

Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia

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Abstract

The southern Gran Sabana (SE Venezuela) holds a particular type of neotropical savanna characterized by the local occurrence of morichales (*Mauritia* palm swamps), in a climate apparently more suitable for rain forests. We present a paleoecological analysis of the last millennia of Lake Chonita (4°39'N–61°0'W, 884m elevation), based on biological and physico-chemical proxies. Savannas dominated the region during the last millennia, but a significant vegetation replacement occurred in recent times. The site was covered by a treeless savanna with nearby rainforests from 3640 to 2180 cal yr BP. Water levels were higher than today until about 2800 cal yr BP. Forests retreated since about 2180 cal yr BP onwards, likely influenced by a higher fire incidence that facilitated a dramatic expansion of morichales. The simultaneous appearance of charcoal particles and *Mauritia* pollen around 2000 cal yr BP supports the potential pyrophilous nature of this palm and the importance of fire for its recent expansion. The whole picture suggests human settlements similar to today – in which fire is an essential element – since around 2000 yr ago. Therefore, present-day southern Gran Sabana landscapes seem to have been the result of the synergy between biogeographical, climatic and anthropogenic factors, mostly fire.

Keywords:

Fire, Gran Sabana, Human occupation, Last millennia, Charcoal, *Mauritia*, Neotropics, Paleoecology, Vegetation change

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Introduction

Savannas are among the most important vegetation formations of the American tropics (Huber, 1987). Palynological studies show that neotropical savannas have been common during the Holocene, especially in the lowlands (e.g. Wymstra and van der Hammen, 1966; Behling and Hooghiemstra, 2001), and emphasize the importance of the last millennia for the shaping of present savanna landscapes (Rull, 1992; Behling

and Hooghiemstra, 1998; Rull, 1999). In northern South America, neotropical savannas are mainly shared between Colombia (Llanos Orientales) and Venezuela (Orinoco Llanos). In addition, there is another relatively large savanna extension between Venezuela, Brazil and Guyana, which in Venezuela is called the Gran Sabana (Huber, 1995b), lying on a mid-altitude plateau, where the present study is located ([Fig. 1](#)).

Although there are several high-resolution paleoecological and paleoclimatic studies of the last millennia in Venezuela (e.g. Rull et al., 2010a), records of this type are scarce in the Gran Sabana (GS). Previous paleoecological studies reveal that during the Late Glacial and Holocene, the southern GS experienced several climatic and vegetation changes. For example, a pronounced and relatively rapid vegetation shift occurred during the Younger Dryas, which ended with the establishment of treeless savanna. This coincided with variations in the hydrological balance (precipitation/evaporation ratio) and possibly with temperature (Montoya et al., 2011). The Mapaurí record ([Fig. 1](#)), showed a dramatic change from cloud forests to savannas at the beginning of the Holocene, also linked to temperature and moisture changes (Rull, 2007). In both cases, fire seems to have played a potentially important role in the vegetation change. Two other middle Holocene records from the Divina Pastora (DV) and Santa Teresa (ST) localities show that, during the last five thousand years, the landscape was dominated by treeless savannas. However, forests were located close to these sites and/or expanded their range between 5400 and 4100 cal yr BP in DV, and 5100 to 3900 cal yr BP in ST. After this time, the climate became drier and the forest extension decreased in size (Rull, 1992). Wetter conditions returned by 2700 cal yr BP, which resulted in the establishment of modern morichales (palm swamps dominated by the palm *Mauritia flexuosa*), rather than the expansion of forests. Similar results were obtained in the Encantada pollen record, with the initiation of morichal around 1200 cal yr BP (Montoya et al., 2009). In a nearby site called Urué ([Fig. 1](#)), the vegetation trends during the last two millennia could be reconstructed in more detail. At the beginning of this period, around 1700 cal yr BP, several recurrent forest fire events triggered a secondary succession that determined a significant forest reduction and the expansion of savannas, as well as the establishment of morichales (Rull, 1999). This study highlighted the effect that fires had upon Gran Sabana vegetation and the low resilience of its forests. Based on the available evidence, it could be assumed that both climatic oscillations and fire have had similar effects over the GS vegetation, that is, the reduction of forest cover and the expansion of savannas, with the establishment of morichales, thus shaping the nowadays southern GS landscape (Rull, 1992). According to Rull (1998b), the morichales, a unique neotropical vegetation type strongly linked to poorly drained and seasonally flooded soils at altitudes below around 1000 m, would have been expanding their range since the Last Glacial Maximum, favored by both climate and fire. Montoya et al. (2009) hypothesize that *M. flexuosa* would be considered a pyrophilous element, as it seems an active colonizer of river margins where gallery forests have been removed by fire.

In this paper, we report the paleoecological study of a lake sediment core from Lake Chonita, in the southern GS, based on pollen and spore analysis, as well as charcoal and non-pollen palynomorphs (NPP), and some physico-chemical measurements (magnetic susceptibility, bulk density and organic matter concentration). The aim is to reconstruct the vegetation changes that occurred during the last three millennia, to analyze the savanna/morichal dynamics and the shaping of present-day southern GS landscapes, as well as to discuss the potential paleoclimatic and/or anthropogenic forcings involved, with emphasis on human occupation timing and fire regimes. The implications of these results for *Mauritia* biogeography, in a regional northern South America context, are also discussed.

Study area

The GS is a vast region of about 18,000 km² located in SE Venezuela (4°36' to 6°37'N and 61°4' to 74°2'W, [Fig. 1](#)). The GS is part of an undulated erosion surface developed on the Precambrian Roraima quartzites and sandstones, and forms an altiplano slightly inclined to the south, ranging from about 1450 to 750 m elevation in a North–south gradient (Briceño and Schubert, 1990; Huber, 1995a). The climate has been described as submesothermic ombrophilous, with annual average temperatures of around 18 to 22°C and precipitation values of 1600–2000 mm yr⁻¹, with a dry season (<60 mm/month) from December to March (Huber and Febres, 2000). Concerning vegetation, the GS is a huge island of savanna within the normally forested Guayana landscape. These savannas form wide and more-or-less continuous treeless grasslands, locally intermingled with forests developing typical forest–savanna mosaics (Huber, 1994). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b), as is the norm in surrounding regions, has led to several hypotheses related to edaphic conditions, climate changes, and anthropogenic fires (Eden, 1974; Fölster, 1986; Rull, 1999; Fölster et al., 2001; Dezzio et al., 2004; Huber, 2006).

