

Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE Venezuela): Palynological evidence from El Paují record

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Abstract

This paper shows a Holocene paleoecological reconstruction based on a peat bog sequence (El Paují, 4°28'N–61°35' W, 865 m elevation) located in the transition zone between the Gran Sabana (SE Venezuela) savannas and the Amazon rainforests. Paleoecological trends are based on the analysis of pollen and pteridophyte spores, algal and animal remains, fungal spores, and charcoal particles. The whole record embraces the last ca. 8000 cal yr BP, and was subdivided into five pollen zones, representing the following vegetation succession: savanna/rainforest mosaic (8250–7715 yr BP), dense rainforests (7715–5040 yr BP), savanna/rainforest mosaic (5040–2690 yr BP), secondary dry forests (2690–1440 yr BP), and peat bog in an open savanna landscape (1440 yr BP–present). These vegetation changes have been attributed to the action of climate and/or land use changes, as well as the corresponding synergies between them. Fire has been determinant in the landscape evolution. Based on the reconstructed fire and vegetation shifts, a changing land use pattern could have been recognized. Between the early and the mid Holocene (ca. 8.3–5.0 kyr BP), land use practices seem to have been more linked to shifting agriculture in a rainforest landscape – as is usual in Amazon cultures – with medium fire incidence affecting only local forest spots or surrounding savannas. More extensive forest burning was recorded between ca. 5.0 and 2.7 kyr BP, followed by land abandonment and the dominance of drier climates between 2.7 and 1.4 yr BP. The modern indigenous culture, which prefers open environments and makes extensive use of fire thus preventing forest re-expansion, seem to have established during the last 1500 yr. Therefore, a significant cultural replacement has been proposed for the region, leading to the present-day situation. Changing human activities have been instrumental for ecological evolution in this savanna–rainforest transitional region, as well as for the shaping of modern landscapes.

Key words: Fire, Gran Sabana, Amazon rainforests, Indigenous land management, Savanna/forest boundary, Ecological succession.

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1. Introduction

The paleoecological and paleoclimatological researches conducted in northern South America have been improving consistently (e.g., Behling and Hooghiemstra, 2001; Bush et al., 2004; Rull et al., 2010a) since studies first began several decades ago (e.g., Wymstra and Van der Hammen, 1966). However, given the vast extent of the region and the different ecosystems present (Colinvaux et al., 2000), many areas have barely been studied, which in some cases prevents the development of a regional

perspective on vegetation–climate– human interactions over time. Indeed, in northern South America (north of the Equator) research efforts have focused mainly on: 1) mountains or highlands (vertical landscapes), where the altitudinal distribution of vegetation can allow the reconstruction of temperature shifts (e.g., Hooghiemstra, 1984; Stansell, 2009); and 2) generally flat lowlands and midlands (horizontal landscapes), where the vegetation changes have usually been interpreted as responses to trends that primarily involve moisture (e.g., Behling and Hooghiemstra, 2001; Berrío et al., 2002a; de Toledo and Bush, 2007). Within these horizontal landscapes, large tracts of forest intermingle with savanna patches, which in some places can become the dominant plant formation (Huber, 1995a; Behling and Hooghiemstra, 2001). In Amazonia, variations in the coverage of both plant formations have been documented since the Last Glacial interval and have generally been interpreted as the result of past climatic oscillations (e.g., Behling, 1996; Colinvaux, et al., 1996). In addition to climate, humans have been an important factor in shaping the present-day landscape of the northern South American lowlands (Sandford et al., 1985; de Toledo and Bush, 2007). Contrary to previously thought on the subject, Amazonia has suffered different levels of pressure owing to anthropogenic disturbances prior to the arrival of Europeans (Bush and Silman, 2007). Human presence has been reported for the region since the Late Glacial, followed by a Holocene expansion (Cooke, 1998). In light of these findings, several paleoecological studies have been addressed, mainly in Amazonia, to discern the possible anthropogenic impact of ancient cultures, either by themselves or coupled with climate shifts (e.g., Bush et al., 2000, 2007a,b). Nevertheless, although it is a growing field, the scarcity of the surveys and their scattered nature continue to prevent the development of a full regional view.

Forest edges and forest–savanna ecotonal boundaries have proven to be good places for paleoecological research due to their sensitivity to climatic shifts, even when such changes are small or of local origin and/or effect (Desjardins et al., 1996; Pessenda et al., 2001; Mayle and Power, 2008). In Venezuela, the Gran Sabana (GS) is characterized by extensive savannas with gallery forests and forest–savanna mosaics (Huber and Febres, 2000). Previous paleoecological studies have revealed that during the Late Glacial and Holocene, the GS experienced several climatic and vegetation changes. For example, a pronounced and relatively rapid vegetation shift occurred during the end of the Younger Dryas and the early Holocene and resulted in the replacement of forest and shrubland formations by treeless savannas (Rull, 2007; Montoya et al., 2011a). This landscape shift coincided with variations in the water balance (precipitation/evaporation or P/E ratio) and possibly also in the temperature. In both cases, fire seems to have played a potentially important role in the vegetation change (Rull, 2007, 2009; Montoya et al., 2011a). Several records show that, during the Holocene, the landscape was dominated by treeless savannas, while forests locally expanded or contracted following moisture variations. Present-day environmental conditions and vegetation were established during the last few millennia, and the typical gallery forests called morichales (palm swamps dominated by the palm *Mauritia flexuosa*) have occupied the GS only in the last 2000 yr onwards, under a high fire-incidence regime (Rull, 1992, 1998a, 1999; Montoya et al., 2009, 2011b). Based on the available evidence, it may be assumed that both climatic fluctuations and fire have had similar effects on the GS vegetation. These effects, namely the reduction of forest cover and the expansion of savannas, with the establishment of morichales, have thus shaped the current GS landscape (Rull, 1992). The incidence of fires in the GS during the last millennia has promoted the hypothesis of an early timing arrival of people to this region; highlighting the important role that human could have in shaping the present-day GS landscape (see Section 2 for further information).

