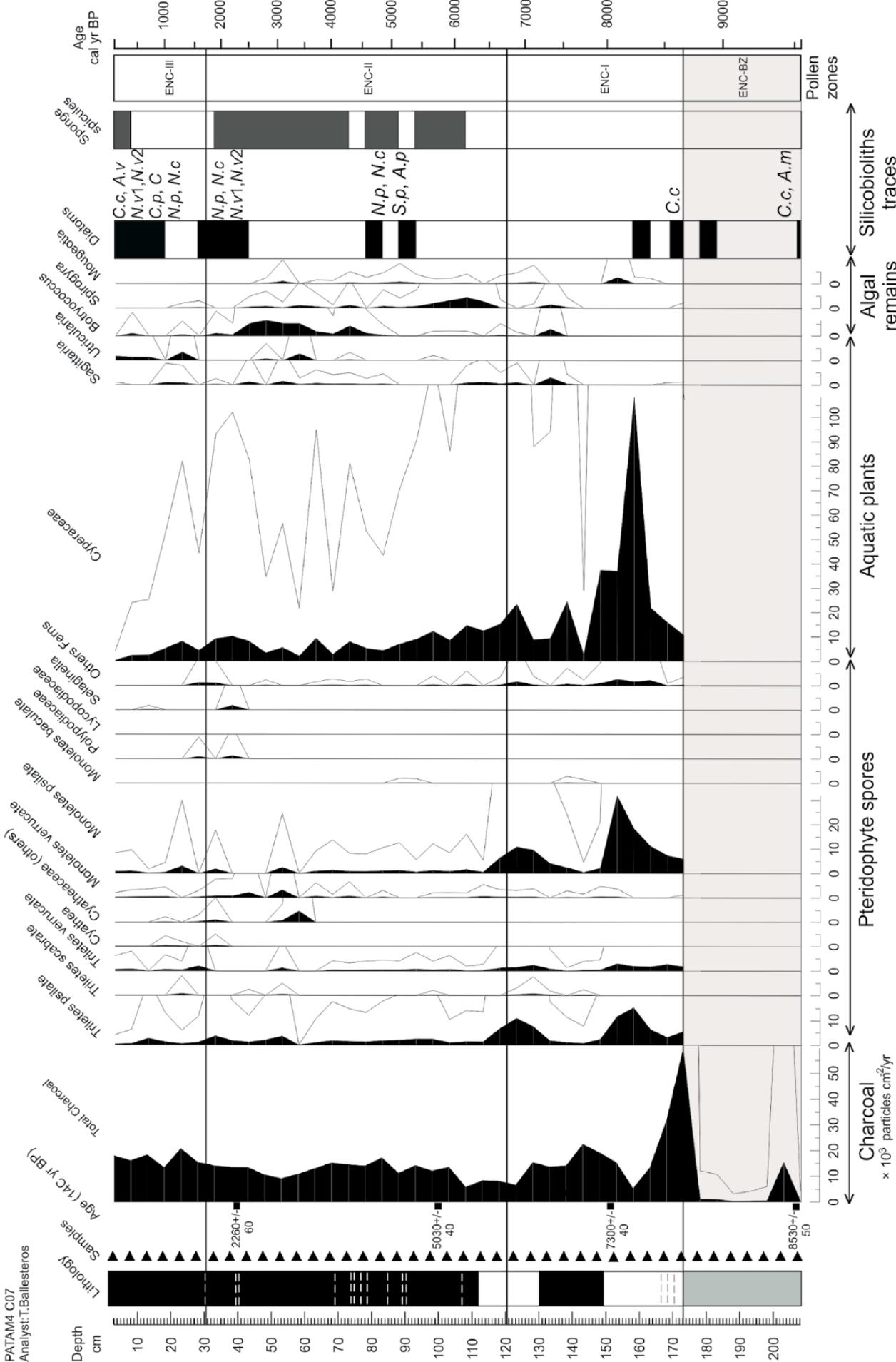
**ENC-BZ (208–173 cm, eight samples).** Palynomorphs were absent (Figures 4 and 5), and therefore, this zone was considered barren (BZ). Charcoal particles remained at low abundances but exhibited a pronounced increase at the boundary with the upper zone (ENC-I).