However, vegetation is not homogeneous throughout the region. The occurrence of shrub and forest patches is more common in northern GS, whereas in the southern region, where our study is located, the savannas are more extensive and the forests are mostly restricted to water courses or mountain slopes. The GS savannas are dominated by C4 grasses of the genera *Axonopus* and *Trachypogon*, with sedges such as *Bulbostylis* and *Rhynchospora*; woody elements are scarce and rarely emerge above the herb layer (Huber, 1995b). According to Huber (1994), there is a special type of vegetation (locally called morichal) where the herbaceous stratum remains ecologically dominant (treeless savanna), but the palm *M. flexuosa* forms characteristic monospecific stands. This vegetation type is especially common around lakes, and in the bottom of river valleys and flooded depressions of the southern GS, up to about 1000 m elevation (Huber, 1995b). The morichales are absent in northern GS due to this altitudinal limit. There is a general lack of knowledge about this palm species' biology and the communities it forms in the Gran Sabana (Ponce et al., 1999). Most GS forests are considered to fall within the category of lower montane forests (also called submesothermic forests, between 800 and 1500 m elevation), because of their intermediate position between lowland and highland forests (Hernández, 1999). Common genera include: *Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignoniaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Clathrotropis* (Fabaceae), *Aspidosperma* (Apocynaceae), *Caraipa* (Clusiaceae), *Dimorphandra* (Caesalpiniaceae), *Byrsonima* (Malpighiaceae), etc., and their composition varies with elevation (Huber, 1995b). The GS shrublands usually occur between 800 and 1500 m elevation and are more frequent at the northern area than at the southern part (Huber, 1995b), where our study site is located. The more common shrub genera are: *Euphonia* (Euphoniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Ochthocosmus* and *Cyrilopsis* (Ixonanthaceae), *Thibaudia*, *Notopora* and *Befaria* (Ericaceae), *Spathelia* (Rutaceae), *Byrsonima* (Malpighiaceae), etc. They usually grow on a rocky, sandstone substrate or deep white sands of alluvial origin (Huber, 1995b).

The GS region is the homeland of the Pemón indigenous group, from the Carib-speaking family. Today they are sedentary, living in small villages, usually in open savannas. Though the GS population density is currently low, the indigenous settlements have experienced an expansion since the arrival of European missions, and today, more than 17,000 people live in the GS (Medina et al., 2004). Fire is a key component of the Pemón culture as they use it every day to burn wide extensions of savannas, and occasionally, forests (Kingsbury, 2001). The reasons for the extent and frequency of these fires are related to activities such as cooking, hunting, fire prevention, communication, magic, etc. (Rodríguez, 2004, 2007). Surprisingly, land-use practices, such as extensive agriculture or cattle raising, typical of other cultures strongly linked to fire, are not characteristic of the Pemón culture (Rodríguez, 2004). The arrival timing of Pemón culture to the GS remains unknown. A recent settlement in the region during the last centuries has been assumed, migrating from Guyana or northern Brazil (Huber, 1995a; Kingsbury, 1999) but this would be constrained by the availability of historical accounts that do not necessarily record the first occupation event (Thomas, 1982; Colson, 1985). Therefore, an early occupation should not be dismissed. There is some archeological evidence consisting of pre-Hispanic remains (spearheads and bifacial worked knives) similar in style to others that are about 9000 yr old found in other Venezuelan localities (Gassón, 2002; Rostain, 2008). In addition, palynological evidence indicating the occurrence of intense and extensive fires during the Younger Dryas (around 12,400 cal yr BP), suggested a potential early human occupation of the GS as one of the potential factors for fire occurrence (Montoya et al., 2011), but a definitive assessment is not yet possible.

Materials and methods

Lake Chonita (4°39'N–61°0'W, 884 m elevation) is located within a private farm called “Hato Divina Pastora” near Santa Elena de Uairén, at the south of the GS region (Fig. 1). The annual precipitation in Santa Elena, at 910 m altitude, is about 1700 mm, with a weak dry season from December to March (Huber, 1995a). The lake is within a treeless savanna landscape, surrounded by scattered morichal patches. In the absence of a known local name for the lake, it will be called Lake Chonita for the purposes of the present study, to be consistent with previous studies developed at the same site (Montoya et al., 2011). The core (PATAM1 B07; 4.67 m long) was obtained in the deepest part of the lake (3.13 m water depth), using a modified Livingstone squared-rod piston core (Wright et al., 1984). The present study is focused on the detailed analysis, and paleoecological interpretation, of the last three millennia interval (0.03 to 0.97 m). A total of nine samples were taken along the whole core for radiocarbon dating, three of them falling within the interval discussed here. Samples were pretreated using standard acid–base–acid procedures (Abbott and Stafford, 1996) and measured at the AMS Radiocarbon Laboratory of the University of California, Irvine (UCI) and Beta Analytic (Beta). Calibration was made using CALIB 6.0.1 and the IntCal09.14c database (<http://calib.qub.ac.uk/calib/>, last accessed on April 2010).

Twenty-eight volumetric samples (2 cm³) were taken in the section studied, at 2–5 cm intervals, for pollen analysis. These samples were processed using standard palynological techniques slightly modified according to the sediment nature (Rull et al., 2010b), after spiking with *Lycopodium* tablets (batch 177745, average 18,584±1853 spores/tablet). The slides were mounted in silicone oil without sealing. Pollen and spore identification was made according to Hooghiemstra (1984), Roubik and Moreno (1991), Tryon and Lugardon (1991), Herrera and Urrego (1996), Rull (1998a, 2003) and Colinvaux et al. (1999). Counts were conducted until a minimum of 300 pollen and spores were tabulated (excluding Cyperaceae and aquatic plants: *Myriophyllum*,

Sagittaria and Utricularia), but counting continued until the saturation of diversity was reached (Rull, 1987). Final counts averaged 533 grains per sample. Pollen taxa were grouped according to the vegetation types previously described (Huber, 1986, 1989, 1994, 1995b; Huber and Febres, 2000). All identified pollen taxa were included into the pollen sum, except for Cyperaceae and the aquatic plants mentioned above. Pollen diagrams were plotted with PSIMPOLL 4.26, using a time scale derived from an age–depth model based on radiocarbon dating, developed with the clam.R statistical package (Blaauw, 2010). The pollen zonation was performed by Optimal Splitting by Information Content (OSIC), and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Only pollen types over 0.4% were considered for zonation. Interpretation was based on comparison with modern samples from previous studies (Rull, 1992, 1999) and the known autoecology of taxa found (Marchant et al., 2002; Rull, 2003). Sample PATAM1_B07/8, 38 cm depth was excluded due to methodological problems. NPP were analyzed on pollen slides, and plotted in percentages based on pollen sum. NPP identification was made according to Montoya et al. (2010) and literature therein. Charcoal counts were carried out in the same pollen slides, considering two size classes (Rull, 1999):

- Type I (smaller microcharcoal particles: 5–100 μm): used as proxy for mostly regional fires, because of their easy dispersion by wind.
- Type II: (larger microcharcoal particles: $\geq 100 \mu\text{m}$): used as proxy for local fires.

Bulk density (BD) was measured on 1 cm^3 samples, taken every 5 cm down-core. The samples were weighed wet, and again after drying in a 60°C oven for 24 h. Total organic matter was measured every 5 cm by loss-on-ignition (LOI) at 550°C (Dean, 1974). There is no measurable calcium carbonate in the sediments, based on LOI measurements made after burning at 1000°C. Magnetic susceptibility (MS) was measured at a 0.5 cm interval using a Tamiscan high-resolution surface scanning sensor connected to a Bartington susceptibility meter at the University of Pittsburgh.