In this paper, we present a paleoecological study of a peat bog sediment core located south of the GS (SE Venezuela), near the Brazilian border, which coincides with the Orinoco–Amazon watershed boundary. The research is based on pollen and spore analysis, combined with charcoal and non-pollen palynomorphs (NPP). The main aims of this study were: (i) to reconstruct the vegetation dynamics and its potential links with local and/or regional climatic changes; (ii) to discern the role played by either climate or fire, or the synergy of both, on plant communities; and (iii) to identify possible evidence of potential pre-Columbian human settlements and the associated land use practices.

2. Study area

The GS covers a 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](#)). Geomorphologically, the GS lies on an undulated erosion surface developed on the Precambrian Roraima quartzites and sandstones, and forms an altiplano slightly inclined to the south, ranging from about 750 to 1450 m elevation (Briceño and Schubert, 1990; Huber, 1995a). The climate has been defined 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 (b60 mm/month) from December to March (Huber and Febres, 2000). Regarding vegetation, the GS present large extensions of savannas within the normally forested Guayana landscape. These savannas form wide and sometimes almost continuous cover of treeless grasslands intermingled with forests, thus developing the typical forest–savanna mosaics (Huber, 1995b). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b) has lead to several hypotheses, basically encompassed in two main categories related to edaphic conditions, and climate change and fires (see: Eden, 1974; Fölster, 1986; Rull, 1999; Fölster et al., 2001; Dezzio et al., 2004; Huber, 2006).

The GS savannas are dominated by grasses of the genera *Axonopus* and *Trachypogon* and sedges such as *Bulbostylis* and *Rhyncospora*; woody plants are scarce, and rarely emerge above the herb layer (Huber, 1995b). There is a transitional type of grasslands between these typical savannas of the GS and those from the highlands, which normally occur on peat bogs and are characterized by the scarcity of grasses, and the dominance of herbs from Rapataceae, Xyridaceae, and Eriocaulaceae families ([Fig. 2](#)) (Huber, 1986). Most GS forests are categorized as lower montane forests 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 in the northern area than in the southern part (Huber, 1994, 1995b), where our study site is located. The most common genera of this vegetation type are: *Euphronia* (Euphroniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Ochthocosmus* and *Cyrrilopsis* (Ixonanthaceae), *Thibaudia*, *Notopora* and *Befaria* (Ericaceae), *Spathelia* (Rutaceae), *Byrsonima* (Malpighiaceae), etc. They usually grow on a rocky, sandstone substrate or deepwhite 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 involve 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). According to the scant evidence available, the Pemón seem to have reached the GS very recently. A tentative recent human occupation during the last centuries has been proposed, based primarily on historical accounts, but they do not necessarily record the first arrival event (Thomas, 1982; Colson, 1985; Huber, 1995a), so an earlier occupation cannot be dismissed. There is some archeological evidence consisting of pre-Columbian remains (spearheads and bifacial worked knives) similar in style to others from about 9000 yr old found in other Venezuelan localities (Gassón, 2002). Moreover, palynological evidence indicating the occurrence of intense fires since the Younger Dryas (around 12,400 cal yr BP), suggested a potential early human presence in the GS (Rull, 2009; Montoya et al., 2011a). In addition, the continued high fire incidence documented during the last two millennia in several southern GS records points to a prior settlement (Montoya et al., 2011b).

3. Material and methods

The study site (4°28'N–61°35'W, 865 m elevation, [Fig. 1](#)) is located near the El Paují indigenous (Pemón) community, in the southernmost part of the GS region, and close to the Brazilian border ([Fig. 1](#)). The closest town is Santa Elena de Uairén (910 m elevation), though there is a closer small village called Icabarú ([Fig. 1](#)). The annual precipitation in Santa Elena is about 1700 mm on average, with a weak dry season from December to March (Huber, 1995a). The peat bog from which the core for this study was collected is situated on a gentle slope surrounded by forests and savannas, and its local vegetation is dominated by *Brocchinia* (Bromeliaceae), *Orectanthe* and *Xyris* (Xyridaceae) ([Fig. 2](#)). Contrarily to most of the Gran Sabana the site is nowadays within the forest domain, with patches of savanna without morichales at both sides of the road from Santa Elena to Icabarú. This locality is representative of a major forest–savanna ecotone between the GS savannas and the Amazon rainforests. In the absence of a local name for the sample site, it will be called El Paují peat bog for the purposes of the present study. The core studied (PATAM5 A07; 2.19 m long) was obtained in the deepest part of the peat bog, using a Russian corer (Jowsey, 1966). A total of 4 samples were taken along the entire length of the core for radiocarbon dating, which was carried out by Beta Analytic (Beta). Calibration was made with CALIB 6.0.1 and the IntCal09.14c database (<http://calib.qub.ac.uk./calib/>, last accessed on December 2010).

Forty-three samples from the sequence studied were taken at 5 cm interval for pollen analysis. These samples were spiked with *Lycopodium* tablets (batch 177745, average $18,584 \pm 1853$ spores/tablet) and processed using standard palynological techniques (KOH, HF and HCl digestion, and acetolysis) slightly modified according to the sediment nature (Rull et al., 2010b). The slides were mounted in silicone oil without sealing. Pollen and spore identification was made according to Roubik and Moreno (1991), Herrera and Urrego (1996), Rull (1998b, 2003), Colinvaux et al. (1999) and Leal (2010). Counts were conducted until a minimum of 300 pollen grains 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). The final counts averaged 357 grains/spores per sample. Pollen taxa were grouped according to the vegetation types previously described (Huber, 1986, 1989, 1994, 1995b; Huber and Febres, 2000). Only identified pollen taxa were included in the pollen sum (spores were excluded), 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 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 0.1% 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). The NPP were analyzed on pollen slides, and plotted as percentages based on the pollen sum. NPP identification was made according to Montoya et al. (2010) and literature therein. Descriptions and illustrations of new morphotypes (named with a code using the IBB prefix and a number) are included in the Appendix. Charcoal counts (only for particles larger than 5 μm) were carried out in the same pollen slides, considering three size classes (Rull, 1999):

- Type I: (smaller microcharcoal particles: 5–100 μm): used as proxy for mostly regional fires, because of the easy dispersion of these particles by wind and/or water.
- Type II: (larger microcharcoal particles: 100–500 μm): used as proxy for local fires.
- Type III: (largest microcharcoal particles: $\geq 500 \mu\text{m}$): used as proxy for high virulence local fire events. Owing to the low concentrations found, only presence/absence data were recorded (Figs. 4 and 5).

