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ORIGINAL ARTICLE

Mid-Holocene vegetation dynamics with an early expansion of *Mauritia flexuosa* palm trees inferred from the Serra do Tepequém in the savannas of Roraima State in Amazonia, northwestern Brazil

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Abstract Transition zones between forest and savanna in northern South America are important areas for improving our understanding of ecosystem dynamics and climate change. The uniquely available mid-Holocene sediment deposits from the Serra do Tepequém plateau in Roraima State, northwestern Brazil, were used to analyze past forest-savanna dynamics through pollen, spores, microcharcoal and loss on ignition (LOI). In this newly studied landscape, two distinct periods of vegetation, fire and climate dynamics have been recorded. The first phase from ca. 7,570 to 6,190 cal BP, with the dominance of savanna vegetation in particular with Poaceae and Cyperaceae and some small forest patches with Moraceae/Urticaceae, *Alchornea* and *Schefflera*, indicates a relatively dry period. Based on the microcharcoal concentration and influx data, frequent regional fires occurred at that time. The second phase from ca. 6,190 to 4,900 cal BP shows a change in the vegetation composition with an increase of *Ilex, Schefflera* and Fabaceae. In this period forest expanded, while savanna became reduced, reflecting an increase of wetter conditions.

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The fire frequency was markedly lower. The first occurrence of *Mauritia flexuosa* palm was at ca. 7,300 cal BP and an early expansion occurred at around 6,600 cal BP. This early expansion of *M. flexuosa* showed a development that was in opposition to the increase of fire and savanna expansion found in other regions in northern South America. The increase of wetter conditions in Serra do Tepequém in the mid-Holocene confirms other results found in savannas of Colombia and Venezuela between 7,000 and 6,600 cal BP.

Introduction

Palaeoecological reconstructions are important for understanding ecosystems and environmental dynamics and furthermore for projecting future climatic scenarios. However, despite the importance of preserving and understanding the Amazonian ecosystems, the number of palaeoecological records is still low (Flantua et al. 2015). Transition zones, such as forest-savanna mosaics, are of particular interest for palaeoclimatic reconstructions, as they are sensitive to disturbances and climatic changes during the past. Examples of such particular areas come from the savannas of northern South America (Hooghiemstra and Berrio 2007; Toledo and Bush 2009; Rull and Montoya 2014). In the Llanos Orientales in Colombia, the Gran Sabana in Venezuela and the Roraima savannas in Brazil different changes were detected in vegetation composition through the Holocene, with similar trends of changes to wetter conditions toward recent times. The forest-savanna mosaics have changed due to the action of climate and/or fires, forming

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different vegetation types of rainforests, shrub lands, and savannas (Montoya et al. 2011a; Rull et al. 2013). In most of the studied records in the area, a regional increase in wetter conditions for the mid-Holocene was detected due to a northernmost position of the Intertropical Convergence Zone (ITCZ) as was reported in several speleothem and geochemical records (Haug et al. 2001; Cheng et al. 2013; Bustamante et al. 2016). As a result, forest vegetation expanded in such savannas (Behling and Hooghiemstra 1999; Toledo and Bush 2009; Rull and Montoya 2014). A further increase in wetter conditions has also been detected for the late Holocene, in which strong human disturbances played a role (Behling and Hooghiemstra 1998, 1999; Meneses et al. 2013; Rull and Montoya 2014).

In the Gran Sabana in Venezuela, the interaction between savanna and forest in the Holocene was characterized by a marked increase of *Mauritia flexuosa* palm, in particular during the last 2,000 years (Montoya and Rull 2011; Rull et al. 2013; Ballesteros et al. 2014). The increase of *M. flexuosa* is interpreted as an indicator of wet environments, since it develops on diverse habitats with common geological and soil characteristics such as anoxic clay or sandy soils, poorly drained and frequent flooded areas, abundant organic material and high water tables (Lasso et al. 2013; Rull and Montoya 2014; Galeano et al. 2015). In addition, the interplay of fire and climate effects on vegetation during the last ca. 2,000 years has been dominated by fires, consequently promoting a continuous trend of savanna expansion, mostly driven by human disturbances (Rull et al. 2013). Similar findings for the late Holocene were reported in the Roraima savannas by Meneses et al. (2013), in which *M. flexuosa* stands have been present together with the expansion of savanna and high signals of fire. Similarly, an expansion of *M. flexuosa* was found in the savannas of Llanos Orientales in Colombia (Behling and Hooghiemstra 1999, 2000). *M. flexuosa* started to expand from ca. 4,000 uncal BP (4,400 cal BP), indicating wet environments that in the late Holocene were highly influenced by humans.

Despite of the effort on the palaeoecological reconstructions for the Gran Sabana and Llanos Orientales, there are only few records from the Brazilian Roraima savannas that studied the past forest-savanna dynamics and even fewer studying the role of fires and human occupation throughout the Holocene (Absy 1979; Desjardins 1996; Reis et al. 2008; Toledo and Bush 2009; Simões Filho et al. 2010; Meneses et al. 2013). The Roraima savannas in northwestern Brazil, which occur in the border area of Guyana and Venezuela, are of particular interest for reconstruction of past vegetation and climate changes. They are part of the "Rio Branco-Rupununi" complex with an area of ca. 61,664 km^2 (Barbosa et al. 2007). This huge area is characterized by particular geomorphological features dominated by a set of dissected plateaus surrounded by intramontane

pediplains, including several residual terrains across the extensive plain areas (Barni et al. 2015). The vegetation is mainly composed of a variety of grasses and sedges surrounded by drainage networks, which are covered by patches of gallery forest usually dominated by stands of *M. flexuosa* palms (known as "Buritizais") (Miranda and Absy 2000; Miranda et al. 2002; Barbosa and Miranda 2004).

Considering that there are few palaeoecological records describing the past vegetation and climate dynamics for the Roraima savannas in Brazil we have selected the plateau of Serra do Tepequém, also known as the "Brazilian tepui" where forest-savanna mosaics and *M. flexuosa* occur. We aimed to study forest-savanna dynamics in a new landscape with a uniquely available sedimentary sequence to contribute to the research on vegetation history and possible human impact in an area of interest for archaeology using pollen, spore, microcharcoal and loss on ignition (LOI) analyses. Our study focuses on detecting a regional increase in wetter conditions for the mid-Holocene using forest-savanna interactions, with an early increase of the palm *M. flexuosa*. We have used the development of this palm and its relation to the fire and savanna dynamics as indicators of wet environments. Furthermore, we compared our new findings with results from other savanna ecosystems such as the Gran Sabana and Llanos Orientales in northwestern South America to detect any similarities or differences.