**ENC-I (173–120.5 cm, 11 samples).** ENC-I coincides both with the physico-chemical Interval B and with the second lithological unit (Figure 2). The pollen assemblage was dominated by herbaceous elements, with Poaceae as the most important taxa. The percentage of herb pollen (*c.* 50–80%) decreased toward the top of the zone and was synchronous with an increase in tree pollen, which can also be observed in the vegetation cover ratio (Figure 4). Woody elements were represented primarily by *Brosimum* (the most abundant), Ochnaceae, *Miconia*, *Solanum*, section *Pachyphylla*, *Cecropia*, and Urticales (others). Pteridophyte spores were primarily dominated by psilate monoletes and psilate triletes (Figure 5), which showed two peaks at approximately 158–153 cm and 128–123 cm, which co-occurred with the peaks of *Miconia* (Figure 4) and maximum abundances of Cyperaceae (at 158–153 cm; Figure 5). *Mougeotia* appeared in the lower half of the zone, whereas *Sagittaria*, *Botryococcus*, and *Spirogyra* appeared for the first time at the top of the zone (Figure 5). Charcoal particles showed the highest values of the entire record at the base of the zone (Figure 4). Regarding the influx values, Poaceae displayed an abrupt maximum at 143 cm, which coincided with a charcoal peak (Figure 6). These values occurred in the lithological/stratigraphical sub-interval B-2.

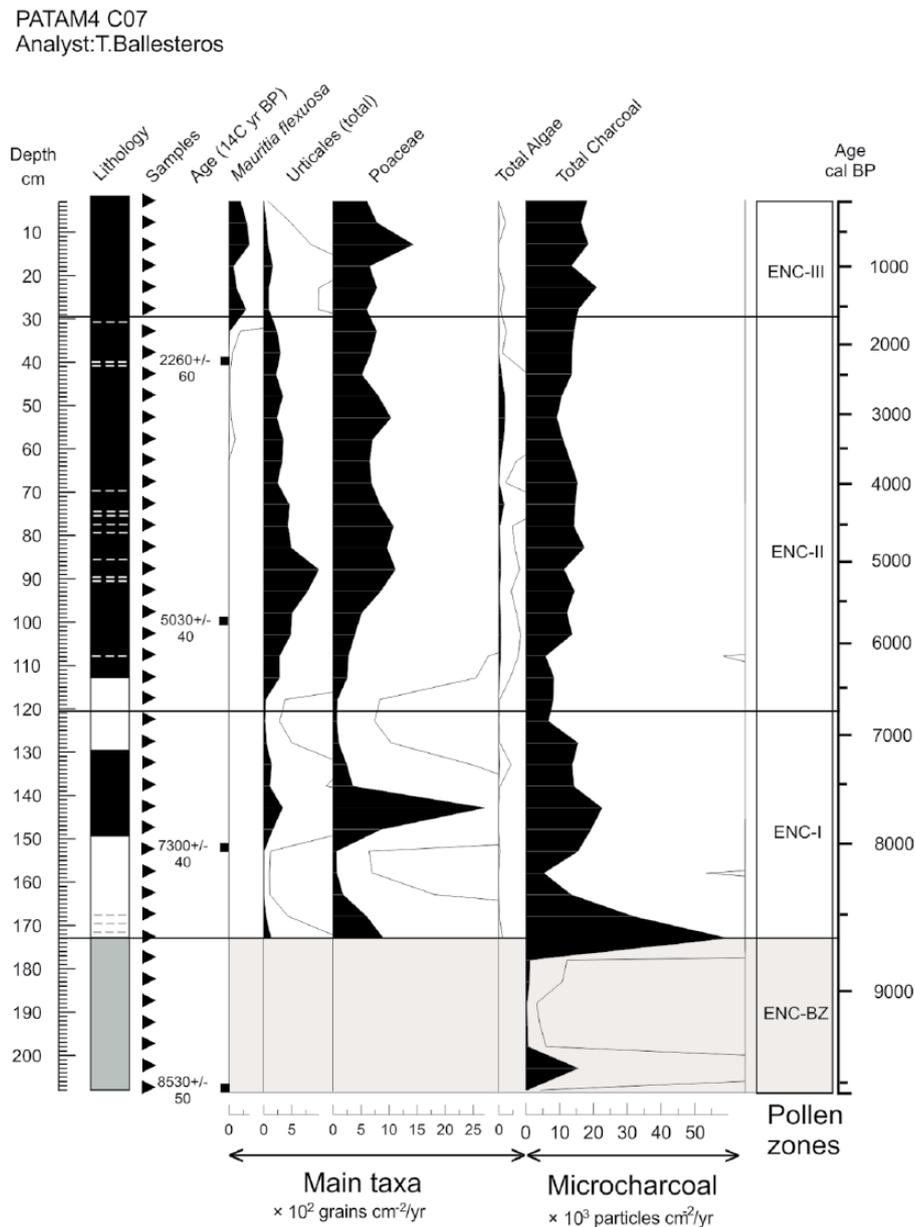
**ENC-II (120.5–30.5 cm, 18 samples).** The ENC-II zone is represented by marked increase in forest elements, primarily Urticales 3–4p, in its lower half. Vegetation cover ratios (in average 1.33) showed the same trend. *Cecropia* was more abundant (2–3%) toward the bottom and the top of the zone. In the lower half of the zone, Urticales reached its highest proportion (>40%) and influx ( $>5 \times 10^2$  grains/cm<sup>2</sup>/yr) (Figures 4 and 6). Among the aquatic elements, *Sagittaria* was nearly constant along the zone and increased slightly near the top (~1.5%). *Spirogyra* was abundant in the lower half (3–4%), while *Botryococcus* was the dominant aquatic element in the upper region of the zone (5–6.5%, Figure 5). Total algal remains had the highest values in the upper half (up to 110 elements/cm<sup>2</sup>/yr; Figure 6). From 103 cm upward, the presence of sponge spicules was almost constant (Figure 5). Charcoal particles presented the lowest values of all the sequences at the base of the zone but exhibited a subsequent increase. Excluding the upper region, this zone broadly coincided with Interval C.