Modern charcoal sedimentation studies have been recently developed in the GS (Leal, 2010). Although they have not been published yet, we used some of their results in the interpretation of the El Paují sequence analyzed here.

4. Results

[Fig. 3](#) represents the age-depth model produced from the results of the AMS radiocarbon dating ([Table 1](#)). The best fit was obtained with a smooth-spline model (Blaauw, 2010). The peat accumulation rates were relatively low between 0.02 and 0.07 cm yr^{-1} , therefore, the resolution of this study is multidecadal to centennial (160 yr per sampling interval in average). This accumulation rate is in agreement with other GS late Holocene sediments (Leal, 2010; Montoya et al., 2011b), and slightly lower than a Late Glacial lake sediment and a Holocene peat sequence (Montoya et al., 2009, 2011a).

The pollen diagram is characterized by alternation between Poaceae, as the dominant herbaceous taxa, and forest elements, mainly Urticales and Alchornea ([Fig. 4](#)). Overall, the record suggests a forested landscape surrounded by open vegetation, except for the upper part, in which open savannas are established. Fire is common during the whole time period under study, especially in the upper levels, where savannas dominate. The remains of aquatic organisms indicate that flooding fluctuated and that the availability of moisture increased towards the top ([Fig. 5](#)). The pollen sequence has been subdivided into five zones, designated PAU-I through PAU-5. Each of these zones will be discussed in detail.

4.1. PAU-I (219–190.5 cm, 6 samples)

The pollen assemblage is dominated by herbaceous elements, but tree pollen is also abundant. Poaceae are the dominant herbs, with percentages fluctuating between 40 and 60%, followed by forest elements, notably Urticales belonging to several morphological types whose identification is still uncertain. Minor herbaceous elements are Drosera, Brocchinia, and Xyris. Among trees, Alchornea, Cecropia, and Weinmannia are also worth mentioning. Shrubs are very scarce ([Fig. 4](#)). The record of charcoal particles shows intermediate values. The most abundant spores are Lycopodium contextum, followed by psilate monoletes and triletes. Cyperaceae dominate the aquatic plants and Mougeotia the algae. Regarding other NPP, Coniochaeta cf. ligniaria, is relatively well represented, followed by Gelasinospora reticulisporea, IBB-37, IBB-39 and IBB-42 ([Fig. 5](#)).

4.2. PAU-II (190.5–125.5 cm, 13 samples)

This zone is characterized by a marked increase in forest elements (mainly Urticales, which reached 50% of the pollen sum, but also Alchornea) at the expense of herbs, notably Poaceae, which fell to percentages around 30% and, to a minor extent, Eriocaulaceae, Xyris and Genlisea ([Fig. 4](#)). No changes in the dominant taxa from the previous zone are evident. Centrolobium appears more consistently, but still with low values. The charcoal particles are also similar in concentration to PAU-I, but with a local peak occurs at the beginning, and a consistent decreasing trend is seen from the middle towards the top of the zone ([Figs. 4](#) and [5](#)). Aquatic plants also show a decreasing trend. L. contextum exhibits a remarkable decrease, which extends through the whole zone. Among the algae, Mougeotia shows an increasing tendency from the middle towards the top of the zone. The other NPP show abundances similar to PAU-I, with three exceptions: a dramatic increase in an unknown remain (IBB-42), a smaller but conspicuous increase of a fungal spore (IBB-41), and the occurrence of several peaks of Assulina ([Fig. 5](#)).

4.3. PAU-III (125.5–85.5 cm, 8 samples)

The pollen assemblage of this zone returns to values similar to those found for PAU-I, with some slight differences. Poaceae increases up to 40% without reaching values typical of PAU-I (60%). Urticales experience a noticeable decrease, from around 60% (PAU-II) to less than 20% ([Fig. 4](#)). Other trees, e.g., Alchornea, Weinmannia, Bonyunia, Pouteria, Centrolobium and Fabaceae (others) increase slightly. There is also a subtle increase in herbs such as Heliamphora, and Xyris.

Charcoal particles increase to the top of the zone and return to intermediate values again. Similar increasing trends are also observed in several pteridophyte spores, mainly L. cernuum and L. contextum ([Fig. 5](#)). Among the algae, Mougeotia has a local maximum in this zone. The more conspicuous changes in other NPP are the abrupt and dramatic declines of C. cf. ligniaria, G. reticulisporea and IBB-42, coeval with an increase in IBB-43 ([Fig. 5](#)).

4.4. PAU-IV (85.5–60.5 cm, 5 samples)

This zone is characterized by an abrupt and conspicuous change in the pollen assemblages (Fig. 4). A sudden decline in Poaceae coincides with a steep increase in *Centrolobium*, reaching a pronounced peak and disappearing at the top of the zone, where Poaceae show a recovery. Fabaceae (others) show exactly the same trends as *Centrolobium*, but with lower percentages. Other trees show values similar to those found in PAU-I and PAU-III, except for *Cecropia*, which has a small local peak around the middle of the zone. Urticales reach their minimum values. There is also a consistent increase in shrubs, though none of them are important individually. Charcoal particles decline to their minimum values at the beginning and remain low throughout the zone (Figs. 4 and 5). Among pteridophyte spores, psilate triletes and *L. cernuum* increase, whereas *L. contextum* and psilate monoletes show a subtle decrease. *Mougeotia* declines abruptly in a manner similar to that of Poaceae, whereas *Actinotaenium*-type consistently appears and increases in this zone. Among the other NPP, IBB-43 peaks and then declines in a similar fashion to that seen for *Centrolobium* and others Fabaceae, IBB-37 increases and peaks at the top of the zone, and IBB-41 declines and almost disappears at the top of the zone (Fig. 5).

