Holocene vegetation dynamics on the Apakará summit of the neotropical Guayana Highlands and potential environmental drivers

Valentí Rull* & Encarni Montoya

Laboratory of Paleoecology, Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), C. Solé Sabarís s/n, 08028 Barcelona, Spain

*Corresponding author. E-mail vrull@ictja.csic.es
Abstract

The Guayana Highlands (GH) are natural laboratories to study the influence of environmental drivers on neotropical ecosystems. The GH summits have been characterized by constant vegetation patterns during the Holocene, except for a few sites close to altitudinal ecotones. Here, we report a new pollen record showing two significant vegetation shifts, from *Myrica* forests to tepuian meadows (5340 cal yr BP) and then to *Chimantaea* shrublands (2720 cal yr BP). These changes are analyzed in terms of potential forcing factors such as regional climate changes, fire and autogenic succession. The first shift occurred shortly after the Holocene Thermal Maximum and the onset of a cooling/drying trend. A charcoal peak was coeval with this change suggesting some potential influence of fire. Autogenic processes related to lake infilling might have also been involved. The second vegetation shift took place during a phase of increased precipitation variability due to a ENSO intensification. The establishment of *Chimantaea* shrublands started at the end of this phase coinciding with another charcoal peak (2300 cal yr BP). These results support the idea of relevant ecological changes in the GH during the Holocene, the apparent vegetation constancy recorded in other GH summits could be due to site insensitivity.

Keywords: Palynology, paleoecology, vegetation history, paleoclimates, Holocene, Neotropics
1. Introduction

The Guayana Highlands (GH), situated between the Orinoco and the Amazon basins in northern South America (Fig. 1A), have been considered a natural laboratory to study the origin of neotropical biotic patterns in terms of the influencing ecological and evolutionary processes and mechanisms, as well as the environmental drivers involved (Rull, 2010). Relevant general aspects that have been studied since the early 20th century in the GH include (i) the classical biogeographical debate between vicarianism and dispersalism, (ii) the chronology, drivers and mechanisms of neotropical diversification, (iii) the relative importance of Neogene vs. Pleistocene speciation and extinction, (iv) the elevational biodiversity gradients and their potential causes, (v) the eventual occurrence of Pleistocene glacial refugia in the tropics, (vi) the robustness of the potential natural vegetation concept (vii) the expected extinction by habitat loss under the effects of global warming or (viii) the more suitable biodiversity conservation strategies, among others (e.g., Chapman, 1931; Tate, 1928, 1938a, b; Mayr and Phelps, 1967; Maguire, 1970; Steyermark, 1979; Huber, 1988; Steyermark and Dunsterville, 1980; Gorzula, 1992; Mayr, 1999; Pérez-Hernández and Lew, 2001; Givnish et al., 2000, 2004, 2011; Huber and Foster, 2003; McDiarmid and Donnelly, 2005; Noonan and Gaucher, 2005, 2006; Rull, 2004a, 2005a, 2006, 2007, 2008, 2010, 2011a, b, 2015; Rull and Vegas-Vilarrúbia, 2006, 2008; Rull and Nogué, 2007; Hopper, 2009; Nogué et al., 2009a,b, 2013; Bernard et al., 2011; Vegas-Vilarrúbia et al., 2011, 2012; Rull et al., 2009, 2013, 2016; Safont et al., 2012, 2014; Salerno et al., 2012; Leite et al., 2015). In spite of the amount and variety of ecological and evolutionary studies conducted to date in the GH, there are still many questions that remain open and demand more research. In this paper, we focus on a relevant ecological topic as is the long-term vegetation dynamics in relation to the potential external and internal drivers of ecological change.

The flat summits of the table mountains, locally called “tepuis”, of the GH hold unique biomes and ecosystems, with amazing biodiversity and endemism patterns, which has led to the
definition of the Pantepui biogeographical province, within the Neotropical realm. Pantepui comprises the assemblage of the ~60 flat summits that constitute the GH, with a total surface of ~6000 km² and an elevation of 1500 to ~3000 m (Huber, 1994; Berry *et al.*, 1995). Though systematic exploration is far from complete (Huber 1995b), almost 2500 vascular plant species (belonging to 630 genera and around 160 families) have been described, of which 62% are endemic to the Guayana Region, 42% are endemic to the Pantepui province, and around 25% are endemic to a single tepui (Berry and Riina, 2005). Local endemism can reach 60% in some tepuis, which is comparable to most oceanic islands (Rull, 2009). Vegetation types and ecosystems atop the tepuis are also unique, not only as compared to other Guayana landscapes but also in a global context (Huber, 1992, 1995c, 2005, 2006). The GH summits are virtually pristine. No mineral resources to exploit have been found, the soils are not appropriate for agriculture and there are no grasslands suitable for cattle raising. Indigenous people living in the surrounding lowlands and uplands do not visit the tepui summits because they are considered to be sacred and forbidden to humans. Tourism and scientific exploration are the only activities that have been developed on Pantepui, using mainly helicopters as transportation (Gorzula and Huber, 1992; Huber 1995d). There is no tourist infrastructure atop the tepuis to facilitate visitation, which maintains the lack of human impact on the summit. The GH are protected by several designations including national parks and a biosphere reserve (Huber, 1995d). In spite of this, some localized but immediate threats linked to uncontrolled tourism have been identified and should be urgently addressed to prevent their further expansion across the GH (Rull *et al.*, 2016).