Results

Lithology and chronology

The lacustrine sequence is characterized, in the studied section, by dark-brown organic-rich sediments. The upper part of the section is characterized by slightly higher magnetic susceptibility values than the lower one, with a major peak between ~30 and 24 cm and a minor peak in the upper 10 cm (between 8.5 and 1.5 cm). The organic matter data shows changes in the relative amounts of organic matter and terrigenous (mineral) sediments in the core ([Fig. 2](#)). Generally, sections with high dry bulk density ([Fig. 2](#)) also have lower organic matter and high in terrigenous sediments. Dry BD shows a high variability and presents its maximum values between ~30 and 24 cm, coinciding with the major MS peak. Organic matter is characterized by a fluctuating trend followed by an abrupt increase in the upper 20–10 cm of the record.

The results of AMS radiocarbon dating were used to produce an age–depth model for the sequence ([Table 1](#)). The best fit was obtained with a smooth-spline function (Blaauw, 2010), and is represented in Figure 2 only for the interval of interest of this study. The sedimentation rate of the whole sequence varies between 0.02 and 0.17 cm yr^{-1} . For the interval studied here, the sedimentation rate ranges between 0.02 and 0.08 cm yr^{-1} . The time interval between samples ranges from 60 to 150 yr.

Palynological zonation

The pollen diagram is dominated by pollen assemblages from two different herbaceous plant formations: a treeless savanna, with a nearby forest in the lower part; and a savanna with morichal, coinciding with a decrease in forest elements, in the upper half (Figs. 3 and 5). The pteridophyte spores are not very abundant, though psilate triletes and monoletes are better represented than others. Regarding NPP, *Botryococcus*, *Coniochaeta* cf. *ligniaria* and *Neorhabdocoela* oocites are the more abundant (Fig. 4). The stratigraphic variations of the pollen and spore assemblages allowed subdivision of the diagram into two zones.

LCH-I (97–37 cm, 14 samples)

The pollen assemblage is clearly dominated by Poaceae, which presents fluctuating values ranging from 40 to 70% of the total pollen sum, followed by trees (mainly Urticales) (Fig. 3). Some forest elements are also present at high to medium abundances, as for example Urticales (the more abundant of them), *Alchornea*, *Byrsonima*, *Cecropia*, *Euphorbiaceae*-type, *Miconia*, *Myrsine* and *Weinmannia*. *Mauritia* appears at the top of the zone, though with low abundance. The percentages of pteridophyte spores are low, but a slight increasing trend can be observed in psilate monoletes and psilate triletes at the top of the zone. Smaller charcoal particles (5–100 µm) remain at low abundances, with an increase at the top of the zone, coinciding with the first appearance of larger particles (N100 µm). Regarding influx index, it can be observed that Urticales, show relatively stable values, with a slight decrease at the top of the zone (Fig. 5). Figure 5 also shows an increasing trend of *Mauritia* and charcoal particles towards the top. Among aquatic elements (algal remains and aquatic or semi-aquatic plants; Fig. 4), *Botryococcus* is the dominant, with strong fluctuations in its concentration and a sharp decrease in the upper part of the zone. Type 91 (HdV. 91) shows an increase at the upper part of the zone, and *Spirogyra* peaks at the top. *Cyperaceae* are also abundant, with minor variations, and *Sagittaria* shows a slightly decreasing trend at the upper part of the zone. Regarding fungal spores and other NPP, the more abundant are *Coniochaeta* cf. *ligniaria*, *Neorhabdocoela* oocites, *Cercophora*-type and *Sordaria*-type, though *Sordariales* also presents a peak at the lower part of the zone (Fig. 4).

LCH-II (37–3 cm, 14 samples)

The pollen assemblage is marked by an abrupt increase of *Mauritia* likely at the expense of trees, in the lower half of the zone, and of trees and Poaceae in the upper part, from around 35 cm upwards (Fig. 3). There is a decrease of *Mauritia* and a return to the former higher values of Poaceae in the intermediate part of the zone (32–18 cm). Above this depth, *Mauritia* increases again synchronously with a decrease in Poaceae. There is a general decreasing trend of nearly all the forest elements, which in some taxa, as *Alchornea* and *Bonyunia*-type, represent almost their complete disappearance. Pteridophyte spores remain at similarly low values to the previous zone. Psilate triletes has higher values at the base of the zone, showing a slightly decreasing trend from ~30 cm upwards. Smaller charcoal particles maintain the increasing trend initiated at the upper part of the previous zone, and experience three abrupt peaks, the first one around 32 to 23 cm, and the other two, of higher magnitude, at 18 and 8 cm, respectively (Fig. 3). Larger charcoal particles remain low at the beginning of the section, and show a pattern similar to smaller particles, but significantly lower in magnitude, throughout the zone. All the biological proxies analyzed show an increase in their influx indices, except for pteridophyte spores (Fig. 3). Figure 5 shows higher

values of *Mauritia* pollen and charcoal particles and lower values of *Urticales* with respect to the former zone. Aquatic elements and fungal spores and other NPP are characterized by lower abundances respect to the former zone, except for *Cyperaceae*, which shows similar values ([Fig. 4](#)). The correlation between *Mauritia* and total charcoal influx index curves ([Fig. 5](#)) was performed, obtaining an R value of 0.718, which is significant for $p < 0.001$.

Discussion

The region around Lake Chonita has remained a savanna during the last three millennia, but a significant vegetation change occurred around 2000 yr ago. Indeed, prior to 2180 cal yr BP, a treeless savanna landscape with nearby forests dominated the site, but the last two millennia have been characterized by forest retraction and the establishment of a morichal, which remains until present. The paleoecological sequence is discussed in the following sections in the context of northern South American savannas, and the contribution of these results to the understanding of the fire–vegetation relationships at South GS.

Paleoecological interpretation

3640 to 2180 cal yr BP

The sedimentary features and the presence of aquatic organisms indicate that the lake probably was already established prior to 3640 cal yr BP. The pollen assemblage of this zone indicates a treeless savanna landscape without morichales. The abundance of forest elements suggests that this formation was probably closer and/or more expanded than today. The continued presence of smaller charcoal particles – indicative of regional fires – together with the continuous presence of *Cecropia* – a secondary colonizer – may indicate some regional fires of low intensity occurred. The lack of coarse charcoal indicates local fires did not occur. The first appearance of larger microcharcoal particles, as proxies for local fires, were recorded at ~2400 cal yr BP. This occurred synchronously with the first appearance, though at low values, of *Mauritia* pollen, and an increase in psilate triletes. These spores have been related with early stages of secondary succession after fire, in other sites of the GS (Rull, 1999). The high values of *Botryococcus* and *Neorhabdocoela* oocites from 3640 to 2800 cal yr BP suggest that lake levels were stable. During this time period climate might have varied from a higher water balance prior to 2800 cal yr BP to lower moisture availability from this date to the end of the interval, as indicated by the lower values of aquatic organisms, mainly *Botryococcus* and *Neorhabdocoela*. This is in agreement with the Encantada record (Montoya et al., 2009), but it does not coincide exactly with other GS records, as for example DV or ST (Rull, 1992). Dating inconsistencies in previous records derived from the use of large quantities of bulk sediment for dating using conventional radiocarbon methods instead of AMS techniques, and the few dates available for a sound age–depth model cannot be dismissed for this time interval.