Study area

Serra do Tepequém belongs to Roraima State in northwestern Brazil (Fig. 1). The sediment core was collected on the plateau in an exposed soil profile (3°47′31.24″N 61°42′15.59″E, elevation 635 m), which is close (100 m) to a spring area that has been influenced by diamond mining during the last decades and more recently by a small riverine formation. A huge area of the upland has been strongly influenced by diamond mining in the last decades (Brasil 1975; Beserra Neta et al. 2015) (Fig. 2c). The plateau possesses a range of elevations, reaching up to 1,100 m a.s.l. above valleys with altitudes of between 500 and 600 m, interrupted by hills and mountains varying from 650 to 900 m up to 1,100 m in height (Nascimento et al. 2012; Beserra Neta et al. 2015). The geomorphology of the area is characterized mainly by erosive scarps, steep slopes, valleys and residual mountains. Geologically this plateau is an erosional remnant of the Roraima formation (Brasil 1975; Almeida-Filho and Shimabukuro 2002), containing mainly sandstones, conglomerates, and minor occurrences of siltstone and claystone, lying over acid to intermediate Early Proterozoic volcanites (rhyolites, rhyodacites, andesites, etc.) of the Surumu Group (Almeida-Filho and Shimabukuro 2002).
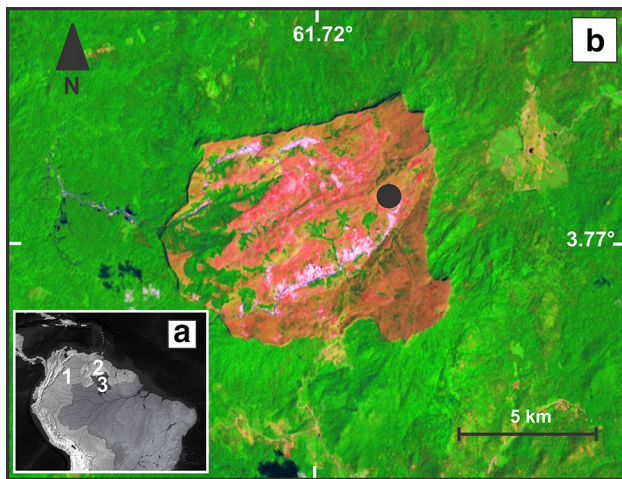
Fig. 1 Location of the Serra do Tepequém sediment core. **a** Location of palaeoecological studies in Savannas of Northern South America: *1* Llanos Orientales-Colombia, *2* Gran Sabana-Venezuela and *3* Roraima savannas-Brazil. **b** False color image of Serra do Tepequém sediment core. The image is composed by mid-infrared band 5, near infrared band 4 and the green band 3 courtesy of the US Geological Survey (USGS 2014). *Black circle* shows the location of the sediment record of Serra do Tepequém. *White to pinkish* areas reflect the exposed soils due to the mining activities in the plateau

The climate in the region (based on the only state-run station, which is located in the capital city Boa Vista) is tropical wet and dry (AWi, after the Köppen classification) (Miranda et al. 2002; Barbosa and Miranda 2004). The mean annual temperature and precipitation are 28 °C and 1,600 mm, respectively (Barbosa and Miranda 2004). The dry season covers the period from October to March with the driest phase in December and March. The wet season occurs from April to September with the wettest phase in May and August (INMET 2015).

The vegetation in the surroundings and on the slopes of the plateau is characterized by tropical rain forest. On the plateau itself the vegetation is mainly composed of grasses with some shrubs, from open grass savannas on the plains to arboreal savannas in the valleys (Nascimento et al. 2012; Beserra Neta et al. 2015). Due to its particular features, the vegetation of the Serra do Tepequém coring site can be classified, as proposed by Barbosa and Miranda (2004), as different savanna types growing along valleys, slopes and on gravel to sandy soils. The main vegetation cover is dominated by grasses from the genera *Andropogon* and *Trachypogon*, and Cyperaceae. Trees from the genera *Aspidosperma, Tabebuia, Mimosa, Piptadenia* and *Cassia* are usually growing in the area. Small patches of *M. flexuosa* palm are found in some areas of the plateau.

Fig. 2 Serra do Tepequém coring site and human impact in the Plateau. **a** Main vegetation growing in the coring area: *M. flexuosa* stands, ferns and grasslands. **b** Coring site, showing the location and scale of the sampled sediments. From 150 to 200 cm, sediments were recovered with a Russian corer following the continuity of the profile. **c** Mining activities located 3 km to the south-west from the coring site. Open and washed soils, disturbed vegetation and artificial channels are observed due to the water pressure used to collect gold and diamonds
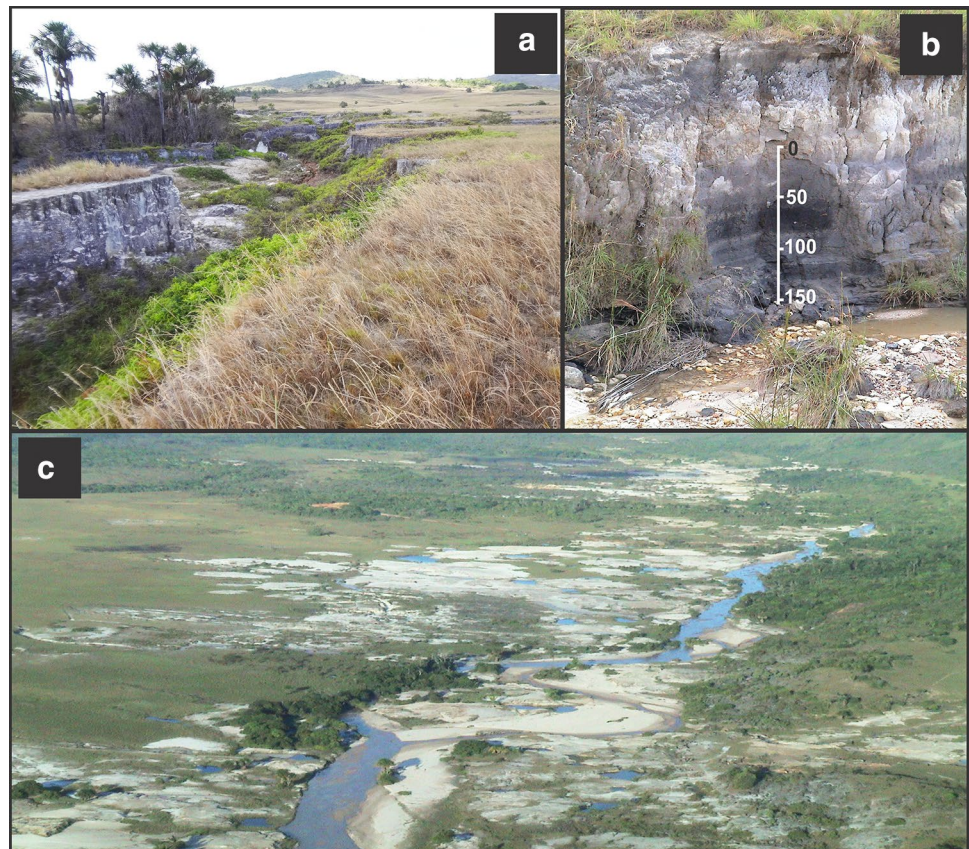
Materials and methods

The 200 cm long continuous sediment core from Serra do Tepequém was recovered in 2004 from an exposed wall in a spring area using 50 cm long split PVC tubes for the first 150 cm of the profile (Fig. 2b). At the same place, directly below the first 150 cm of the core, a Russian corer was used to obtain the sediments from 150 to 200 cm, which were not exposed. Deposited material above 0 cm (see Fig. 2b) was clearly reworked, probably due to mining activities in the area and was not recovered. The core was stored in the laboratory under cold (4 °C) and dark conditions. For palynological analysis, 31 subsamples (0.5 cm^3) were taken at 5 cm intervals along the core. As a result of the mining activities in the area, the first 50 cm of the record are clearly disturbed and reworked, besides which the pollen content was almost zero. Therefore the core was analyzed from 50 to 200 cm depth since our focus for palaeoecological reconstruction was mainly pollen and microcharcoal analysis. Pollen samples were prepared using standard pollen preparation techniques (Fægri and Iversen 1989). One tablet of exotic marker (*Lycopodium clavatum*) was added per sample for the calculation of pollen concentration and influx (Stockmarr 1971). Most of the samples were counted to a sum higher than 300 pollen grains. Spores were excluded from the pollen sum.