The biotic uniqueness and pristine nature of the GH summits and their biota make them especially suitable for the study of long-term vegetation dynamics under natural forcing, without the direct influence of human activities. To date, this type of studies has been conducted on a number of tepuiian summits, which has allowed the main Holocene vegetation trends to be reconstructed (Rull, 2004b, 2005a, b; Nogué *et al.*, 2009a; Safont *et al.*, 2016). Most of these records documented an outstanding vegetation stability during the last 6000 years but two of
them revealed significant vegetation shifts likely linked to climatic changes and fire. The Churí
record, from the same massif as the Apakará summit (Fig. 1B), documented a Late Holocene
upward displacement of a characteristic ecotone that was interpreted in terms of a gentle
warming (Rull, 2004a, b, c). The Uei record is the only case documented so far where
anthropogenic fires have likely affected the tepuian vegetation in the past. According to Safont
et al. (2016), fires which originated in the nearby savanna uplands in the mid-18th century
spread to the summit of the Uei and significantly reduced forests and meadows, favoring
colonization by invader shrubs.

The apparent discrepancy between long-term vegetation constancy and change atop the tepuian
summits during the Holocene was tentatively explained in terms of climatic change intensity
and site sensitivity. On the one hand, it was suggested that the extremely high humidity (over
2500 mm per year) of the GH acted as a buffer preventing moderate climate shifts to
significantly affect vegetation. On the other hand, it was proposed that coring sites near an
altitudinal vegetation ecotone, as is the case of the Churí record, would be better suited to record
vegetation changes than those situated within the elevational range of a given formation (Rull,
2005b). A preliminary paleoecological study from the Apakará summit seemed to support the
hypothesis of site sensitivity (Rull et al., 2011). A significant vegetation shift was recorded
around the middle Holocene, which was tentatively linked to the end of the Holocene Thermal
Maximum and the incoming of cooler and more unstable climates, in terms of precipitation, as
documented in the Cariaco records (Haug et al., 2001) (Fig. 1A). However, this study was of
very low resolution (barely one sample per millennium) and it was recommended to increase the
resolution by intensifying sampling density.

Here, we report the results of a multidecadal to centennial-scale study of the same core aimed at
(i) reconstructing the detailed long-term ecological dynamics of the Apakará vegetation, (ii)
documenting eventual regime shifts and identifying the potential environmental drivers
involved and (iii) testing the existing hypotheses for the apparent spatial heterogeneity of
Holocene vegetation dynamics atop the tepuis. It should be stressed that this study is not aimed to investigate the response of the Apakará vegetation to regional climatic shifts but to reconstruct the Holocene vegetation dynamics of this summit and discuss the potential drivers involved, especially climatic changes, fire and autogenic successional processes. Climate dynamics is also beyond the scope of this study, which is essentially ecological.