Similar trends regarding water levels and climate have been observed in some paleoecological and paleoclimatic records from northern South America. For instance, Lake Valencia ([Fig. 1](#)) had higher water levels from 6000 to 3000 14C yr BP (~6840 to 3200 cal yr BP), except for a short interval of lower lake levels centered at 3300 14C yr BP (~3550 cal yr BP) (Bradbury et al., 1981; Leyden, 1985; Curtis et al., 1999). From this, some of these authors inferred a high precipitation/evaporation ratio (P/E) determined by higher insolation and changes in the latitudinal position of the Intertropical Convergence Zone (ITCZ) (Curtis et al., 1999). Haug et al. (2001) inferred a decrease in precipitation from 5350 cal yr BP in the Cariaco Basin ([Fig. 1](#)), with large

century-scale variations between ~3750 and 2750 cal yr BP. In the Colombian Llanos Orientales, a wetter interval was suggested for the middle Holocene, peaking around 4000 cal yr BP (Marchant and Hooghiemstra, 2004). Such climatic inferences were supported by evidence of forest expansion in different records (e.g. Behling and Hooghiemstra, 1998, 1999, 2000; Berrío et al., 2002). Contrarily, the Rupununi savannas of Guyana ([Fig. 1](#)), would have had a continuous presence of treeless savanna since the middle Holocene, with an increase in Poaceae around 3000 cal yr BP (~3200 cal yr BP) (Wymstra and van der Hammen, 1966). Therefore, a likely forest expansion in the present savanna areas of northern South America prior to 3000 cal yr BP, probably linked to an increase in moisture, seems to be supported by the available evidence. The regional differences found in nearby locations could be related to local climate variations.

2180 cal yr BP to present

The beginning of this time interval was marked by an abrupt local vegetation change, though the general GS landscape continued to be dominated by treeless savannas. The sudden increase of *Mauritia* coincides with a decrease of Poaceae and forest elements. While Poaceae abundance returned to former values at ca. 1920 cal yr BP, the forest did not show any recovery until the present. The increase in fire incidence during this interval could have been decisive in this sense, favoring the establishment of morichal communities, as suggested by several former studies (Rull, 1992, 1998b, 1999; Montoya et al., 2009). The synchrony showed in the influx index between the increment of *Mauritia* pollen and charcoal particles and the decline of Urticales, interpreted in this work as indicative of forest presence according to Gosling et al. (2009), agrees with this assumption ([Fig. 5](#)). The potential establishment of a drier regional climate since 2800 cal yr BP (Bradbury et al., 1981; Curtis et al., 1999; Berrío et al., 2000; Behling and Hooghiemstra, 2001; Berrío et al., 2002; Wille et al., 2003), might indicate some level of climatic influence (or a synergistic fire-climate coupling) on forest retraction. The treeless savanna expanded again from 1920 to 1120 cal yr BP, synchronously with a decrease of *Mauritia* abundance. At the same time, there is a major peak in MS and BD curves. Such synchrony could be interpreted as a higher input of terrigenous sediments to the watershed due to erosion processes caused by the existence of a more open landscape resulting from *Mauritia* clearing. After that, two major charcoal peaks recorded at ca. 1120 and 480 cal yr BP coincide with the morichal expansion. Thus, it is suggested that the present-day landscape around Lake Chonita was established around 1120 cal yr BP. The MS minor peak occurred this time paralleled the *Mauritia* increase and is dated ca. 500 to 50 cal yr BP, which is synchronous with the Little Ice Age (LIA) recorded in the Venezuelan Andes, as a cool and humid interval linked to solar activity cycles (Polissar et al., 2006). In Lake Chonita, the only potential evidence for more humid conditions is the *Mauritia* increase at the top. However, aquatic elements indicate that during the whole interval moisture conditions were more or less stable, and similar to present-day, with minor variations, so a definitive interpretation cannot be made.

The recent appearance and sudden increase of *Mauritia*, or the establishment of present-day morichales, coinciding with an increased fire incidence have also been reported in most sequences in the GS (e.g.: DV, ST, Urué and Encantada) (Rull, 1992, 1999; Montoya et al., 2009). Sudden increases of *Mauritia* and/or slightly drier climate than mid Holocene relative to the last millennia have also been reported in several studies in nearby areas. In the Venezuelan Llanos, *Mauritia* presence was also reported only for the last two millennia, in a climate likely more humid than the previous interval (Leal et al., 2002, 2003). In the Colombian Llanos, the same trends have been

observed, during the last two millennia, in several localities (Behling and Hooghiemstra, 1998, 1999, 2000; Berrío et al., 2000; Behling and Hooghiemstra, 2001; Berrío et al., 2002; Wille et al., 2003). Hence, there is a general agreement regarding the influence of increased human impact, usually through fire, in the establishment of morichales, and the shaping of the present savanna landscapes during the last two millennia.

Mauritia, climate, fire, and human occupation in the GS

Several studies developed in the GS have revealed the continuous persistence of savannas since at least the early Holocene (Rull, 2007; Montoya et al., 2011). However, the taxonomic composition of this biome has shown the dynamic nature of its plant communities. This is the case of morichales, whose occurrence has been traditionally considered indicative of warm and wet lowlands (and midlands) of northern South America. As a consequence, morichal expansions observed in paleoecological records have been generally interpreted in terms of wetter climate (e.g. Rull, 1992; Behling and Hooghiemstra, 1999; Rull, 1999; Berrío et al., 2000; Leal et al., 2002, 2003). The appearance and expansion of *Mauritia*-dominated communities in the Colombian Llanos Orientales (Fig. 6), likely agree with this climatic interpretation. Thereby, this palm was recorded for first time around the middle Holocene, where a wet period was documented for the region (Marchant and Hooghiemstra, 2004). In our study, however, the recent morichal expansion occurred in a climate drier than the preceding phase which, at first, seems contradictory. Nevertheless, this evidence also suggests that climate is not the only factor affecting the morichal occurrence and distribution at southern GS, which appears to be linked strongly to fire incidence or to fire–climate synergies (Fig. 5). The synchrony between increased fire frequency and morichal establishment recorded in several GS sequences together with the correlation degree obtained, as well as the common presence of charcoal particles in palynological slides, supports this view. This is in agreement with the absence of *Mauritia* palm swamps during the Holocene in the GS, despite the occurrence of periods of higher moisture availability, and its later expansion during phases of high fire incidence (e.g. Montoya et al., 2009). This supports the assumed pyrophilous character of *Mauritia* and the morichales it forms (Montoya et al., 2009), favored by human-induced forest clearing by fire. Another potential factor involved would be geographical. According to Rull (1998b) *Mauritia* has been expanding its range since the end of last glaciation, so it is possible that this palm did not reach the GS until the last two millennia. This would also help to explain its former absence in the GS during Holocene periods, with assumedly optimal ecological conditions, when it was indeed present in the Colombian Llanos Orientales (Fig. 6). Overall, this suggests that the present-day distribution of this palm could be the result of a synergism between biogeography (post-glacial expansion), climate (humid conditions) and human disturbance (fire). Unfortunately, the lack of charcoal data for most of the available neotropical records prevents a regional synthesis of the potential effect of fire upon *Mauritia* communities.