Pollen and spore identification was based on reference literature (Roubik and Moreno 1991; Carreira et al. 1996; Rangel-Ch et al. 2001; Rull 2003; López-Martínez et al. 2010; Leal et al. 2011; Montoya et al. 2012) and the pollen reference collection at the Department of Palynology and Climate Dynamics (University of Göttingen, Germany). The grouping of the pollen taxa into the ecological groups was been done according to Marchant et al. (2002), Leal et al. (2013) and the Brazilian flora checklist (REFLORA 2015). The zonation of the pollen diagram was obtained using the method of optimal splitting by sums of squares, using the pollen and pollen-spores data to detect differences. The number of statistically significant zones was evaluated using the broken stick model

(Bennett 1996). All illustrations and calculations were done with Psimpoll (Bennett 2009). Pollen based indices were calculated using the program R version 3.2.0 (R development core team 2015) and the vegan package version 2.3.0 (Oksanen et al. 2015). Pollen-spores sample diversity was plotted based on rarefaction analysis to a base of 10 counts ($E(T_{10})$) and pollen-spores richness using rarefaction to a base of 400 counts ($E(T_{400})$) according to Matthias et al. (2015).

Microcharcoal particles (from 10 up to 150 μm) were counted on the pollen slides without differentiation and expressed as concentration (particles/cm^3) and influx (particles/cm^2/year). LOI analysis was done according to Heiri et al. (2001). Subsampling was carried out each cm along the core to calculate the organic matter content (LOI 550 °C).

For radiocarbon dating, six samples were submitted to the AMS NTUAMS Laboratory of the National University of Taiwan (Table 1). Radiocarbon dates were calibrated with the curve IntCal13 for the northern hemisphere (Reimer et al. 2013). Calibration and age depth model were performed with R (R development Core Team 2015). The age-depth model was constructed using Bayesian statistics with the package Bacon (Blaauw and Christen 2011), which reconstructs accumulation histories for sediment deposits and helps to identify outliers in the data. All radiocarbon dates were included for the analysis. The accumulation rate prior was set as a gamma distribution with a mean of 20-year/cm and shape of 2 and beta distribution with strength of 4 and mean of 7.31 sections were used (each 5 cm) for the age-depth model. The core segment (68–50 cm) above the dated lower core section was calculated by the software by extrapolation.

Landsat 7 imaging for the study area map was obtained from the earth explorer web page of the US Geological Survey (USGS 2014). This false color elevation image is composed of the shortwave mid-infrared band 5, near-infrared band 4 and the red band 3. The image thus composed was used to show land–water boundaries.

Table 1 List of the AMS radiocarbon dates from the Serra do Tepequém core

Depth (cm)	Lab code	Dated material	^{14}C year BP	Age cal BP (weighted average, 2σ)
68	NTUAMS-1770	Bulk sediment	4,534 ± 39	4,848–5,065
74*	NTUAMS-573	Bulk sediment	6,981 ± 25	7,357–7,472
102	NTUAMS-716	Bulk sediment	5,443 ± 19	5,906–5,942
122	NTUAMS-717	Bulk sediment	6,019 ± 21	6,458–6,569
144*	NTUAMS-774	Bulk sediment	5,018 ± 48	5,372–5,601
200	NTUAMS-718	Bulk sediment	6,625 ± 23	7,093–7,190

*Dates rejected for age depth modeling

Results

Stratigraphy and chronology

The sediments of the Serra do Tepequém core are mainly composed of grey–brown to black organic clay and sandy deposits (Table 2). Thin layers of charcoal mixed with sand are found along the core and are more frequent between 130 and 70 cm. The organic matter content (LOI 550 °C) increases from the bottom to the top reaching values up to 18%. Higher values are found between 100 and 70 cm and the lowest at the bottom and top of the core (at 200 and 50 cm). Detailed inspection of the core after fieldwork indicated that the upper core part (50–0 cm) has been reworked (Fig. 2b). In some parts between 50 and 0 cm, sediments are very compact with a high amount of gravel (ca. 0.5 cm diameter), in other sections they are fragmented without obvious stratigraphy. The LOI values for this section are between of 3 and 5% (ESM—Online Resource 1).

A total of six AMS ^{14}C dates was obtained from bulk sediment (Table 1). The age at 74 cm gave the oldest age of the set of samples making it clearly an outlier, probably due to reworked material that was included in the bulk sediment for radiocarbon analysis. The other dates span between 7,140 and 4,950 cal BP. Three dates from the middle of the sequence (at 144, 122 and 102 cm) are not in stratigraphic order. These dates allow two possible alternative age depth relationships. First, building the model with the date at 144 cm and rejecting the two dates at 122 and 102 cm as too old, or second, rejecting the date at 144 cm as too young. Although the presence of too old dates is conceptually easier to understand, ages that are too young may occur due to roots or fungal and bacterial growth (Wohlfarth et al. 1998). As there is no other indication whether one date is more reliable than the other, we favor the more parsimonious solution of rejecting the date at 144 cm as being too young to be included in our model. Furthermore, keeping the dates at 122 and 102 cm brings them onto a near linear trend with the uppermost date at 68 cm adding confidence to this choice. Regardless of these conceptual considerations we have used the Bayesian age-depth modeling routine Bacon with all the radiocarbon dates, since it has outlier detection capabilities (Blaauw and Christen 2011). Running Bacon without any previous assignment of outlier probability of certain dates, we obtained the age model that we would have favored conceptually, with the dates at 144 and 74 cm detected as outliers and therefore not considered in the final age depth model (Fig. 3).

The Bayesian model provided ages spanning from 7,570 to 4,900 cal BP (200–50 cm core depth), comprising part of the mid-Holocene. The resulting time resolution between the analyzed samples is between 100 and 300 years.

On the other hand, caution should be taken when interpreting the ages from 68 to 50 cm, since they are extrapolated and might reflect different deposition times as shown by the stratigraphy and LOI changes (Table 2; Fig. 5).

Description of the pollen diagram

Both pollen and pollen-spores data suggest a division of two main zones T1 (200–100 cm; 20 samples) and T2 (100–50 cm, 11 samples). T2 is divided into two subzones T2-a (100–75 cm) and T2-b (75–50 cm). In total 77 pollen types were identified and grouped into four ecological groups: Grassland, palms, forest and spores (Figs. 4, 5). Pollen concentration oscillates between 217,500 and 277,460 grains/cm^3 and pollen influx between 1,480 and 16,800 grains/cm^2/year. Pollen-spores sample diversity ($E(T_{10})$) and pollen-spores richness ($E(T_{400})$) increase towards the top of the core. Considering that rarefaction to low counts ($E(T_{10})$) as a diversity indicator (Matthias et al. 2015), has not been tested in this kind of tropical ecosystem, we have also applied the Shannon index (Hill 1973) to our pollen samples for comparison (ESM—Online Resource 2). The results are highly correlated ($R^2 = 0.9955$) and we selected the representation as rarefaction to a base of 10 counts ($E(T_{10})$) as a conceptually simpler representation of pollen type diversity within the sample. Microcharcoal concentration and influx decrease from bottom to top of the core (200 to 50 cm).