4.5. PAU-V (60.5–0 cm, 11 samples)

Another significant shift in the pollen assemblages occurs in this zone. *Centrolobium* disappears from the record permanently, Fabaceae (others) abruptly declines, and the pollen assemblage is dominated by grasses again, reaching percentages similar to those found for PAU-I. All trees are at their minimum values, while shrubs maintain the percentages found in PAU-IV. Some herbs, notably *Brocchinia* and *Stegolepis*, increase. The charcoal concentration reaches its maximum values and shows two major peaks, one at the base of the zone and the other near the top (Figs. 4 and 5). A remarkable change seen in pteridophyte spores is the increase of psilate triletes, which mirrors the charcoal curve. There is a general increase in Cyperaceae and in algal remains, notably *Actinotaenium*-type, *Mougeotia* and *Botryococcus*, which was scarce or absent in the previous zones (Fig. 5). Among the fungal spores, IBB-43 notably declines, following similar trends than *Centrolobium* and others Fabaceae. *C. cf. ligniaria* and *G. reticulispora* recover to values typical of PAU-I and PAU-II, whereas *Gelasinospora* sp. and IBB-9 increase slightly. IBB-37 remains similar to the previous zone, and IBB-41 is scarce until the middle of the zone, from where occurs a slight increase. IBB-42 shows a comparatively small peak at the top of the zone.

5. Paleoecological interpretation

The results presented above indicate that the vegetation around El Paují peat bog has experienced significant changes during the last 8000 cal yr BP. The forests and savannas have repeatedly expanded and retreated, likely due to climate shifts, human activities, or synergies between both. This section deals with the paleoecological interpretation in terms of vegetation, climate and human pressure. Comparisons with other records from the GS and northern South America are also drawn to evaluate the spatial extent of the recorded changes. The time intervals discussed correspond to the pollen zones of the diagram (Figs. 4 and 5).

5.1. 8250 to 7715 cal yr BP

The dominance of Poaceae over forest elements suggests two alternative interpretations of the vegetation during this interval. The coring site could have been characterized by open savannas surrounded by forests dominated by several Urticales, or it could have been characterized by forest–savanna mosaics. The landscape would have been similar to the present, but the forests would have been closer or more extended. Fires seem to have been present since the beginning, as an important vegetation disturbance element (Figs. 4 and 5). The similarity between the Type I and Type II charcoal curves suggests a moderate incidence of local fires (Leal, 2010). The presence of fungal spores usually associated with dead and charred plant material remaining after fires (mainly *C. cf. ligniaria* and *G. reticulispora*) (van Geel and Aptroot, 2006), together with the occurrence of *Cecropia* – a common pioneer tree in early successional stages after fire disturbance (Behling and Hooghiemstra, 1999; Marchant et al., 2002; Mayle and Power, 2008) – supports the interpretation that local fires were common during this time interval. Aquatic elements suggest a hydrological balance (P/E ratio) lower than present (Fig. 5). Conditions drier than today have been also reported at Lake Valencia (Fig. 1), for the same interval (Leyden, 1985). The Cariaco Basin record (Fig. 1) also shows reduced precipitation values between 8.3 and 7.8 cal kyr BP (Haug et al., 2001). In the Colombian Llanos Orientales (Fig. 1), palynological evidence shows that the vegetation was more open than it is today, suggesting lower moisture availability (Wymstra and Van der Hammen, 1966; Behling and Hooghiemstra, 1998; Berrío et al., 2002a). Thus, it seems that a phase of reduced hydrological balance occurred over northern South America between these dates, probably due to a southward displacement of the Intertropical Convergence Zone (ITCZ) (Haug et al., 2001). In the El Paují record, the occurrence of local fires would have also contributed to the development of open savanna patches. The occurrence of local and regional fires has been documented in the Gran Sabana region since the Late Glacial and the early Holocene, and has been interpreted as a potential evidence of early human occupation (Rull, 2007, 2009; Montoya et al., 2011a). The record examined here would support this hypothesis.

5.2. 7715 to 5040 cal yr BP

The high values of Urticales, dominating the forest elements, is typical of closed-canopy neotropical rainforests (Gosling et al., 2009), and indicates a remarkable vegetation shift from open or mosaic vegetation to a densely forested landscape. The increasing trend in *Mougeotia* would suggest a weak, progressive increase in the P/E ratio, and the decrease in charcoal is indicative of a slight but progressive decline in local fires (Fig. 5). The synergistic action of these two factors would have led to the observed vegetation change. However, this trend is significant only for the upper half of the zone. The charcoal peak found at the beginning of the zone coincides with a decline in Poaceae (Fig. 4). It is plausible to suppose that fires acted on savanna vegetation and thus allowed forest recovery. The wetter climate prevailing during the upper half of the zone probably favored forest persistence. Unfortunately, the unknown origin and ecological requirements of the NPP IBB-41 and IBB-42 prevent these NPP from contributing to the interpretation, but their association with forest expansion and increasing forest density would be useful for identifying the potential use of these NPP as indicators. If fire incidence is linked to human activities, this time interval would have been characterized by a decrease in human pressure to forest favoring its recovery. Archeological and paleoecological studies have widely reported the presence of early human settlements in nearby areas since the mid Holocene or earlier, despite the absence of evidence for plant cultivation (e.g., Saldarriaga and West, 1986; Gassón,

2002; de Toledo and Bush, 2007). At a regional level, paleoclimatic studies have yielded contrasting interpretations. For example, conditions drier than those occurring today have been reported for several GS sequences (Montoya et al., 2009; Leal, 2010) and for the Lake Valencia catchment (Bradbury et al., 1981; Leyden, 1985; Curtis et al., 1999). A progressive increase in precipitation has been reported in the Cariaco Basin, coinciding with the Holocene Thermal Maximum, which occurred during this time interval (Haug et al., 2001). In Colombia, drier conditions have also been reported for the Llanos Orientales (Behling and Hooghiemstra, 1998, 2000; Berrío et al., 2002a) and the Cauca Valley (Berrío et al., 2002b) (Fig. 1), as well as for Amazonia (Mayle and Power, 2008). The El Paují record suggests a likely similar climate to PAU-I in the bottompart of the zone – drier than today – despite the forest increment registered.