The existing evidence suggests that fire is a key factor to understand the GS environmental history. As mentioned before, the GS has been the homeland of the Pemón indigenous group at least during the last 300 yr. The intensive and extensive use of fire by this culture is well documented (Kingsbury, 2001; Rodríguez, 2004, 2007), and has been often related to the current extension of savannas and forests (Dezzeb et al., 2004; Huber, 2006). The high amount of charcoal in different neotropical records has been postulated as indicative of human settlements, even in the absence of changes in land use (Bush et al., 2007). Moreover, there is some archeological evidence of human populations synchronous with charcoal peaks around the Orinoco Basin, frequently located close to water courses (e.g.: Saldarriaga and

Webs, 1986). The continuous presence of local fires at Lake Chonita since about 2000 yr ago (Figs. 3 and 5), suggests an earlier human occupation of the lake catchment. If so, one possible scenario is that once humans arrived, they made fires for different reasons, and the forest suppression favored the morichal establishment where edaphic conditions were suitable. In this case, humidity seems to have played a minor role in the palm establishment, due to the time elapsed between the decrease in water levels and the *Mauritia* expansion (Figs. 3 and 4). The progressive soil degradation caused by the maintained fires should be also considered (Dezzeo et al., 2004). Conversely, the synchrony between increases in charcoal and *Mauritia* after 2000 yr ago point to this possible early human settlement at South GS, not necessarily of the Pemón culture, but a similar culture at least in regard to the use of fire. The extensive use of palms by many indigenous cultures from the Neotropics supports this assumption (Heckenberger and Neves, 2009).

Biogeographic considerations on Mauritia

Given the results presented here, some considerations regarding morichal communities seem pertinent. Figure 6 shows the age of modern-day *Mauritia* community establishment in different paleoecological records from northern South American savannas. *Mauritia* pollen can be present both in monospecific palm formations (with percentages from 10 to 30% or more), and in mixed or gallery forests (with percentages from 1 to 4%) (Rull, 1992). Thus, the age marks not the first appearance of *Mauritia* pollen in the record, but the formation of a modern morichal community. In a northern South American context, the Holocene colonization of the GS by *Mauritia* seems to have occurred later than in the savannas from the Orinoco lowlands (Fig. 6). This would be due in part to anthropogenic factors (i.e. time of arrival of fire-prone cultures), but the physical isolation of the GS from any other savanna patch would have also played a role. *Mauritia* has no long-distance dispersal by wind, and its seeds are commonly transported by animals (mousses, opossums, squirrels, agoutis, peccaries, and others) or by water (Ponce, 2002). Therefore, a physical connection is needed for *Mauritia* expansion. At present, there is no such connection in the GS. One possibility is that *Mauritia* reached the GS during a phase of a general savanna expansion, which would have caused a less fragmented pattern, but there is no any paleoecological record suggesting such a framework after around 2000 yr ago. It is also possible that humans were the dispersal agents, as it is known that this palm is widely and intensively used by indigenous cultures for housing, food, and other relevant activities (Henderson et al., 1995; Gomez-Beloz, 2002; Heckenberger and Neves, 2009). In this case, physical connection is not mandatory, as humans could have migrated from one savanna patch to another through the rainforest. Concerning the source, colonization from the north is unlikely because the northern GS is a physical barrier due to its elevation, around 400–500 m higher than required for *Mauritia*, whose upper limit is around 1000 m altitude. For *Mauritia* to reach such elevations and cross this barrier, an increase of ca. 2.5–3.0°C in the annual average temperatures would be needed by 2000 cal yr BP, but this has not been found in the GS records to date. Therefore, the GS populations of this palm species should come from elsewhere. With the presently available – though very scarce – data, the more likely source seems to be the Amazon Basin (Rull, 1998b). This should be considered a working hypothesis, which needs further palynological analysis (including charcoal records) combined with anthropological and archeological studies. Emphasis should be placed on the precise delimitation of present-day *Mauritia* distribution, which is still largely unknown, and the design of a coring strategy able to produce a network of sites with dated first appearances of the *Mauritia* pollen, in order to follow the spatio-

temporal colonization patterns. Intraspecific phylogeographic studies would also help to reconstruct migrational patterns and potential genetic variability among populations, to help test biogeographical hypotheses based on paleoecological results.

Conclusions

The palynological study of the upper part of the lake Chonita sequence, from southern GS, allows for the reconstruction of vegetation changes during the last three millennia. Although savannas were the dominant vegetation type, two different savanna landscapes are recognized: a treeless savanna with forests more extensive and/or closer than today prior to 2180 cal yr BP (with likely higher water levels prior to 2800 cal yr BP), and a savanna with morichal, under intensive fire regimes thereafter. The abrupt and dramatic increase of *Mauritia*, and the concomitant decrease of forest elements occurred around 2000 cal yr BP could have been caused by fire. At the same time, a shift to drier conditions than in the mid-Holocene has been reported in nearby localities suggesting that a regional climate change should also be considered, but given the preference of *Mauritia* for humid climates, the hypothesis of fire is better supported. The synchronous appearance of *Mauritia* and charcoal, together with the disappearance of forests, support the hypothesis of a potential pyrophilous nature of this palm (Montoya et al., 2009). The continuous occurrence of local fires during the last two millennia around Lake Chonita suggests the presence of human settlements well before the assumed colonization around the last centuries. The results presented here highlight the importance of the interplay between climate and fire to explain the present-day GS vegetation. The colonization of the GS by *Mauritia* appears to have occurred later than in the Colombian Orinoco Llanos, probably because of a later human occupation and the physical isolation of these savanna patches with respect to the main northern South American savanna areas. Further studies are required to test this hypothesis, but it seems that the present geographical patterns of *Mauritia*, and the monospecific communities it forms, are the result of the synergy between biogeographic, climatic and anthropogenic factors, with human-made fires as a major cause.

Appendix A

Localities depicted in Figure 6. The different sequences are ordered chronologically, by the time of appearance of *Mauritia* or *Mauritiella* palm stands or morichales, expressed as cal yr BP. Fire column refers to the coincidence between morichal pollen and charcoal increase. N marks those localities where morichales were already present at the beginning of the record. Elev.: Elevation (in meters); Carim: Carimagua; ND: no data; GS: Gran Sabana.