Table 2 Description of the sediments from the Serra do Tepequém core

Core depth (cm)	Description of sediments
0–50	Light brown sandy to silty reworked sediments with gravel and roots from grasses
50–70	Dark grey sandy to silty sediments with some fractions of gravel
70–115	Black organic clay sediments mixed with charcoal and some sandy layers
115–130	Layered sandy sediments alternating with bands of black organic clay and charcoal
130–143	Clay to silty sediment mixed with a small proportion of fine yellowish sand
143–168	Dark gray organic clay to silty sediments with charcoal
168–200	Sandy clayey sediment combined with thick layers of coarse sand and charcoal
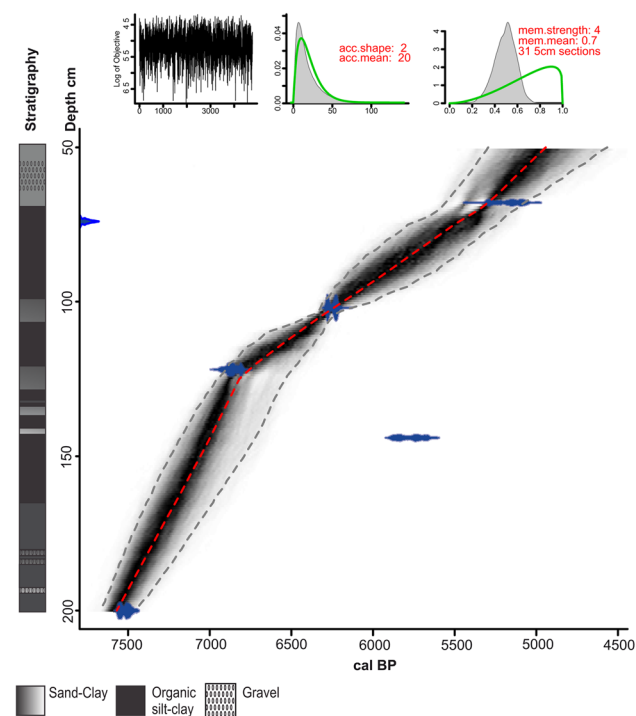
Fig. 3 Stratigraphy and chronology for the Serra do Tepequém sediment core. The stratigraphy is shown on the *left side*. *Upper panel* shows three graphs: (*left*) the Markov Chain Monte Carlo iterations for the Bayesian Bacon model; (*middle*) prior (*gray line*) and posteriori (*filled gray curve*) distributions for the accumulation rate; and (*right*) prior and posterior distributions of the memory. The *lower panel* shows the calibrated distribution of the radiocarbon dates and the age-depth model *darker greys* indicates the likelihood; *grey stippled lines* show 95% confidence intervals; *white dashed curve* shows single 'best' model based on the weighted mean age for each depth (Blaauw and Christen 2011)

Pollen zone 1 T1 (200–100 cm; 20 samples)

This zone is characterized by high percentages of the ecological group grassland (61–80%). Poaceae (38–72%) and Cyperaceae (6–29%) are frequent in this zone showing an opposed development, Poaceae increasing while Cyperaceae decreases and vice versa. Palm pollen grains have low percentages during this zone. The first occurrence of *M. flexuosa* pollen is at 170 cm core depth. At the end of the zone *M. flexuosa* increases up to 10%. Forest pollen taxa (14–32%) are dominated by Moraceae/Urticaceae (9–23%). Other forest taxa with values lower than 5% such as *Alchornea* (0–4%), *Schefflera* (0–2%), Melastomataceae (0–4%) and *Sloanea* (0–3%) increase towards the top of the zone. Fern spores have a high representation at this interval with values between 7–41%. *Sticherus*-type is the most frequent (11–33%) at the core depth from 200 to 165 cm. Later, the values are reduced towards the top of the zone with 3–17%. Other ferns are represented at this interval in low proportions. Fungal spores occur only in this zone

with *Gelasinospora* (0–1%). The Non Pollen Palynomorph (NPP) TEP-2 (Fig. 6) is present only in this zone with values of 0–7%. Pollen concentration at the base of this zone is relatively low compared with the upper part. Values vary from 21,000–80,000 grains/cm³ from 200 to 160 cm depth and more abrupt changes in concentration occur from 23,000 up to 277,000 grains/cm³ from 160 to 105 cm depth. Pollen influx values show a similar trend to pollen concentration. Microcharcoal particles have the highest concentration of the record; lower values are found at the bottom from 200 to 170 cm (530,000–1,500,000 particles/cm³). From 165 to 105 cm microcharcoal particles reach values of 3,200,000 particles/cm³. Microcharcoal influx has the highest values of the record (51,000–310,340 particles/cm²/year) from 200 to 130 cm depth; afterwards values start to decrease. Pollen-spores richness ($E(T_{400})$) and pollen-spores sample diversity ($E(T_{10})$) tend to increase towards the top of the zone.

Pollen zone 2 T2 (100–50 cm; 11 samples)

Subzone T2-a (100–75 cm)

Mauritia flexuosa and grassland vegetation dominate this zone. The main grassland taxa reduce in pollen values (26–49%). Poaceae oscillates between 23–42% and for Cyperaceae values are between 3–6%. Palm pollen is dominant (31–57%) and is mainly represented by *M. flexuosa* (22–49%) and *Mauritiella* (3–8%). *Wettinia*-type starts to occur at this zone with values of 0–7%. Forest pollen taxa are reduced (10–20%). Moraceae/Urticaceae pollen is less frequent (4–13%), but other taxa such as *Ilex* (0–4%) and *Qualea paraensis* (0–2%) increase their percentages in this zone. Fern spores have also changed their frequency (3–19%). *Sticherus*-type is markedly reduced with values between 0–2%, *Lycopodiella cernua* starts to increase (0–4%) as well as trilete verrucate (1–9%). Pollen concentration fluctuates from high values at the bottom to low values at the top of the zone (112,000–277,000 grains/cm³). Pollen influx performs similarly with values between 3,100–9,700 grains/cm²/year. Microcharcoal concentration decreases towards the top (840,000–1,400,000 particles/cm³); the same trend is found for the microcharcoal influx (30,300–59,400 particles/cm²/year).