5.3. 5040 to 2690 cal yr BP

During this interval, a clear shift to more open vegetation occurs after forest clearing. A climatic explanation of this vegetation shift is unlikely, as it occurs under wetter climatic conditions, as suggested by the maximum in algal remains (Fig. 5). An increase in local fires, as indicated in the charcoal increase, is the preferable interpretation. Therefore, expansion of savanna would be a consequence of forest burning, probably caused by humans. The NPP IBB-41 and IBB-42 again follow the same trends as the *Urticales*-dominated forest, supporting their close relationship with this vegetation type (Fig. 5). The same conclusion follows from the data on *C. cf. ligniaria* and *G. reticulispora*. The inferred wetter climate during this interval is supported by similar studies in nearby regions (Rull, 1992; Montoya et al., 2009; Leal, 2010). This interpretation is also in agreement with regional trends indicating an increase in the hydrological balance around 4000 cal yr BP (Marchant and Hooghiemstra, 2004), when a local maximum of *Mougeotia* is recorded in El Paují (Fig. 5).

5.4. 2690 to 1440 cal yr BP

The most conspicuous vegetation shift in the El Paují sequence took place during this interval. A dense forested landscape returned at the expense of grasses, but this time the forest was dominated by *Centrolobium* and other trees of the family Fabaceae, whereas *Urticales*-dominated forests were either absent or distant from the site (Fig. 4). The savannas were strongly reduced in extent and probably consisted of patches within a predominantly forested landscape. This strong vegetation shift coincides with the drier climates inferred from the aquatic elements and a dramatic decline in the incidence of fire (Fig. 5). *Centrolobium* is a genus of deciduous trees (Allen and Allen, 1981) typical of the dry seasonal semideciduous forests of lowland Amazonia (Garcia et al., 2004; Toniato and de Oliveira-Filho, 2004; Ortuño et al., 2011). *Centrolobium* species are able to regenerate from roots (Martini et al., 2008; Hayashi and Appezzato-da-Glória, 2009), becoming one of the more important invaders of the earlier phases of secondary forest regeneration after the abandonment of intense land use and/or after fire (Gould et al., 2002; Park et al., 2005; Bertoncini and Rodrigues, 2008). Therefore, the most likely interpretation of PAU-IV is the rapid invasion of the site by *Centrolobium*-dominated dry forests after the sudden cessation of fires around 2700 cal yr BP. The increase registered in shrub taxa, frequent formation in dry secondary forests although not individually important, supports this interpretation (Fig. 4). On the other hand, the synchronous appearance and further decline of IBB-43, point to a close relationship of this unknown NPP with *Centrolobium* and Fabaceae (others) (Fig. 5). A possible explanatory factor is mycorrhizal symbioses, which are important in contemporary Amazon forests, especially in forest regeneration stages where Fabaceae trees, including *Centrolobium*, are commonly dominant (Marques et al., 1997, 2003). This possibility should to be confirmed through further studies. The overall landscape picture suggests the establishment of drier climates favoring the

development of secondary dry forests, and it also suggests the abandonment of the site by humans. The slight *Cecropia* increase and the non-recovery of the *Urticales*-dominated rainforests, which require higher levels of moisture availability to develop, are consistent with such a scenario. Several studies from the northern South American lowlands support the occurrence of regional drier climates since around 2800 cal yr BP (Bradbury et al., 1981; Curtis et al., 1999; Berrío et al., 2000, 2002a; Haug et al., 2001; Montoya et al., 2011b).

5.5. 1440 cal yr BP to present

During this time interval, forests retreated and savanna vegetation expanded and dominated the landscape (Fig. 4). Locally, the present-day vegetation was established in the El Paují peat bog, as indicated by the increase of *Brocchinia* and the appearance of *Stegolepis* (Fig. 2). This vegetation shift coincides with an increased P/E ratio given the values of the aquatic elements observed, being the maximum P/E values found during this period, in contrast with the hydrological balance inferred for former Holocene times (Fig. 5). The establishment of savannas instead of forests under these climatic conditions would seem contradictory. Therefore, climate would not be the best explanation for the landscape shift. The dramatic increase in fire around 1400 cal yr BP would be a more likely driver for the observed savannization (Figs. 4 and 5). This information suggests the return of human populations to the site and the establishment of different patterns of land use. Indeed, whereas the middle Holocene fires were compatible with the occurrence of rainforests, during the last 1400 yr forests seem to have been burnt until their almost eradication from the site. In this sense, the current El Paují landscape seems to have established in the last 1500 yr onwards synchronous with the highest fire activity, probably owing to a strong human impact. Fires have persisted through the entire interval, and show a second peak around 220 yr ago (AD 1730), more than 200 yr after the European colonization (see below, Section 6). The increase in human disturbance recorded in El Paují, leading to the present-day vegetation patterns, has been also documented at the regional level. In other GS records, forest retraction and savanna expansion coincide with an increased fire incidence and the local establishment of morichales around lakes and rivers (Rull, 1992, 1999; Montoya et al., 2009, 2011b; Leal, 2010). The same patterns can be observed in the Colombian Llanos (Berrío et al., 2000, 2002a; Behling and Hooghiemstra, 2001). It therefore seems that human activities have played a major role in shaping current savanna landscapes in northern South America.

6. Discussion and conclusions: human occupation and land use Practices

This section discusses the results presented above and the interpretation of the pollen data in terms of human occupation and landscape management, mainly in relation to fire practices. The consistent presence and abundance of charcoal, as a fire proxy, throughout the record strongly suggests a consistent human occupation during the Holocene in the El Paují area. The continuous presence and abundance of some taxa that serve as indicators of secondary succession after human disturbance, notably *Cecropia* and psilate trilete spores, support this interpretation (Rull, 1999; Mayle and Power, 2008). Similar fire records have been documented for the neighbor Guyana during the Holocene, and have been linked to human activities (Hammond et al., 2006). However, the positive feedbacks between climate, humans and vegetation features (because the vegetation is the chief source of the fuel for fires) could have played a role. For example, the savanna expansion recorded at the base of the sequence (PAU-I, ca. 8250 to 7715 cal yr BP) occurred during a phase of regional dry climates (Mayle and Power, 2008), and probably favored the occurrence of fires.