**Figure 5.** Diagram showing the elements outside the pollen sum, such as the aquatic and semi-aquatic plants, pteridophyte spores, algal remains, and silicibolioliths traces. The abundances are expressed in percentages with respect to the pollen sum. Silicibolioliths traces are expressed as barren (empty space) and present (filled space). Diatoms taxa: C.c = *C. cyllopuncta*, A.m = *Achnanthisidium minutissimum*, N.p = *Nitzschia palea*, N.c = *Nitzschia capitellata*, S.p = *Sellaphora capitellata*, S.p = *Sellaphora pupula*, A.p = *Amphora pediculus*, N.v1 = *Navicula viridula* var. *rostellata*, N.v2 = *Navicula viridula* var. *rostellata*, A.v = *Amphora veneta*, C.p = *Cocconeis placenticula* var. *euglypta*, and C = *Craticula* sp.



**Figure 6.** Diagram showing the influx values of the main taxa, total algae, and microcharcoal particles. Calibrated ages shown on the right side are based on the age–depth model outputs.

**ENC-III (30.5–3 cm, six samples).** The pollen assemblage of the ENC-III zone showed an abrupt change in composition. *M. flexuosa* increased dramatically from 1.5% to 27.7%, while pollen of woody taxa underwent a drastic reduction from >40% to 3% (Figure 4). From 23 to 18 cm, *M. flexuosa* declined, whereas a tree pollen recovery (32%) was observed, synchronous with a subtle decrease in charcoal particles (Types I and II). A return to former *Mauritia* values was recorded shortly thereafter and was coeval with a severe reduction of pollen of woody taxa to *c.* 3%. Urticales and *M. flexuosa* influx values followed similar trends with their respective relative abundances, confirming the trends inferred from the percentage values (Figure 6). In the upper region, Poaceae dominated the pollen assemblage, reaching almost 70% of the pollen sum. Pteridophyte spores were common but occurred in low percentages (Figure 5). Aquatic elements remained at low abundances (< 2%, Figure 5). Charcoal particles showed values that were roughly similar to those of the previous zone ( $\sim 16 \times 10^3$  particles/cm<sup>2</sup>/yr).