Subzone T2-a (75–50 cm)

Low values of microcharcoal concentration and an increase of forest elements dominate the zone. Grassland taxa continue to decrease in the record (27–36%). Poaceae have values between 21–30% and Cyperaceae between 2–5%. Palm dominance is slightly reduced (27–43%). *M. flexuosa* pollen reduces its frequencies (22–31%) but other
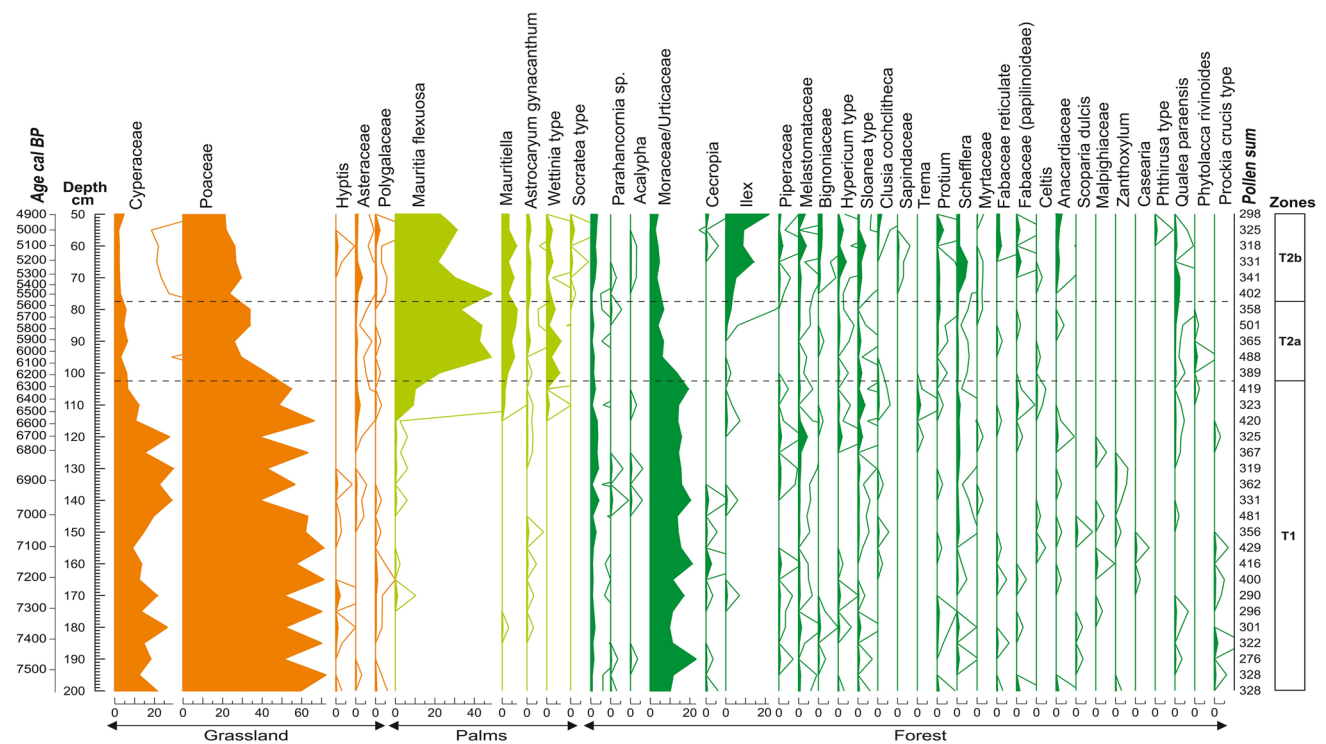
Fig. 4 Pollen and spores percentage diagram showing the taxa grouped into ecological groups: grasslands, palms and forest. The exaggeration factor of each taxon was set to 10

palm taxa remain with similar values and slight variations. Forest pollen taxa are increasing their representation with values between 26–46%. Moraceae/Urticaceae pollen is less frequent (3–4%) while other forest taxa increase their frequencies, for example *Ilex* (5–21%), *Alchornea* (2–4%), *Schefflera* (1–5%), *Sloanea* (1–3%) and *Hypericum*-type (1–3%), among others. Pollen concentration is decreasing toward the top of the zone (35,000–106,000 grains/cm^3). Pollen influx has values between 1,500–3,100 grains/cm^2/year. Microcharcoal concentration decreases towards to the top (400,000–700,000 particles/cm^3); the same trend is observed for the microcharcoal influx (17,000–26,000 particles/cm^2/year). Pollen-spores sample diversity and pollen-spores richness have the highest values of the record in this zone.

Interpretation and discussion

### Chronology of the sediment core Serra do Tepequém

Our results reflect the usefulness and robustness of the Bayesian age depth modeling used in Bacon, since it reproduces our conceptual considerations and provides realistic age uncertainties. Our dataset provides a good illustration for the power of the outlier detection incorporated in Bacon

(Blaauw and Christen 2011). The supposed too young age at 144 cm might be the result of long period of storage before applying radiocarbon dating analyses as reported in other AMS ^{14}C analyses (Wohlfarth et al. 1998). The sediment core was stored for more than 10 years after recovery, which could favor the growth of some bacteria or spores in this section. Moreover, this part of the section was sampled from a cleaned exposed profile and fungal growth or the presence of rootlets or other young material cannot be discounted. Nevertheless, even if we had chosen the alternative age depth model most of the assigned sample ages would have differed only in the order of few hundred years. Thus, despite the problem of reversed dates, this mid-Holocene pollen diagram represents one of the better dated records for tropical South America.

The mid-Holocene at Serra do Tepequém

Period I (7,570–6,190 cal BP; zone T1)