It is noteworthy that, despite the persistent presence of fire disturbance, rainforests experienced a remarkable expansion between 7715 and 5040 cal yr BP. The expansion of the rainforests was probably favored by fires developed in savanna vegetation, by wetter climates, or by both factors. The coexistence of wet climates, rainforests and fires would be explained by land use practices similar to those currently found in many neotropical forested landscapes, in which small forest spots (known locally as conucos) are cleared and burned for shifting agriculture (Fig. 6). The absence of pollen from cultivated plants does not weaken this interpretation. Pollen from this source is typically absent from pollen records in the whole Guayana region, even in modern conuco areas (Rull, 2007, 2009; Leal, 2010). The rainforest reduction and savanna expansion recorded between approximately 5.0 and 2.7 cal kyr BP coincides with an increase in fire incidence and suggests more intense forest burning either at a regional or at a local scale. Regional burning is a more likely possibility because large charcoal particles, used as proxies for local fires, do not increase during this period. After that, humans seem to have abandoned the study area more or less suddenly, as suggested by the abrupt decline of fire incidence around 2.7 cal kyr BP. The site was then colonized and occupied by secondary dry forests until about 1.4 cal kyr BP, probably under drier climates and in the absence of human pressure. Humans then returned, but their patterns of land use were totally different from those used during the previous period of human occupation. Indeed, fire incidence increased and remained at a high level until the present. These fires probably prevented any reestablishment of the forest, despite the return of wetter climates. The situation is very similar to the nowadays Pemón practices of frequent and extensive fires that affect both savannas and forested areas.

According to this interpretation, a remarkable shift in land use patterns occurred between the mid- and late Holocene, separated by an interval of reduced or null human pressure between around 2.7 and 1.4 cal kyr BP. These differences could be interpreted as the sequential occurrence of two different cultures at El Paují: a first forest-like indigenous culture with lower pressure upon landscape, concurrent with the presence of rain forests; and a second savannalike indigenous culture coinciding with the savanna establishment and expansion. An eventual change of land use within the same indigenous group is unlikely. Based on anthropological evidence, the arrival of the present-day Pemón culture in the region has been proposed to have occurred very recently, around last centuries (Thomas, 1982; Colson, 1985). However, aleoecological indicators of the Pemón presence, namely the onset of modern fire regimes and the expansion of *Mauritia* palm stands in the GS, support an earlier colonization by this culture, at least since ca. 2000 yr ago (Rull, 1998a; Montoya et al., 2011b). It must also be recognized that the El Paují area, as mentioned above (Section 3), is located near the biogeographical boundary between the open GS savannas and the Amazon rainforests (Fig. 1), which coincides with the limit between the GS Pemón and the Amazon Yanomami groups. The Pemón show a marked preference for open landscapes, which is linked to the extensive use of fires, while Amazon Yanomami live in forested habitats and practice shifting agriculture (Huber, 1995a). Therefore, early to mid Holocene landscapes and land use, as suggested by the El Paují record, are more consistent with the local presence of Yanomami-like groups, whereas the late Holocene scenario seems more appropriate for the Pemón culture. Therefore, the modern indigenous culture inhabiting El Paují area, and the Gran Sabana in general, could have arrived to the area around 1500 yr ago, earlier than prior evidence suggest, but some 500 yr later than in other Gran Sabana localities (Montoya et al., 2011b). The absence of *Mauritia* palm stands along the whole time interval studied is noteworthy in comparison with other GS sequences. A possible explanation is that some features of the El Paují forested landscape, as the absence of permanent water-saturated soils or the distance to water courses (See Section 5.5), are not as suitable as the open savannas for morichal development, but differences in human practices according to

the dominant habitat cannot be excluded. This interesting question is open and deserves further research.

The more recent paleoecological and fire trends from the El Paují record could be related with European colonization. Indeed, a regional decline in the indigenous population occurring around AD 1600 seems to have been caused by the consequences of European contact (Bush and Silman, 2007). This decline would be reflected in the El Paují record by the significant charcoal minimum at AD 1630 (23 cm; 320 cal yr BP). The colonization of the Guayana region and its surroundings by the Europeans started in the 16th century, when several military expeditions from different countries (notably Spain, Great Britain and The Netherlands) competed for the possession of the mythical El Dorado. Spanish conquerors and missionaries were established in the 17th century and remained until the first half of the 18th century, when their activities were banned by the Venezuelan government (Huber, 1995a). The charcoal peak at AD 1730 coincides with this period and would reflect burning, either by the Spaniards just before their departure or subsequently by the indigenous population following their recovery and the resumption of traditional fire practices.

In general, the observed ecological shifts in the El Paují area have been greatly affected by human activities since the early Holocene; hence, the role developed by humans in shaping the modern El Paují landscape has been crucial, with fire as the main driver. Further studies should hopefully provide more detail in the ecological development in this ecotonal area between the Gran Sabana and the Amazon rainforests, especially during the last millennia, when present-day cultures established.