#### Statistical analysis

Figure 7 shows the results of the CCA along the biplot of the first two axes, which explain 47.88% of the total variance (Axis

1 = 28.42%, Axis 2 = 19.46%). Positive values on Axis 1 are represented by TN and, to a lesser extent, by TOC, the inc/coh ratio (indicator of the organic matter content of the sample; see Croudace et al., 2006; Sáez et al., 2009; Ziegler et al., 2008), Co and Fe, whereas negative values are represented by Ti, Zn, and Zr and, to a lesser extent, by As, Ni, Rb, K, Mn, Si, Sr, and BD. Charcoal and MS represent the positive values on Axis 2, whereas algae and Br have more influence on the negative values.

Within the space defined by these two axes, samples are clustered according to the previously defined pollen zones. Pollen zone ENC-I falls on the negative side of Axis 1 and the positive side of Axis 2, which is linked to a suite of elements (As, Ni, Rb, K, Mn, Si, Sr, and BD). Pollen zone ENC-II is situated in the middle of Axis 1 and the negative side of Axis 2, showing a widespread arrangement of samples that are linked to a variety of elements (such as TOC, TN,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and algae). Zone ENC-III is located on the positive sides of both axes, showing no relationship with physico-chemical proxies.

Charcoal and *M. flexuosa* showed no significant relationship when considering the whole diagram; however, when only zone ENC-III is taken into account (*Mauritia* is absent from the other

pollen zones), the linear correlation between charcoal and *M. flexuosa* is positive and significant ( $r = 0.68$ ;  $p = 0.015$ ). Charcoal also shows a strong positive relationship with psilate spores ( $r = 0.66$ ;  $p < 0.001$ ), and these are highly associated with *Miconia* ( $r = 0.70$ ;  $p < 0.001$ ).

## Reconstruction of environmental changes

The environmental variations in the sediments of Lake Encantada allowed us to differentiate four periods.

### Period 1: 9700–8700 cal.yr BP (from 213 to 173 cm)

The presence of well-rounded and sorted siliclastic sediments together with the highest sedimentation rates (0.04 cm/yr) suggests that these sediments were likely deposited in a fluvial environment. We believe that flowing waters would have prevented the deposition and/or preservation of most biological proxies.

### Period 2: 8700–6700 cal.yr BP (from 173 to 120 cm)

Pollen analysis suggests that during this period, the landscape was covered by open savanna with scattered small forest patches. Regional fires peaked and decreased several times, and when fires decreased, the forest patches expanded. This expansion is indicated by the wind-pollinated taxa of the Moraceae family (Figure 4; Burn et al., 2010) (*c.* from 8500 to 8000 cal. yr BP and *c.* from 7500 to 7000 cal. yr BP). After more intense burning events, *Miconia* increased in parallel to a significant increase in psilate-fern spores. Both *Miconia* and pteridophytes with psilate spores are colonizers of burnt areas during early stages of succession (Berry et al., 1995; Hernández and Fölster, 1994; Marchant et al., 2002). In the GS, a similar assemblage formed by *helecholes* (fern communities), intermingled with patches of shrubs (*matorrales*), is considered to be a degrading successional stage after secondary forest burning (Fölster et al., 2001; Rull, 1999). Conversely, when regional fires increased, the forest and *helecholes-matorrales* retreated and the savanna expanded (*c.* from 8000 to 7500 cal. yr BP). Around *c.* 7700 cal. yr BP, higher  $\delta^{13}\text{C}$  values (indicative of  $\text{C}_4$ -land plants; Meyers and Lallier-Vergés, 1999), higher C/N ratios (Figure 3), and greater Poaceae-influx values coincided with the enhancement of fires (Figure 6). According to modern plant surveys (see Supplementary material, available online), most herbs in GS have  $\text{C}_4$ -photosynthetic pathway. This evidence confirms the dominance of expanding open vegetation when fires were more intense. Other paleorecords from the area indicate that this period was dry across the greater region (*Llanos Orientales*: Behling and Hooghiemstra, 1998; Amazonia: Mayle and Power, 2008) which is also consistent with a previous work in the GS (Montoya et al., 2011b) and the evidence presented here.