Low to high values in the organic matter content, variation in the texture of the sediment core and the change from high to lower sediment accumulation rates in this period, suggest a marked change in climate with a strong effect between dry and wet periods. Such an effect was mainly dominated by the latitudinal influence of the Inter Tropical
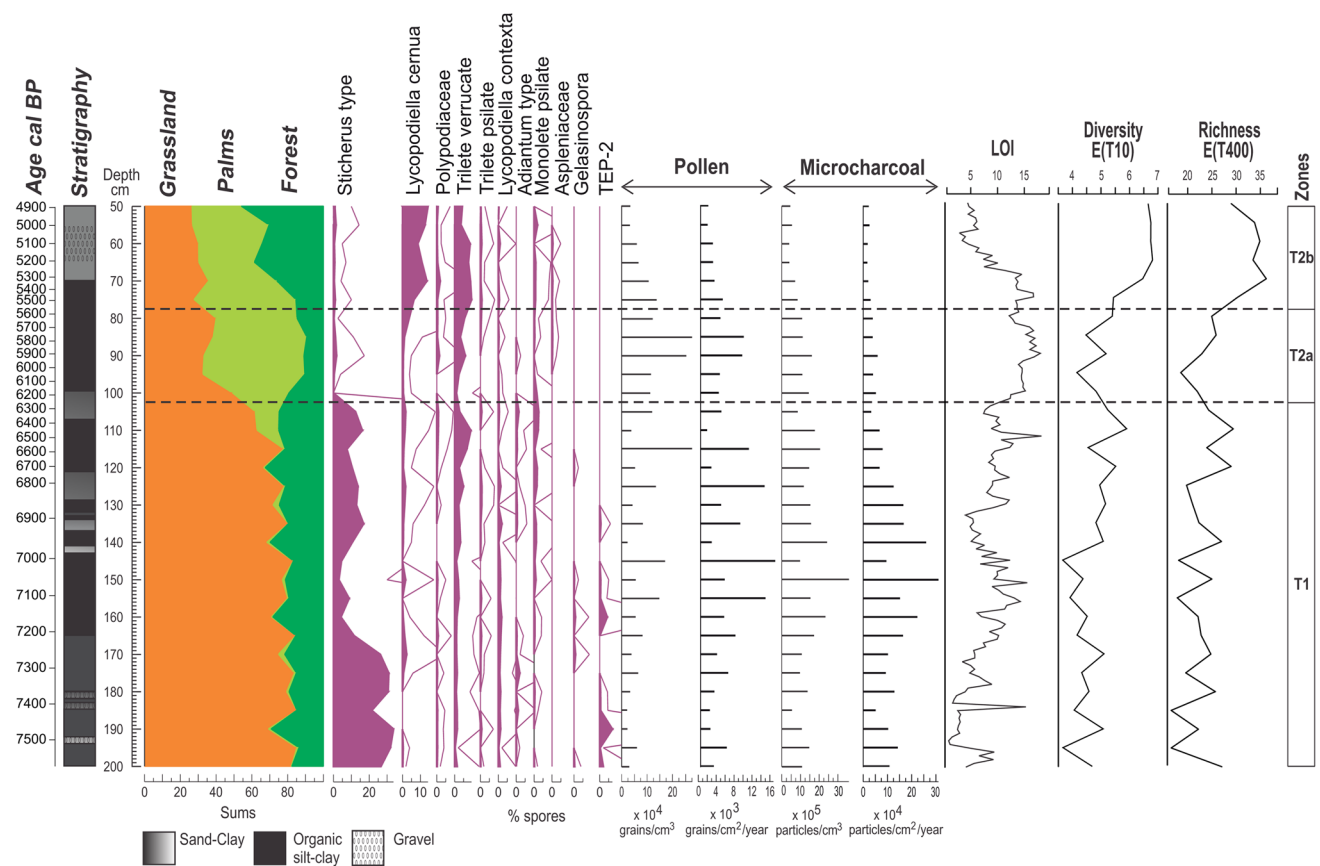
Fig. 5 Pollen sum diagram showing the sum of each ecological group, spore percentages, pollen and microcharcoal concentration, pollen and charcoal influx, LOI, pollen-spores sample diversity ($E(T_{10})$) and pollen-spores richness $E(T_{400})$)
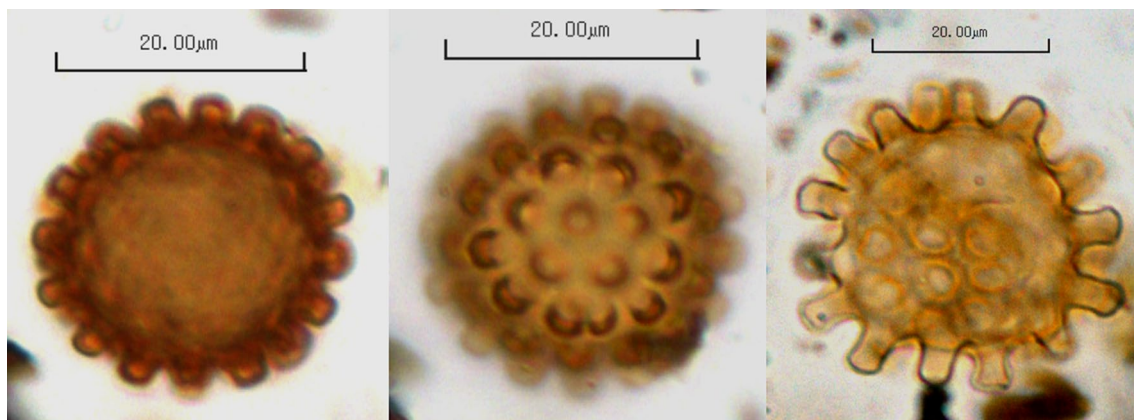
Fig. 6 TEP-2, single circular microfossils with tubular protuberances and 22–26×21–25 μm size. The tubular protuberances are ca. 2 μm in diameter and ca. 2.5 μm in length. The space between tubules is ca. 2–2.5 μm. This macrofossil was reported from a dry period when open areas (grasslands) dominated

Convergence Zone (ITCZ) in the area (Cheng et al. 2013; Bustamante et al. 2016). The effect of a longer dry period, due to a longer southward migration of the ITCZ, contributed to the development of more exposed soils that were eroded when the input of water increased in a wet period (Fig. 5). According to Nascimento et al. (2012) the study

area is located between residual mountains and intermountain valleys containing the drainage system of Serra do Tepequém. These characteristics are related to the geomorphological origin of the plateau, which is a synclinal valley (Luzardo 2006). Consequently, the sediment composition of the coring site is probably not only reflecting marked

changes between periods, but also local changes in the drainage system in which the Serra do Tepequém sediment core is located.

Regarding the vegetation changes in the studied site, small forest areas were mainly represented by some species of Moraceae/Urticaceae, *Alchornea* and *Schefflera*, and the dominance of Poaceae and Cyperaceae indicated relatively large savanna areas. The high presence of the fern spore *Sticherus*-type may also indicate open areas (Rull 1999), besides the presence of an active channel with running water coming from the spring area. Regional fires were present at this time with the highest signal in the record able to be correlated with the dominance of savanna and the considerable cover of the ferns in our study site (Rull 1999). As a local signal of fires and burned soils the fungal spore *Gelasinospora* was detected. Such a spore occurred only for this period, which therefore supports the hypothesis of probable local fires in a dry period in the area (Fig. 5) (van Geel 1978; Dietre et al. 2016; Herzschuh et al. 2016). Another potential indicator of fires is the NPP TEP-2 (Fig. 6), which only occurred when high peaks of microcharcoal were detected and coincided with some maxima of *Gelasinospora*. The ecological background and origin of TEP-2 are unknown, preventing its inclusion as a support of our interpretations. All these features compared with our sedimentological findings indicate that a longer migration of the ITCZ toward the south facilitated the expansion of grasslands and other creeping pteridophytes (i.e., spores of *Sticherus*-type, *Lycopodiella contexta* and *L. cernua*) between 7,570 until 7,060 cal BP (200 to 150 cm) (Fig. 5). The regional signal of fire might also indicate a dry period; however, the impact of human fire use for hunting could have played a role.

For the period between ca. 6,960 to 6,580 cal BP (140 to 115 cm) pollen and microcharcoal influx are showing a change in vegetation cover (Fig. 5). The reduction of Poaceae, the increase of Cyperaceae, and the sparse occurrence of *M. flexuosa*, might confirm the beginning of wetter conditions in the study area, together with a physical change in the drainage system, as is reflected in change of sediments in the core. Sediment composition had more variation than in earlier times, showing a reduction in organic matter content and an increase of sandy sediments until 6,710 cal BP (120 cm). At that time the influence of the Atlantic sea surface temperature (SST) on the ITCZ started to restrict the southward extent of this convective system, therefore reducing the length of the dry season in the area (Haug et al. 2001; Cheng et al. 2013). Even though such a marked change is observed in the different proxies, statistical analyses do not support another subdivision or zone for this period.

From ca. 6,580 to 6,190 cal BP, *M. flexuosa* rapidly started to expand together with other forest and fern species, colonizing former dry areas. From the physiological point of view, *M. flexuosa* juvenile plants are shade intolerant and need open areas to succeed (Lasso et al. 2011). At that time, open areas were available and an increase in accumulation of organic matter began, consequently allowing the expansion of young palm juveniles. As to the changes in sediment texture and organic matter content, they are to be expected since spring water availability seems to be dependent on the rainfall and ground water from the plateau. The increase in available moisture in the study site is also reflected in an increase of forest in the area.