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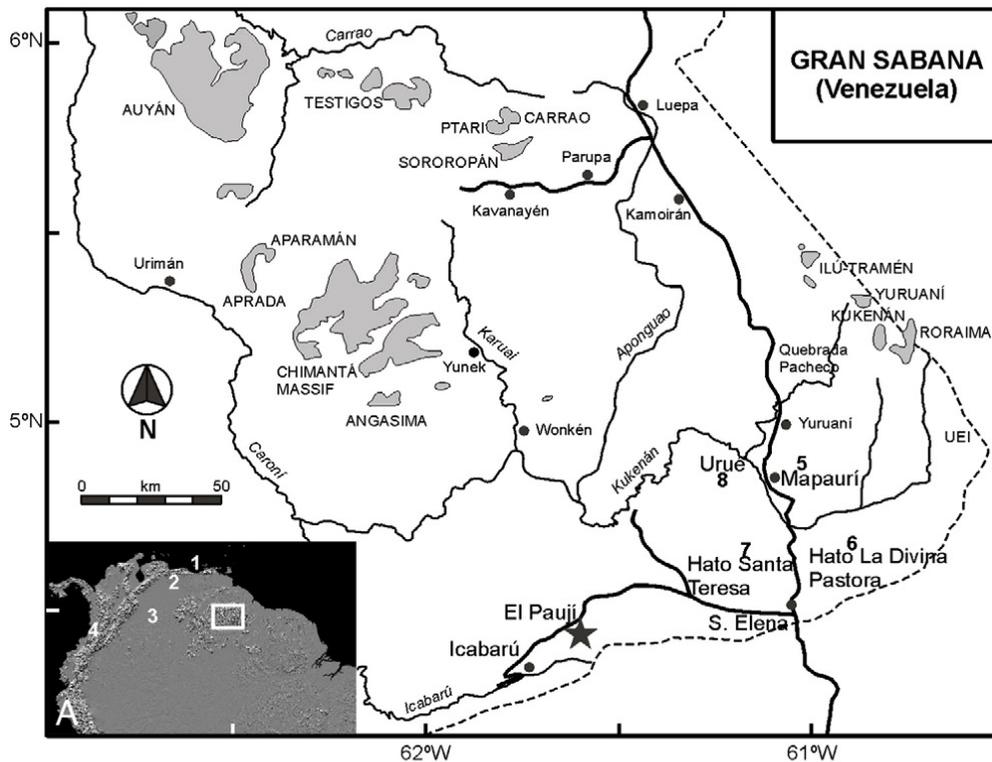


Fig. 1. A. Location of the study area and its position within northern South America. (Radar image courtesy of NASA/JPL-Caltech.) The coring site is indicated by a black star. Numbers indicate the sites with palaeoecological information mentioned in the text: 1 — Cariaco Basin (Venezuela); 2 — Lake Valencia (Venezuela); 3 — Colombian Llanos; 4 — Cauca Valley (Colombia); 5 — Mapaurí (Gran Sabana); 6 — Lake Chonita (Gran Sabana); 7 — Lake Encantada (Gran Sabana); and 8 — Urué (Gran Sabana). B. Google-earth image of present-day forest/savanna contact at the study. The coring site is marked with a white star. GS: Gran Sabana.



Fig. 2. Image of the current landscape and the local vegetation of El Paují peat bog. Yellow spots are the leaves of the columnar bromeliads of the genus *Brocchinia* that identify and characterize the peat bogs of the Gran Sabana. Note the location of the peat bog between grasslands and forests, and the absence of *Mauritia flexuosa* palm stands or morichales (Photo: V. Rull).

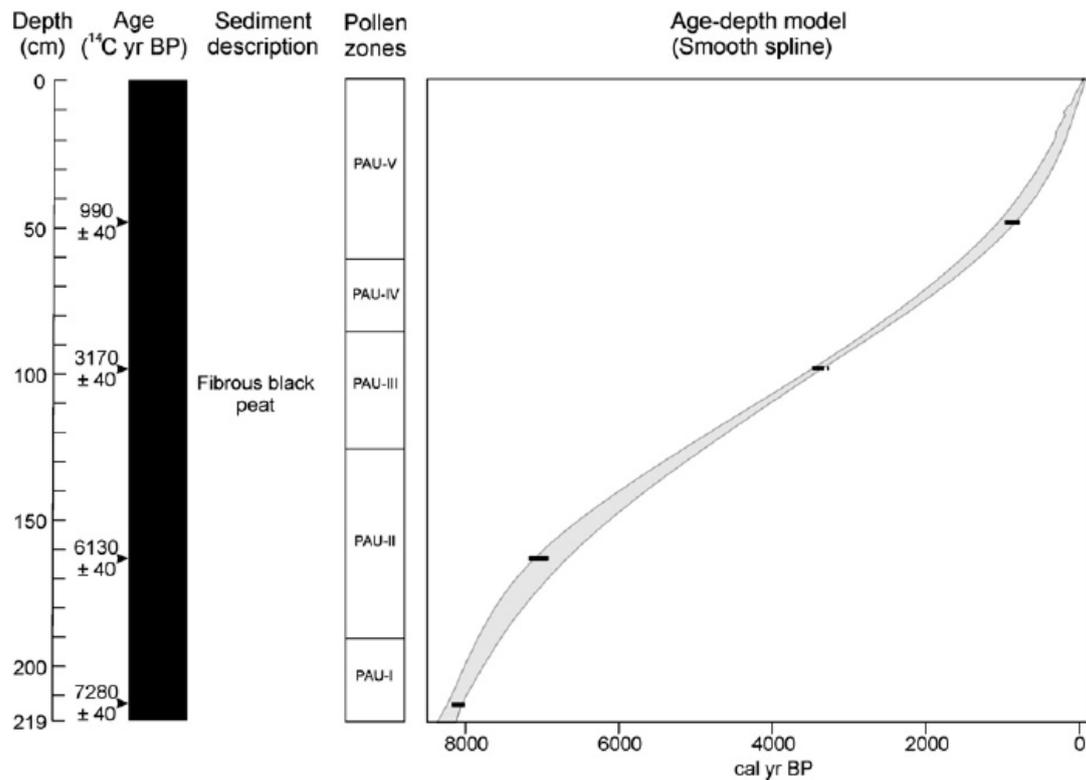


Fig. 3. Core stratigraphy, with radiocarbon ages, sediment description, pollen zones and age-depth model of the sequence.

Table 1

AMS radiocarbon dates used for the age-depth model (WA: weighted average).