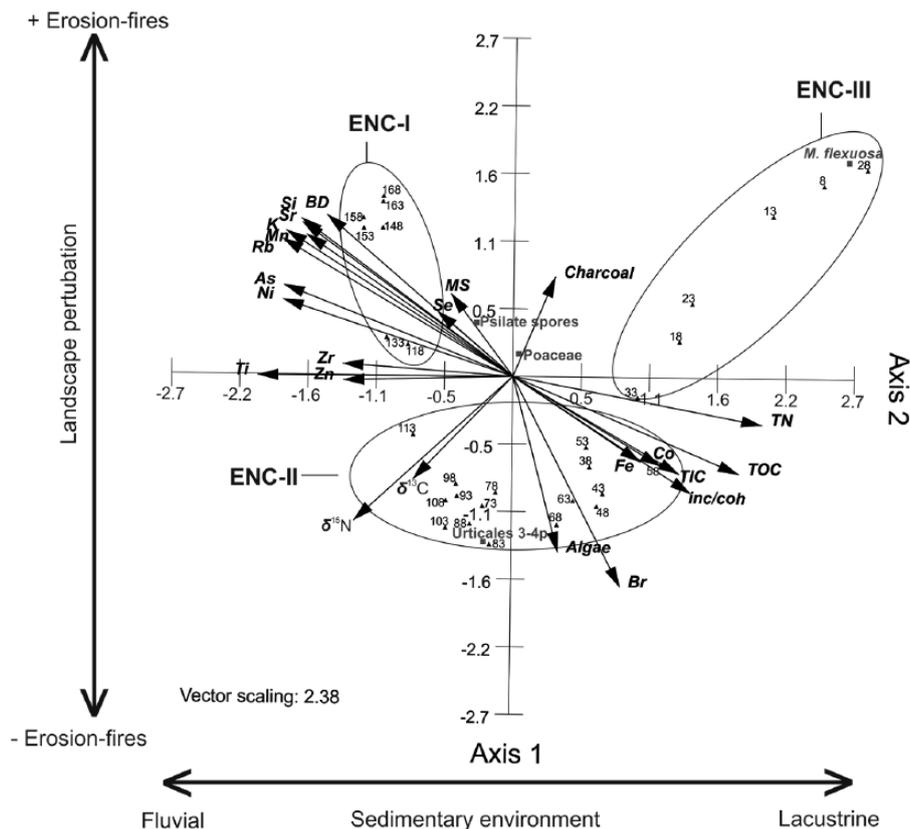
At the beginning of the period, the abrupt change from clastic sediments to yellowish-white clays (Interval B-1) might indicate the change from fluvial to lacustrine conditions. Most geochemical (TOC and TN) and biological (algal influx) proxies suggest that the aquatic productivity was negligible or not preserved in the sediments (Figures 3 and 6). During the periods from 8700 to 8000 cal. yr BP and from 7200 to 6700 cal. yr BP yellowish-white clays (Intervals B-1 and B-3) were deposited (Figure 3). The change in sediments combined with higher terrigenous inputs (Figure 3) indicates the disconnection with the fluvial system (Figure 3). Based on the analysis of biological proxies, we believe that these intervals represented wetter conditions. Conversely, during the period from 8000 to 7200 cal. yr BP, the lithological change to brown clays (Interval B-2) suggests the deepening of the water body. However, based on palynological results, we

suggest that during this interval, the conditions were drier. According to the MS results (Figure 3) and Axis 2 of the CCA (Figure 7), the intense erosional events may be interpreted as soil instability caused by fires (see a detailed explanation in section 'Interpretation of the environmental gradients: Canonical correspondence analysis (CCA)') instead of being driven by enhanced rainfall, which commonly occurs in tropical regions (Warrier and Shankar, 2009). Evidence may be indicating a temporal connection with the fluvial system. Thus, the interplay of fires, open landscape, and long-distance transport of terrigenous elements (Figure 7) might have promoted high erosion events. Poaceae pollen grains are airborne and waterborne transported (Brown et al., 2007) and hence can be transported to a long distance. So the high amount of Poaceae pollen grains during Interval B-2 (Figure 6) would have been locally and extra-locally sourced. On the other hand, the decrease in the  $\delta^{15}\text{N}$  values ( $<0\text{‰}$ ) suggests the lake primary productivity might be ruled by nitrogen-fixing bacteria (Figure 3). In summary, this period might be considered as highly variable, with an alternation of drier and wetter intervals. We tentatively suggest that disconnection–connection dynamics with the fluvial system could have been driven by variations in the river's drainage pattern.