N°	Locality	Coordinates	Elev.	Region	Morichal	Fire	Reference
1	Chenevo	4°5'N - 70°21'W	150	Colombia	6330	ND	Berrio et al., 2002
2	Angel	4°28'N - 70°34'W	200	Colombia	4290	ND	Behling & Hooghiemstra, 1998
3	Carimagua	4°4'N - 70°14'W	180	Colombia	4260	ND	Behling & Hooghiemstra, 1999
4	Sardinas	4°58'N - 69°28'W	80	Colombia	4030	ND	Behling & Hooghiemstra, 1998
5	Mozambique	3°58'N - 73°3'W	175	Colombia	3720	ND	Berrio et al., 2002
6	Margaritas	3°23'N - 73°26'W	290	Colombia	2500	Yes	Wille et al., 2003
7	Loma Linda	3°18'N - 73°23'W	310	Colombia	2330	ND	Behling & Hooghiemstra, 2000
8	Agua Sucia	ND	260	Colombia	2230	ND	Wijmstra & van der Hammen, 1966
9	Chonita	4°39'N - 61°W	884	Venezuela, GS	2175	Yes	This publication
10	Sta. Barbara	9°33'N - 63°40'W	80	Venezuela	>1960	ND	Leal et al., 2002, 2003
11	Sta. Teresa	4°43'N - 61°5'W	880	Venezuela, GS	1700	ND	Rull, 1992
12	Div. Pastora	4°42'N - 61°4'W	800	Venezuela, GS	1500	ND	Rull, 1992
13	Encantada	4°42'N - 61°4'W	867	Venezuela, GS	1220	Yes	Montoya et al., 2009
14	Urué	5°2'N - 61°10'W	940	Venezuela, GS	990	Yes	Rull, 1999
15	Carim-Bosque	4°4'N - 70°13'W	180	Colombia	>1190, 80	ND	Berrio et al., 2000

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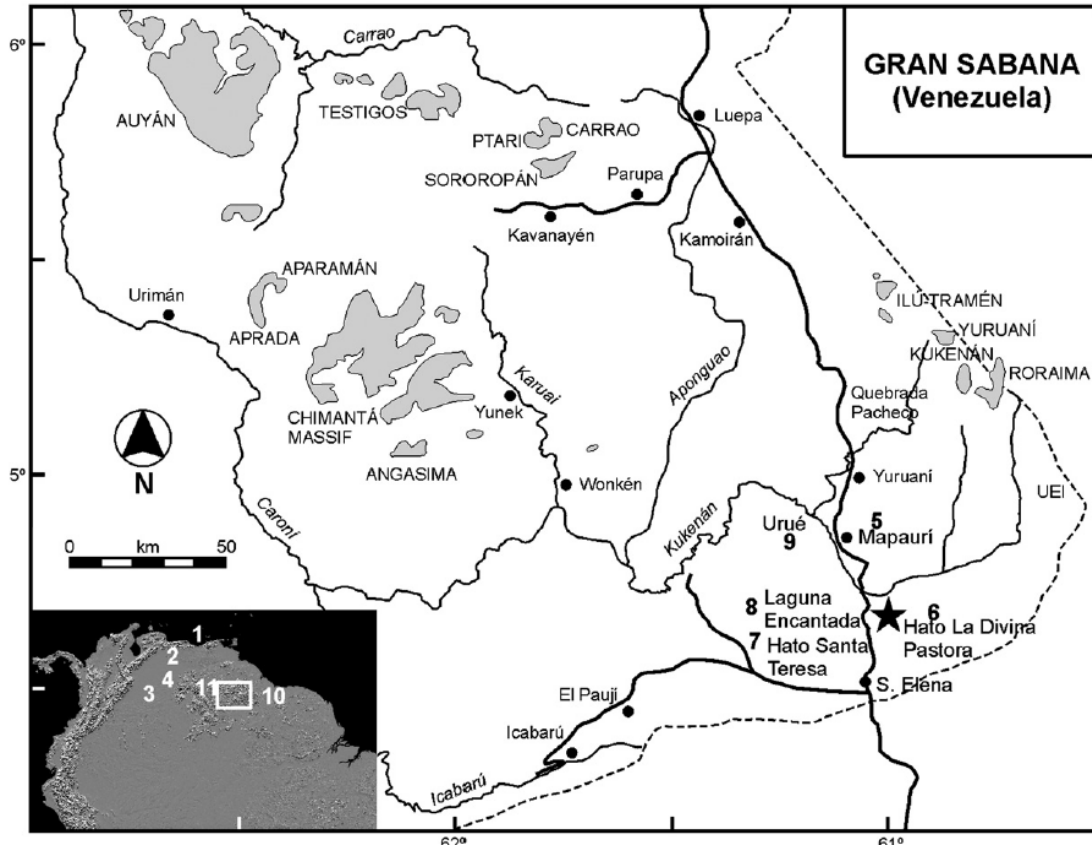


Figure 1. Location of the study area and its position within northern South America. (Radar image courtesy of NASA/JPL-Caltech). The coring site is indicated by a star. Numbers indicate the sites with paleoecological information mentioned in the text: 1 — Cariaco Basin (Venezuela); 2 — Lake Valencia (Venezuela); 3 — Colombian Llanos; 4 — Orinoco savannas (Venezuela); 5 — Mapauri (Gran Sabana); 6 — Divina Pastora (Gran Sabana); 7 — Santa Teresa (Gran Sabana); 8 — Lake Encantada; 9 — Urué (Gran Sabana); 10 — Rupununi savannas (Guyana); and 11 — Canaima (Gran Sabana).

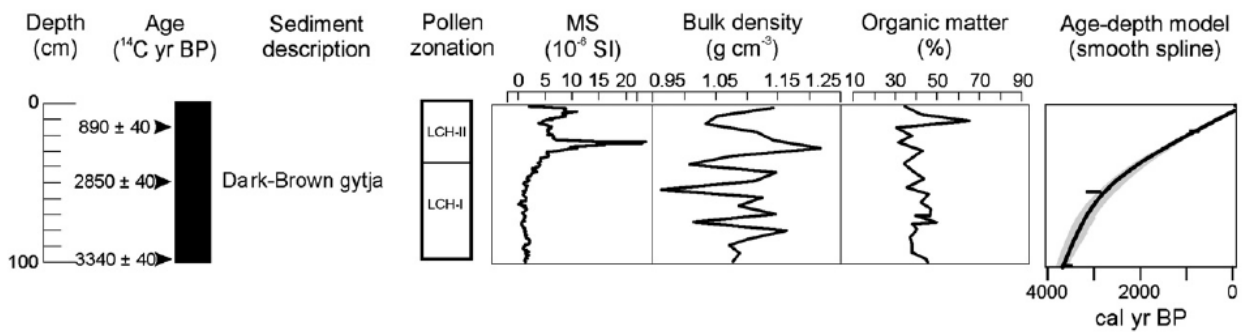


Figure 2. Core stratigraphy, with radiocarbon ages (in radiocarbon years, uncalibrated ages) and sediment description; pollen zones, physical parameters curves and age–depth model of the study section. MS: Magnetic susceptibility.