Period II (6,190–4,900 cal BP; zone T2)

A period with more humid conditions than before is detectable by the presence of more organic sediments together with the reduction trend of microcharcoal concentration and influx toward younger times. At this time the effect of the ITCZ in Serra do Tepequém is reflected in a reduced dry season, due to a more northward position and the changes in sediments might be also related to the development of a swampy area. These wetter conditions are also visible in the vegetation composition and in the increase of plant diversity as indicated by the pollen-spores richness (Fig. 5). A swampy area covered by *M. flexuosa* and other palms was dominant, and a notable reduction in grasslands, fire and *Sticherus*-type occurred (subzone T2-a, Figs. 4, 5). Rull (1999) showed that some fern spores have a similar performance to charcoal. Both were more abundant in the first phase of the record (T1), and were declining when the charcoal content diminished in this period (T2). The reduction in *Sticherus*-type and microcharcoal in Serra do Tepequém is followed by an increase in forest taxa and replacement by creeping pteridophytes (increase in spores of *Lycopodiella cernua, L. contexta* and Polypodiaceae) growing in the savanna (subzone T2-b).

The forest-savanna mosaic persisted, but with the expansion of the swampy area and new forest taxa. The input of coarse sediments to the rill became reduced as well as the regional signal of fire and grasslands. Such reduction of fire due to the increase of wetter conditions has been also found in the Venezuelan savannas for the early mid Holocene (see Climatic conditions section below) (Rull et al. 2013). Another possible explanation for the reduction of the charcoal signal in the sediments of Serra do Tepequém may be the effect of the closeness of the canopy in the area, which might not have allowed charcoal to accumulate easily.

Starting at 6,190 cal BP, conditions were favorable for *M. flexuosa* to spread out. A swampy area was completely developed and new colonizer species became established. A marked reduction in grasslands is evident, indicating the increase of moisture at that time (Fig. 4). A balance

between forest and savanna became established such as in other records (Behling and Hooghiemstra 2000). The pollen-spores sample diversity started to increase, reaching continuous higher values at the end of the period.

From 5,330 cal BP until the end of the record at 4,900 cal BP, the increase in forest elements and the relatively low pollen and charcoal concentrations may indicate an increment of run-off water in the rill, bringing coarse eroded sediments to the coring site. The expansion of forest is supported by the study on *M. flexuosa* seedlings by Galeano et al. (2015). These authors argued that the distribution pattern of this palm is influenced by rain seasonality combined with local heterogeneous conditions like drainage, flooding and slope, which allow terra firme forest species to establish on better drained places and displace *M. flexuosa* seedlings. At the end of this second period, better drained places were available for forest to colonize Serra do Tepequém (Fig. 5).

The characteristics of the sediments from 0 to 50 cm made it difficult to develop the palaeoecological analyses and interpretation toward recent times. As explained before, this section of sediments of the Serra do Tepequém core was reworked with a mixture of compacted and fragmented sediments. Also the pollen content was very low and oxidized, which did not permit the pollen analysis of this section. The main reason for the reworked material is related to the intense gold and mining activities that the plateau has been experiencing during the last 100 years (Almeida-Filho and Shimabukuro 2002). Many areas are now bare soils due to the water pressure used to wash the plateau surfaces (Fig. 2c), which changed the soil properties and removed the organic content.

A possible human impact during the mid-Holocene

Human impact on Serra do Tepequém during mid-Holocene times might not be excluded. The earliest reported human occupation for the Roraima savannas was found in Pedra Pintada (Reis et al. 2008) at 100 km toward the east from Serra do Tepequém. Such occupation dates ca. 4,000 uncal BP (ca. 4,400 cal BP), even though for Amazonian lowlands the earliest occupation is indicated at ca. 11,200 uncal BP (ca. 13,000 BP) (Roosevelt et al. 1996). In our record, the dry conditions detected from the huge amount of charcoal particles and savanna dominance could be also a signal of human impact in the area, but, since our record does not include a macro charcoal analysis to detect a local signal of charcoal, such assumptions should be taken with caution. A possible sign of local fires in our study site is the presence of *Gelasinospora* fungal spores, an indicator of past local fire occurrence (Dietre et al. 2016; Herzschuh et al. 2016). The presence of this spore together with the layers of charcoal found

in the sediments (Table 2) may indicate possible human influence in the area. In addition, the changes in forest and fern composition for the wettest period of our record possibly indicate an abandonment of the land. Our study shows that the area has a potential for archaeological research, which would allow us a clear view of the role of ancient cultures in relation to vegetation changes and fire.

The mid-Holocene at Roraima savannas in Brazil

Despite the nature of Serra do Tepequém, an isolated plateau surrounded by tropical rainforest lying ca. 15 km from the main savanna region of Roraima, we expect that the effect of the ITCZ on vegetation development shows similar trends. The oldest sediment record from Roraima State is Lago Caracaranã with an age of ca. 10,020 uncal BP (11,500 cal BP) (Simões Filho et al. 2010; Cordeiro et al. 2014). This studied site covers the entire Holocene and was analyzed using mineralogical analyzes such as TOC, charcoal, silicate, kaolinite and quartz. The results suggest that between 7,600 and 6,000 cal BP there was an expansion of the dry season. These conditions increased the erosion in soils with high input of quartz, kaolinite and calcite into the lake. Furthermore, the study of Cordeiro et al. (2014) in the same lake showed that the highest maxima in the microcharcoal record are from the early to mid-Holocene, also pointing to a dry period. At Serra do Tepequém the effect of a longer southward migration of the ITCZ was also reflected in more open vegetation and a high signal of regional fires (zone T1) (Figs. 4, 5). Simões Filho et al. (2010) suggested that the beginning of the wetter conditions in Roraima State started at 6,000 cal BP, with a reduction of fires from mid- to late Holocene as suggested from the microcharcoal analyses (Cordeiro et al. 2014). This coincides with the maximum vegetation cover of *M. flexuosa*, the high values of LOI and the reduction of microcharcoal at the Serra do Tepequém coring site. Although the study of Lago Caracaranã does not use palynological data and has a different geomorphological setting from Serra do Tepequém, the effect of a southward position of the ITCZ is reflected by a dry period for ca. 7,600 and 6,000 cal BP with a change to wetter conditions toward more recent times. Furthermore, the Holocene vegetation dynamics in the eastern part of the Roraima savannas were reconstructed by Toledo and Bush (2009) at Jacaré Lake, which is located 7 km from Lago Caracaranã. They found vegetation changes related to forest expansion from 5,700 to 4,700 uncal BP (ca. 6,500 to 5,400 cal BP) coinciding with the findings of wetter conditions at Lago Caracaranã and Serra do Tepequém.