### Period 3: 6700–1700 cal.yr BP (from 120 to 30 cm)

The pollen assemblage showed a remarkable compositional and structural change in plant communities during this period. The vegetation shifted to patches of dense rainforest within savanna from 6700 to 5400 cal. yr BP. As noted by modern ecological studies (Leal et al., 2013; Rull, 1999), the percentages of herbs and tree pollen would indicate the occurrence of a forest–savanna mosaic during this period. Forest was highly dominated by Urticales with 3–4p pollen grains, *Brosimum*, Sapotaceae, *Cecropia*, *Pourouma*, and *Hyeronima*. Urticales values suggest that an evergreen tropical forest with a closed canopy was established nearby or patchily distributed in the location (Gosling et al., 2009). An additional local environmental reconstruction for the area was provided by a peat core extracted from the shore of Lake Encantada (Montoya et al., 2009). This sequence also showed a notable development of forest roughly at the same time interval. Hence, it seems to indicate that dense forest patches expanded locally. However, the palynological signal of some regional forest expansion expressed by the arrival of some windborne pollen grains to the sampling location cannot be disregarded. The rainforest development occurred when fires (regional and local) declined dramatically, which enabled *Cecropia*, as a pioneer tree, to colonize the land cleared by the fire disturbances (Burn et al., 2010; Marchant et al., 2002) and subsequently rainforest expanded. Because of the humidity requirements of rainforests and the higher abundances of *Spirogyra*, we consider this to be a period of higher available moisture during forest development.

In the upper half of this period, a clear shift to more open vegetation occurred. The region near Lake Encantada was dominated by either open savanna with forest patches or reduced forest–savanna mosaic, under higher fire intensity and moisture availability and then before 5400 cal. BP. This is supported by maximum values of aquatic elements (e.g. *Botryococcus*, deeper water inhabitant; Figure 5). Similar forest development and wetter climates during the middle to late Holocene are supported by similar studies from other locations in the GS (Montoya et al., 2011b; Rull, 1992), and in the neighboring savannas of Colombia *Llanos Orientales* and northern Amazonia (Behling and Hooghiemstra, 2000; Pessenda et al., 2010; Figure 1a). This increase in humid conditions was the opposite of the trend toward drier conditions that occurred in the northernmost South American Andes (Vélez



**Figure 7.** Biplot of the canonical correspondence analysis (CCA).

Numbers correspond to the sample's core depth (cm). ENC-I, ENC-II, and ENC-III correspond to pollen zones. Barren zone ENC-BZ is not included.

et al., 2003). Thus, the wet climate inferred in our study fits with regional climatic trends recorded in localities north of the Amazon basin, which would have been strongly influenced by moisture coming from the basin.

The sedimentological change to brown clays and the pronounced increase in Br, TOC, and TN (Figure 3) occurred at the base of the Interval C. Probably the lake became more productive.

#### Period 4: 1700 cal.yrBP–the present (from 30 to 3 cm)

In the period from 1700 cal. yr BP to the present, the vegetation experienced an abrupt change toward the establishment of treeless savanna with *morchales* stands (*Mauritia* palm), that is, the modern-day landscape. The continuous presence of small *helechales* indicates a network dynamic of fern patches. Rull (1999) interpreted these communities as a transitional stage from open secondary forest cleared by fires to open savanna with *morchales* (Rull, 1999). The high percentage of *M. flexuosa* pollen in sediments indicates the local occurrence of *morchales* (Rull, 1999). According to its ecology, this palm seems to be opportunistic and able to colonize new habitats created by fire and poorly drained soils resulting from wet conditions (Rull, 1999). Although fire evidence is not conclusive with regard to the initial establishment of the *morchales* (Figures 4 and 7), the correlation analysis ( $r = 0.68$ ;  $p = 0.015$ ) indicates some level of fire influence on this plant community, which is also suggested by several former studies (Montoya et al., 2009, 2011c; Rull, 1999). On the other hand, the marked rise in TOC and slight rise in TN indicate an increase in primary lake productivity, which occurred in synchrony with decreased  $\delta^{15}\text{N}$  values and algae scarcity. These results suggest that aquatic productivity was almost entirely dominated by nitrogen-fixing bacteria. The scarcity of algal remains and

predominance of bacteria might indicate drier conditions and/or nutrient-limited conditions.