Laboratory	Sample	Depth (cm)	Sample type	Age (yr C14 BP)	Age (cal yr BP) 2σ	Age (cal yr BP) estimation (WA)
Beta-247285	PATAM5_A07/10	45–50	Wood	990±40	898–1006	957
Beta-247286	PATAM5_A07/20	95–100	Wood	3170±40	3341–3480	3405
Beta-247287	PATAM5_A07/33	160–165	Wood	6130±40	6890–7164	6918
Beta-251877	PATAM5_A07/43	210–215	Wood	7280±40	8013–8174	8144

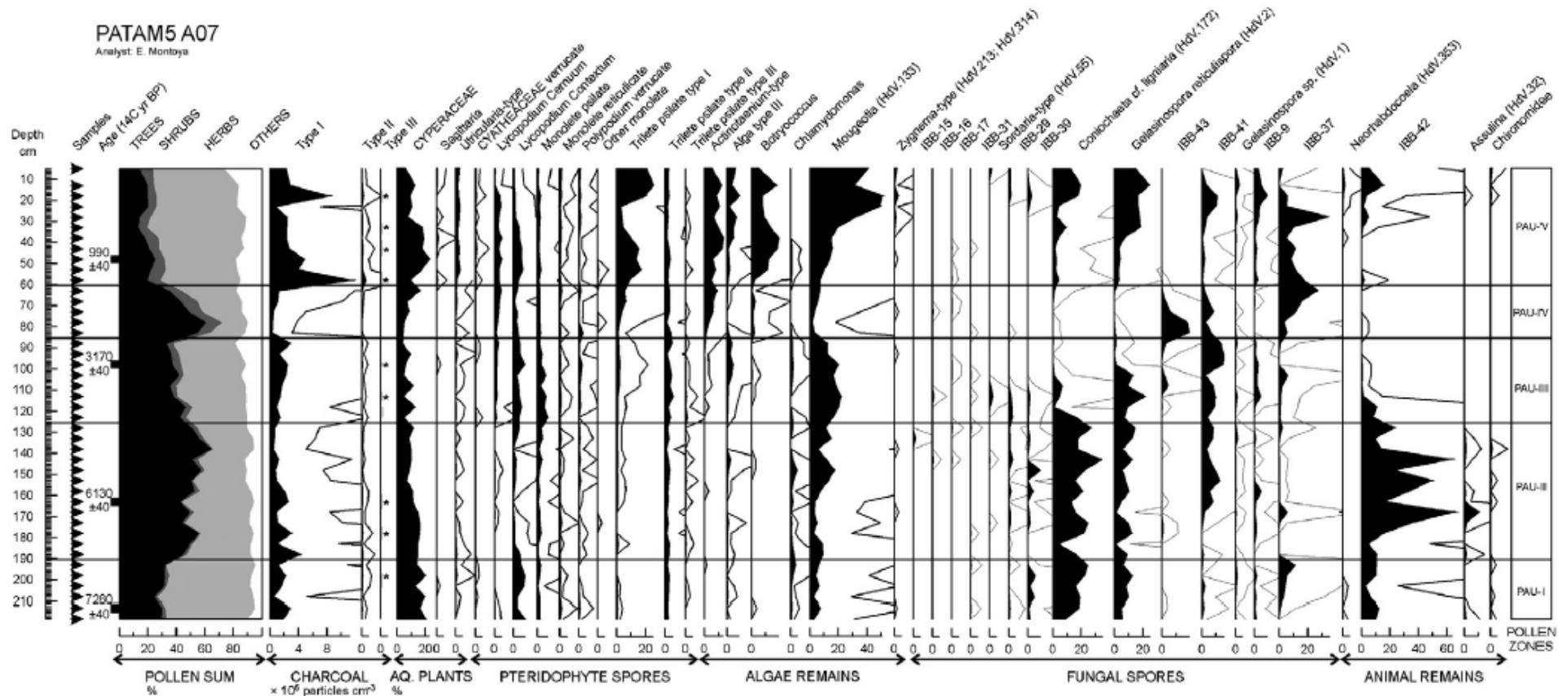


Fig. 5. Diagram showing the elements outside the pollen sum, namely aquatic and semi-aquatic plants, pteridophyte spores, algae remains, and non-pollen palynomorphs. The abundances are expressed in percentage respect to the pollen sum. Solid lines represent $\times 10$ exaggeration. AQ. PLANTS = Aquatic and semi-aquatic plants; HdV = Hugo de Vries Lab; and IBB = Institut Botànic de Barcelona.

Appendix. Descriptions of unknown NPP

IBB-9 (Plate I): Ascospores ellipsoid one-celled, 21.8–33.4×13.0–17.0 µm; smooth wall or slight longitudinal sub-parallel striae over the entire spore-length, with two protruding apical pores. This morphotype could be related to Types 47–48 from SW Pacific Islands (Macphail and Stevenson, 2004) and/or Type UG-1187 described in East African lake sediments (Gelorini et al., 2011).

IBB-37 (Plate I): Fungal spores, two (three) septate, 17.1–25.8×11.8–16.5 µm; apical end rounded, and basal cell pale or hyaline and narrow. This morphotype could be related to Type 86 described for SW Pacific Islands (Macphail and Stevenson, 2004).

IBB-39 (Plate I): Ascospores slightly lemon-shaped, three-septate, 19.5–29.3×8.1–17.0 µm; constricted at the septum.

IBB-41 (Plate I): Fungal spores, 13.1–18.8×8.6–11.7 µm; wall with pronounced protuberances that confer it a highly irregular and variable aspect.

IBB-42 (Plate I and II): Globosemicrofossil of unknown origin, 112.4–153.2×62.3–100.7 µm. It presents a likely apical aperture or more easily breakable zone, more constricted than the main body (32.3–47.8 µm), and a basal end that can be presented as: (1) closed and rounded end with a likely inner hole; or (2) open end with two prominent terminations with rounded spines form. It appears frequently broken. Perhaps the basal zone differences represent the same morphotype before (close) and after (open) it breaks. This morphotype has been found in this sequence at high abundances in a zone (PAU-II, from 7715 to 5040 cal yr BP) where the water level did not show any significant change in the bottom part, but an increase in forest elements (Mainly Urticales) was recorded.

IBB-43 (Plate I): Ascospores fusiform, 12.3–21.3×6.3–10.2 µm; with two apical pores. This morphotype has been found in this sequence at high abundances in a zone (PAU-IV, from 2690 to 1440 cal yr BP) where it was recorded an abrupt increase of *Centrolobium* and other Fabaceae tree synchronous with the disappearance of fires.

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