A regional overview of the mid-Holocene vegetation changes in northern savannas in South America

The establishment of M. flexuosa

The best documented history of forest-savanna dynamics from near Serra do Tepequém comes from the southeastern part of the Gran Sabana region of Venezuela, with records from ca. 12,000 cal BP to the present (Leal et al. 2013; Ballesteros et al. 2014; Rull and Montoya 2014; Rull et al. 2015). The Gran Sabana region lies on sedimentary rocks, sandstones, claystones and conglomerates of the middle Proterozoic Roraima formation showing similar geological features as those found at Serra do Tepequém (Almeida-Filho and Shimabukuro 2002; Montoya et al. 2011b). For the Roraima formation, Serra do Tepequém is the first record reporting an early establishment with a continuous occurrence of *M. flexuosa* stands in the mid-Holocene, starting at ca. 6,600 cal BP. The increase of this palm is related to wetter conditions together with a local availability of water. In our study site, regional fires showed a marked decrease towards the mid to late Holocene, with an increase of *M. flexuosa* and forest taxa expansion due to the increase in wetter conditions (Fig. 5). These features show a different development of *Mauritia* stands compared with those reported by Rull et al. (2013) in the Gran Sabana region and Meneses et al. (2013) at the southern part of the Roraima savannas for the late Holocene. In Serra do Tepequém, a higher signal of regional fires was present when grasses and open vegetation were the dominant vegetation in the area. These features are in agreement with the expansion of savannas in the Gran Sabana region and the southern part of Roraima, but not when there was the expansion of *M. flexuosa* and forest taxa. This development might be explained as the effect of the ITCZ on the plateau. A wetter period favored the development of taxa that were able to grow in frequently flooded areas, as is reported in the sedimentological record of Serra do Tepequém. Such wetter conditions could be a factor in the reduction of the microcharcoal signal, since a reduction of fires would be expected in a wetter environment. But as mentioned before, forest canopy can also be a limiting factor for microcharcoal deposition in the sediments and it should be considered as a possible explanation.

At the llanos Orientales in Colombia (Berrio et al. 2002; Hooghiemstra and Berrio 2007), the expansion of *Mauritia* was found around ca. 4,000 to 3,500 uncal BP (4,400 to 3,700 cal BP) and, as was found earlier in Serra do Tepequém, the development of these palms is related to the change to wetter conditions in the savanna with a shorter dry season and increased precipitation. For the late Holocene an increase in human impact is linked to savanna expansion and recurrent fires (Behling and Hooghiemstra

1998, 2000; Berrio et al. 2002; Velez et al. 2005; Hooghiemstra and Berrio 2007). As fires were not analyzed in these records, the interplay of *M. flexuosa* and fire cannot be compared. However, Serra do Tepequém reflects similar development of *M. flexuosa* when savanna vegetation was also contracting in the Llanos Orientales records (Hooghiemstra and Berrio 2007).

Climatic conditions: the effect of the ITCZ on different records

The latitudinal effect of the ITCZ for the mid-Holocene in northern South America had an influence on the length of the dry and wet seasons in each study area (Cheng et al. 2013; Bustamante et al. 2016). The timing and impact on the diverse study sites might vary due to the different latitudinal positions and local features that were then conditioning the dynamics between forest and savanna expansion.

Conditions were drier in Serra do Tepequém for the recorded period between ca. 7,570 to 6,600 cal BP before the expansion of forest and *M. flexuosa* started, as the ITCZ was in a southward position at that time (Cheng et al. 2013). This is also shown in the records from El Paují (Montoya and Rull 2011; Montoya et al. 2011a; Rull et al. 2013) and Laguna Encantada (Rull et al. 2013; Ballesteros et al. 2014). These records display the dominance of open vegetation when fires were more intense. After these dry conditions, charred particles began to be reduced in the three records, indicating a wetter climate. As a result, around 7,000 cal BP at the Laguna Encantada and El Paují, the rainforest expanded (Rull et al. 2013; Ballesteros et al. 2014). In the case of Serra do Tepequém, the forest-savanna mosaic remained stable with more dominance of savanna grasslands and a high regional fire signal until ca. 6,600 cal BP when *Mauritia* stands showed their highest expansion in the record. Ballesteros et al. (2014) also reported a synergistic action between reduction in fires and wetter conditions that determined the development of rainforest around ca. 6,700 uncal BP (7,500 cal BP) in Laguna Encantada. Such changes in vegetation and fires due to a change from dry to wetter conditions are comparable with speleothem records (Cheng et al. 2013). Records from northeastern Brazil and eastern Amazonia showed a drastic shift from severely dry to substantially wet conditions in the region (Cheng et al. 2013). The llanos Orientales records show changes in climate from dry to wetter conditions at different time scales. For the western part of these savannas the climate changed to wetter conditions from ca. 7,100 and 6,100 uncal BP (8,000 and 7,000 cal BP) and for the eastern part from ca. 6,400 and 5,300 uncal BP (7,300 and 6,000 cal BP) (Hooghiemstra and Berrio 2007). Serra do Tepequém shows similar patterns from the period between ca. 6,960 and 6,580 cal BP in which wetter conditions began to be

noticed. Afterwards at ca. 6,200 cal BP the full development of *M. flexuosa* palm stands and the change in composition of forest then corroborate a more dynamic and humid environment. Behling and Hooghiemstra (2000) considered that the vegetation of the mid-Holocene period was little influenced by humans in the savannas of the Llanos Orientales, but this assumption should be considered with caution since they have not included a charcoal analysis to confirm possible human practices and fire regime dynamics in the area. Those authors also concluded that the dynamics of the forest–savanna boundary are determined primarily by precipitation change, and to a lesser extent by changes in fire frequency, soil conditions and biotic factors. In our study site, precipitation change also played an important role in the dynamics of the forest-savanna mosaics, but the local conditions of the study site, such as the geomorphological origin of the plateau (altitude, drainage system, isolated plateau etc.), are influencing the dynamics on vegetation at the same level (Luzardo 2006). The effect of local fires cannot be strongly argued with our results, but at a regional scale the fire signal is showing an effect.

Conclusions

The regional increase in wetter conditions during the mid-Holocene was detected in Serra do Tepequém, and was reflected in changes in the deposition of sediments, vegetation and fire dynamics. Our results show that a dry period with reduced wet seasons occurred around 7,570 to 6,190 cal BP. In that period, a forest-savanna mosaic mainly dominated. Grassland taxa and creeping pteridophytes were present in the area, in agreement with other palaeoecological records reporting dry conditions for northern South America.

The Serra do Tepequém sediments reveal an increase in wetter conditions between ca. 6,190 to 4,900 cal BP. Such changes promoted new arrangements of forest, pteridophytes and an early increase in *M. flexuosa* palm. As wetter conditions intensified, our findings exhibit a decrease in savanna vegetation together with a reduction of regional fires and hence new forest species starting to colonize the study area.

The timing of the change to wetter conditions in Serra do Tepequém is slightly different compared with the records of the Llanos Orientales and Gran Sabana, probably due to the latitudinal influence of the ITCZ and the particular geomorphological features of each studied site. Our results are complementary with the Gran Sabana findings of the records for el Paují and Laguna Encantada with an increase in moisture around ca. 7,000 and 6,600 cal BP. Regarding the Llanos Orientales in Colombia, changes from dry to wetter conditions with similar timing and vegetation arrangements were found in the record from Laguna Sardinas.

Our study shows that the early increase in *M. flexuosa* developed differently to the increase in fire and savanna expansion found in the savanna region in Venezuela. The *M. flexuosa* expansion in Serra do Tepequém may indicate a local geomorphological and climatic setting besides a possible land use derived from ancient cultures in the area. Human impact should be corroborated with further palaeoecological and archaeological studies in the region, as it is not completely clear what impact such cultures had on vegetation.

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