#### Interpretation of the environmental gradients: Canonical correspondence analysis (CCA)

Chemical elements such as Ti, Zr, and Zn are usually associated with terrigenous inputs of sediments to the lake, whereas total nitrogen (TN) and TOC commonly reflect variations in the organic productivity of the lake (Cohen, 2003). A careful analysis of the sample distribution in the plane defined by the two first CCA axes reveals that they are stratigraphically ordered, with the deepest elements located on the left side of the graph (sandy lithological unit 1) and the uppermost elements located on the right side (clayish lithological unit 3). Therefore, the first axis could be related to the suggested progressive change from a fluvial sedimentary environment to a lacustrine one.

Despite the absence of archaeological evidence, previous paleoecological studies in the southern GS suggest that the consistent presence and abundance of charcoal (fire proxy) could be related to land highly managed and altered by humans for at least the last two millennia (Montoya and Rull, 2011; Montoya et al., 2011c). Thus, Axis 2 might reflect changes in the anthropogenic management of the catchment. The presence of charcoal particles associated with MS at the positive end of Axis 2 suggests that the burning of vegetal cover could initiate or enhance the erosion of the soils. When fires were reduced and *Cecropia* established (Figure 4), the development of middle to late successional rainforest might have been favored, as indicated by the presence of Urticales (Burn and Mayle, 2008; Gosling et al., 2009) on the negative side of Axis 2. The algae were located parallel to Urticales 3–4p, suggesting a positive relationship with forest expansion and a negative relationship with fire frequency.

## Discussion and conclusion

### *The role of environmental drivers in the southeastern GS*

**Interplay between climate and fire.** Climate alone was not the determining factor affecting the vegetation dynamics during both dry (~8700–6700 cal. yr BP) and wet (~6700 cal. kyr BP–the present) periods. The moisture content of a fuel source, which is determined by the preceding rainfall, affects how readily it will burn, thus acting as a regulator of fire in tropical systems (Cochrane and Ryan, 2009). Thus, higher available moisture restricted the incidence of fire (Figure 7). Hence, the predominance of savanna during early to middle Holocene would be the result of the positive feedback between dry conditions, fires, and grassy vegetation. A similar reinforcing feedback of open savanna occurred near Mapauri record during early Holocene (Rull, 2007; Figure 1a). When climate conditions turned wetter ~6700 cal. yr BP, fire ignition was reduced. After longer fire-free intervals, trees would have reached a fire-suppression threshold through the development of a sufficient canopy cover, which prevented the growth of grasses (Hoffmann et al., 2012a). The synergistic action between reduced fires and a wetter climate appears to be a determinant in the development of rainforest. Thus, we suggest that during early to middle Holocene, the fire regime may have been unaffected by humans.

Despite the wetter conditions that occurred since ~5400 cal. yr BP, the savanna expansion would have been the result of forest burning, which could be caused by fires set by humans (Montoya et al., 2011b). The coexistence of wetter conditions, forest vegetation, and fires might be explained by land-use practices similar to those currently found in many neotropical forested landscapes (e.g. slash-and-burn), in which small forest spots are cleared and burned for shifting agriculture (known locally as *comucos*). Shifting cultivation practices apparently occurred in the El Paují region, south of Lake Encantada, from 7700 to 2700 cal. yr BP (Montoya et al., 2011b; Figure 1a). Considering a lag of about 2300 years between the start of *comucos* in El Paují and Lake Encantada, paleoecological results might suggest that semi-nomadic and forest-like indigenous culture migrated northward from the southernmost part of the GS. Fires increased after 6200 cal. yr BP and since 5400 cal. yr BP forest retreated gradually. The forest communities in the GS have been considered low resilient to burning (Fölster et al., 2001). However, this evidence might indicate that forest communities may have been resilient and recurrent burns could have reduced their resilience. This ecological feature of GS forest communities needs further assessment. An apparent shift in land-use practices toward more extensive use of fire in open landscapes was recorded ~2000 years ago and continued to the present in several of the GS localities (El Paují, Lake Chonita, Urué, Divina Pastora, Santa Teresa; Montoya et al., 2009, 2011b, 2011c; Rull 1992, 1999; Figure 1a). In El Paují, humans appear to have abandoned the study area around 2700 cal. yr BP, although the area could have been populated again from 1400 cal. yr BP onward by a different culture (Montoya et al., 2011b). A change to a new-savanna-like culture could have also occurred near Lake Encantada around 1700 cal. yr BP. Drier conditions may have been influential in the maintenance of savanna vegetation and continuity of fires. Recurrent burns were required to maintain the openness of the landscape and allowed the development of highly flammable vegetation, which drove the ecosystem to a treeless savanna state during the last two millennia (Montoya and Rull, 2011).