Table 1

AMS radiocarbon dates used for the age–depth model for the whole record. Asterisks mark the dates included in the interval under study. The estimated ages have been extracted from the calibrated ages (WA: Weighed average).

Laboratory	Sample	Depth (cm)	Sample material	Age (yr 14C BP)	Age (cal yr BP) 2 σ	Age (cal yr BP) estimation (WA)
Beta-279600*	PATAM1_B07/3	13	Pollen extract	890 \pm 40	731–915	800
Beta-277185*	PATAM1_B07/11	51	Pollen extract	2850 \pm 40	2855–3078	2730
Beta-277184*	PATAM1_B07/22	98	Pollen extract	3340 \pm 40	3471–3643	3660
UCI-43705	PATAM1_B07/32	144	Wood	4080 \pm 40	4497–4655	4640
UCI-43706	PATAM1_B07/49	212	Wood	6465 \pm 25	7323–7403	7380
Beta-277186	PATAM1_B07/70	298	Pollen extract	9590 \pm 60	10,738–11,164	10,690
UCI-43537	PATAM1_B07/87	362	Wood	9720 \pm 70	11,063–11,251	11,380
Beta-247284	PATAM1_B07/93	392	Wood	10,440 \pm 40	12,128–12,530	12,340
UCI-43614	PATAM1_B07/99	402	Wood	11,005 \pm 45	12,699–13,078	12,740

PATAM1-B07

Analyst: E. Montoya

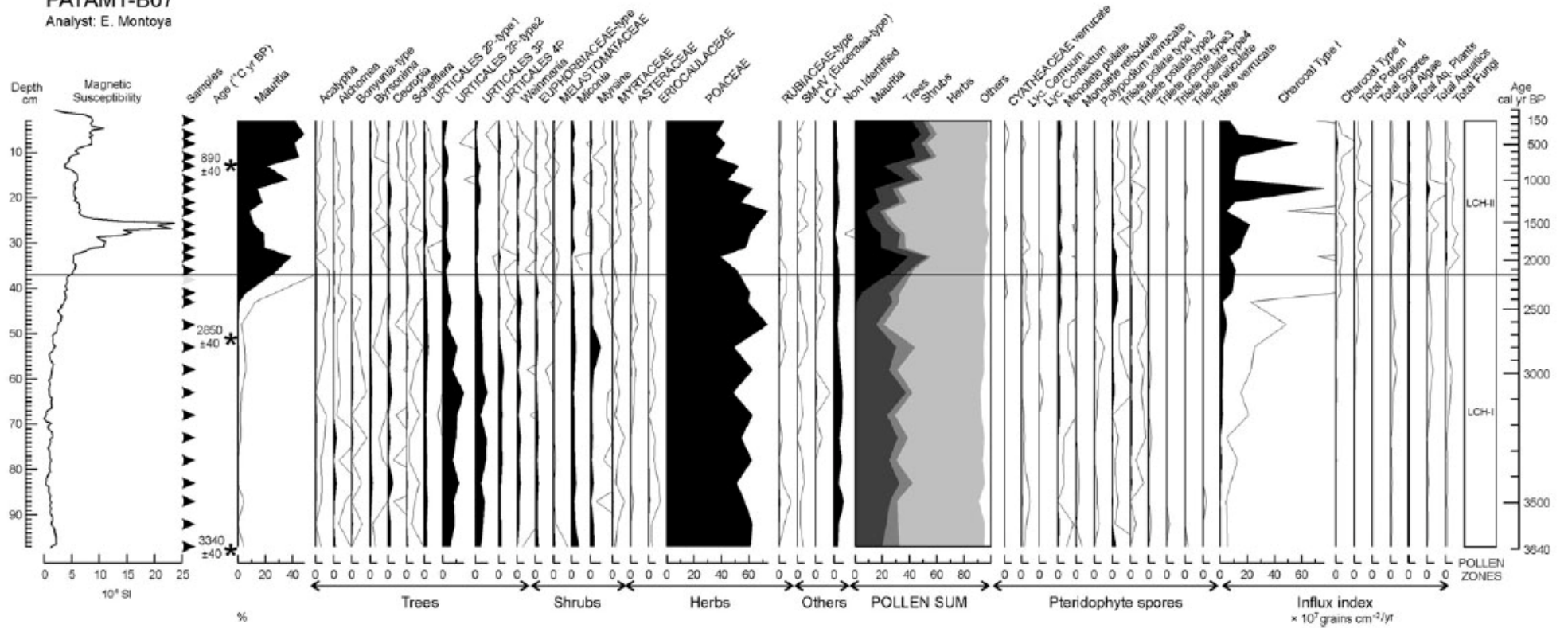


Figure 3. General pollen diagram expressed in percentages. Solid lines represent ×10 exaggeration. Excluded sample (38 cm depth) is marked in gray. Time scale has been done according to the age depth model obtained for the sequence (Fig. 2).