**Interplay between erosion and fire.** In the GS, soil erosion is greatly enhanced when the organic-rich surface layer is lost along with the forest vegetation (Fölster, 1986). Thus, the prolonged loss of forests could be associated with the progressive loss of soil water and nutrients, which could have subsequently hindered reestablishment of tree species. Moreover, because of the shallow

root system (Dezzeo et al., 2004), calcium deficiency and limited water retention capacity of the soils, tree mortality (Fölster et al., 2001) and drying of the soils might have been significantly affected by fire. Therefore, the synergism between fire and erosion could have resulted in forest instability, promoting an increase in soil erosion and nutrient loss. This synergism would have favored the establishment of the grass stratum. This process was likely triggered by fires but maintained by enduring soil-stress conditions. Rull (1992) suggested that the burning of the GS forests has initiated a degenerative and irreversible process that when coupled with soil degradation (Rull et al., 2013) results in the savanna expansion (Rull, 1992, 1999). The interplay between fire, erosion, and the grass vegetation was probably intensified around 5400 cal. yr BP, enabling the landscape change to open savanna with forest patches. That state remained until ~2000 years ago, when the shift of land-use practices allowed surpassing the tipping point toward an irreversible expansion of savanna, reinforced by drier climates. Thus, due to the opening of the landscape, the synergistic action between fire and erosion appears to have increased during the last 2000 years.

The Lake Encantada record, combined with former paleoecological studies (e.g. El Paují, Chonita, Urué), allows for the reconstruction of the regional picture of environmental change and land-use patterns in the southern GS and for the assessment of competing hypotheses (climate, fire, soils) for explaining the maintenance of the savanna.

### *Relationship between GS savannas and other moist savanna areas*

Although the GS has different vegetation types, human history, and lower climatic variability than the Brazilian savannas (Cerrado biome), it shares a long history of fire regime, poor soil conditions (e.g. low pH, high aluminum concentrations, poor nutrient availability), and climatic fluctuations during the Holocene. Humid climate conditions would also favor the establishment of forest instead of savanna (Oliveira-Filho and Ratter, 2002). It is widely accepted that climate, soils, and fire have been highly interactive in their effect on Cerrado vegetation (Oliveira-Filho and Ratter, 2002). The complex interaction of these factors in the GS was first assessed and recognized in this study. Climate alone does not explain the current predominance of savannas in these two humid regions. We consider that, as in Cerrado biome (Pinheiro and Monteiro, 2010), climate has been the trigger of this assumed interaction in vegetation history of the GS during the early Holocene. Seasonal and/or dry climate may have produced conditions prone to fires (Oliveira-Filho and Ratter, 2002) in Cerrados, and our evidence shows that that this also occurred in the GS. Recurrent fires apparently tended to prevent forest recovery and caused soil impoverishment in these two regions (Cerrados: Oliveira-Filho and Ratter, 2002). In some areas of Cerrado, the transition from forest to savanna seems to have been related to edaphic factors rather than to fire action (Pinheiro and Monteiro, 2010). However, limited data in the GS (this study) suggest that fires would have primarily driven this vegetation shift. Fires and soils have shown to be selective agents of savanna vegetation (e.g. fire-adapted and fire-dependent species) in the Brazilian savannas (Pinheiro and Monteiro, 2010), in which environmental factors are better understood (Oliveira-Filho and Ratter, 2002). Therefore, further assessment of the role played by fires and soils and the interplay between these two drivers is required in the GS. Since the middle Holocene, the failure of Cerrado (Ledru et al., 1998) and GS forests (Montoya et al., 2011b) to expand into savanna may be largely caused by human-induced fires through shifting cultivation (Pivello, 2011), overriding the effect of wetter conditions (Ledru, 1993; Montoya et al., 2011b). We believe that the interplay between fires and soil conditions has played a role in the vegetation history in humid neotropical savanna areas and that humans may have largely influenced it.

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