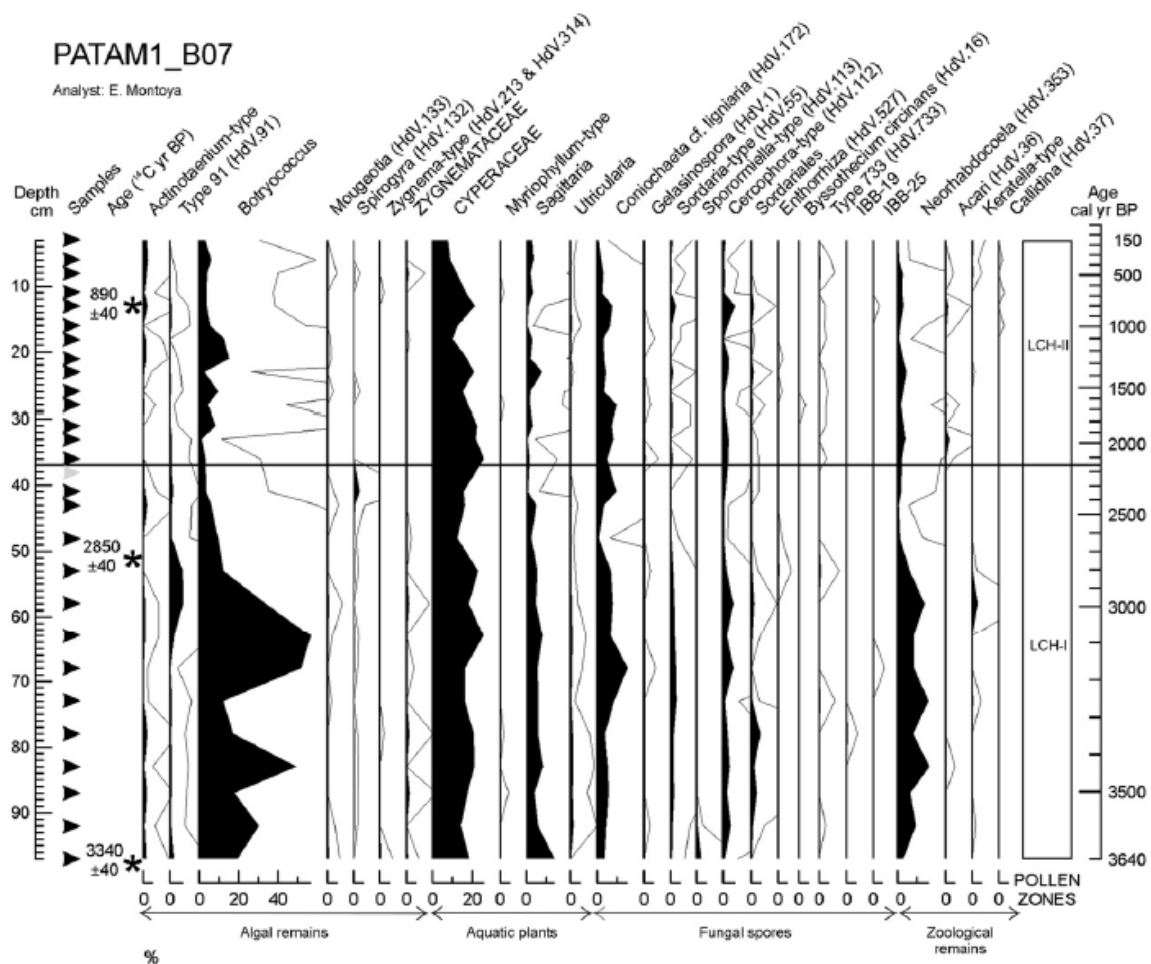


Figure 4. General non-pollen palynomorphs (extra pollen sum taxa) diagram expressed in percentages respect to pollen sum. Solid lines represent $\times 10$ exaggeration. HdV: Hugo de Vries Lab; IBB: Institut Botànic de Barcelona. Excluded sample (38 cm depth) is marked in gray. Time scale has been done according to the age depth model obtained for the sequence (Fig.2).

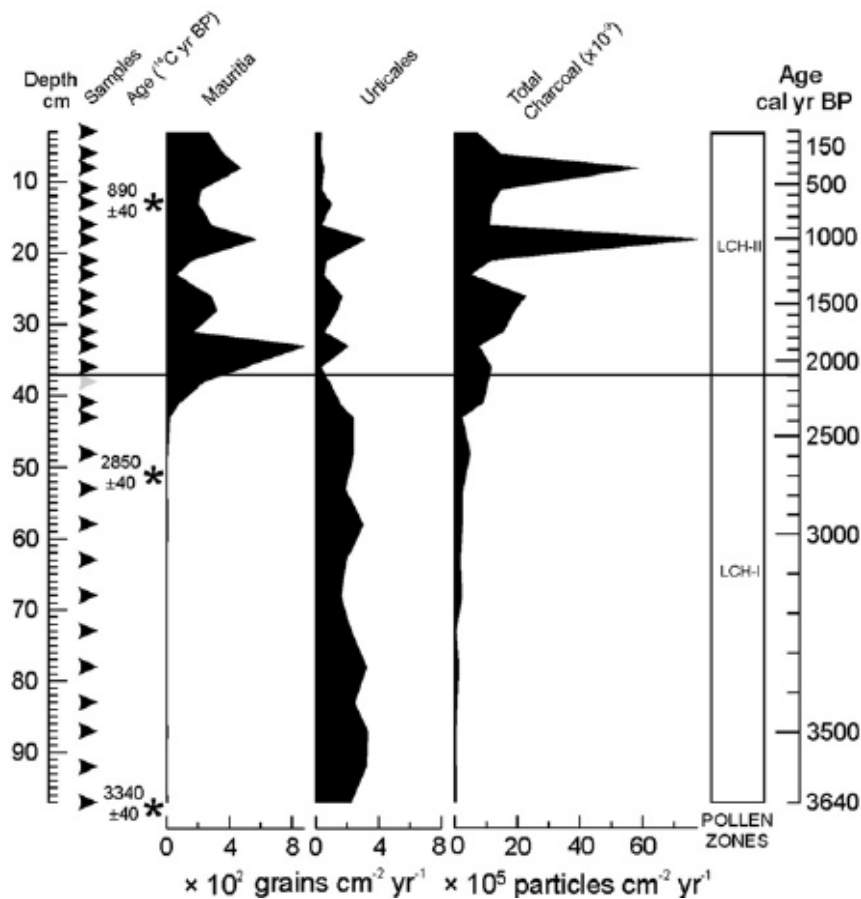


Figure 5. Influx index diagram of *Mauritia* pollen, *Urticales* pollen as indicative of forests following Gosling et al. (2009) and total charcoal particles. Excluded sample (38 cm depth) is marked in gray. Time scale has been done according to the age-depth model obtained for the sequence (Fig. 2).

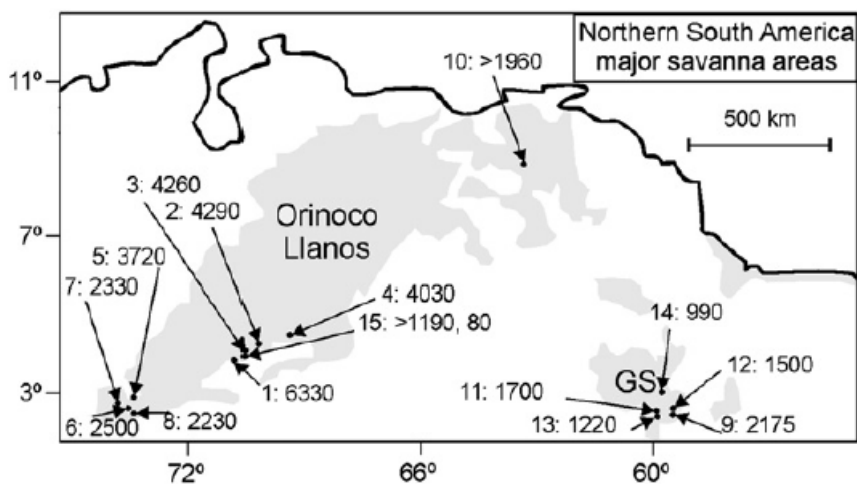


Figure 6. Location of sequences where morichal establishment has been reported in northern South American savannas. Map extracted from Behling and Hooghiemstra (2001) and Eva et al. (2004); present-day savanna areas are marked in gray. Numbers are referred to: (i) the sequences properly, they are ordered chronologically and showed at appendix; and (ii) the age (expressed in cal yr BP) of the morichal establishment. GS: Gran Sabana; N marks those localities where morichales were present at the beginning of the record, so the palm establishment must have occurred earlier. See appendix for all information related.

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