2. Material and methods

2.1. Study site

The Apakará summit is part of the Chimantá massif, one of the largest tepuian complexes of the GH with a total surface area of >600 km² (Figs. 1B and 2A). Like the other table mountains of the Guayana region, the Chimantá massif is formed by the Precambrian quartzites/sandstones of the Roraima Group, overlying the igneous/metamorphic Guayana Shield (Fig. 1A). The flat summits of this massif range from 2200 to 2600 m elevation at their tops (Huber, 1995a). The coring site was located at 5º 19’ 22” N and 62º 13’ 34” W, at 2170 m elevation. There is no weather station near the site but it is known that, at these elevations, the GH have mesothermal ombrophilous climates with average annual temperatures between 12 and 18 ºC and a total annual precipitation ranging from 2500 to 3500 mm, with low seasonality. Additional moisture is provided by dense mists, which are frequent in these summits. Winds and thunderstorms are also common, especially when the Intertropical Convergence Zone (ITCZ), which seasonal latitudinal displacement controls the seasonal precipitation regime in northern South America, is close to the region (March to November) (Huber, 1995a). Inter-annual climatic variability is controlled by the El Niño Southern Oscillation (ENSO) of 4-year periodicity, in average, which is responsible for the intensification of land-sea temperature contrasts, which strongly affects the evolution of trade winds and the intensity and distribution of precipitation (Poveda et al., 2006). A common sequel is the occurrence of wetter or drier than average rainy seasons.
The vegetation of the Chimantá massif has been subdivided into four main categories, namely forests, shrublands, meadows and pioneer vegetation. The more characteristic forests are gallery forests dominated by *Bonnetia roraimae* (Bonnetiaceae) growing along water courses (Fig. 2B). Among shrublands, the more representative are the so called “paramoid” shrublands – owing to their physiognomic resemblance with the Andean páramo vegetation dominated by several species of the endemic genus *Chimantaea* (Asteraceae) (Fig. 3). Broad-leaved meadows dominated by *Stegolepis ligulata* (Rapateaceae), endemic to the Chimantá, are the more extended. Grassy meadows are rare. Pioneer vegetation grows on sandstone outcrops and is composed of a variety of species from other formations, lichens and mosses are also frequent in these rocky environments (Huber, 1992, 1995c). The coring site was in the margin of a large paramoid shrubland (Fig. 3) patch dominated by *Chimantaea mirabilis* (Asteraceae) and the bambusoid grass *Myriocladus steyermarkii*, surrounded by meadows, with gallery forests along the nearby river and scattered shrub stands on sandstone outcrops (Rull *et al.*, 2011). The more relevant components of the paramoid shrubland and the surrounding vegetation are listed in Table 1. The site is close to the upper limit of the tepuian meadows dominated by *Stegolepis ligulata*, which is around 2200-2300 m (Huber, 1992). The *Chimantaea mirabilis* shrublands occur between 1900 and 2500 m elevation (Huber, 1995c; Pruski, 1997).

2.2. Methods

The peat core analyzed in this paper (PATAM9-A07; 2 m depth) was obtained with a Russian corer in February 2007. Radiocarbon dating of nine plant macrofossil samples was conducted by Beta Analytic and the Kek Carbon facility of the University of California (Table 2). The age-depth model was performed with clam.R, version 2.2 (Blaauw, 2010), using the calibration of Reimer *et al.* (2013). Samples for pollen analysis were processed using standard methods including KOH, HCl and HF digestions, acetolysis and mounting/storing in silicone oil (Bennett and Willis, 2001). *Lycopodium* tablets (batch nº 177745; 18,584 spores/tablet) were added before chemical processing. Counting was conducted until a minimum of 300 pollen and spores.
and the saturation of diversity (Rull, 1987). The pollen sum included all pollen types with the exception of aquatic plants (Alismataceae, Onagraceae). Identification was based on local pollen and spore morphological studies (Salgado-Labouriau and Villar, 1992; Rull, 2003; Leal et al., 2011; López-Martínez et al., 2010) and other regional floras and atlases (e.g. Roubick and Moreno, 1991; Tryon and Lugardon, 1991; Colinvaux et al., 1999; Bush and Weng, 2006).

Charcoal particles were identified and counted in the same palynological samples, only particles >5μm were considered. Pollen diagrams were plotted and zoned with psimpoll 4.27 using the Optimal Splitting by Information Content (OSIC) method (Bennett, 1996). Statistical analyses were performed with MVSP 3.22. The interpretation of the pollen diagram in terms of vegetation succession was based on previous studies of modern pollen sedimentation in relation to the vegetation types (Rull, 2005c).

3. Results

3.1. Lithology and age-depth model

Lithologically, core PATAM09-A07 was composed mainly of dark-brown peat, except for two layers (190-200 cm and 140-145 cm) of clayey peat and a layer (170-190 cm) of gyttja (Fig. 4). Regarding chronology, the best fit (GOF = 14.09) was obtained with a linear interpolation model (Fig. 4). According to this model, the core encompasses the last ~8500 years (8556 to 268 cal yr BP). The base of the section exhibits extremely low accumulation rates (0.030 mm a⁻¹) coinciding with the basal clayey peat. The change to gyttja was accompanied by a huge increase in accumulation rates, which increased by >30 times starting slightly before 6000 cal yr BP. This situation lasted until about 5800 cal yr BP, when accumulation rates declined to moderate levels (0.209 mm a⁻¹).
A total of 97 pollen and spore types were identified, excluding those which were unidentifiable owing to mechanical deformation or bad preservation (unknown). Types above 0.2% were depicted in the percentage diagram individually whereas the others (<0.2%) were included in the category called “other dicots”, in the case of pollen, and “other pteridophytes”, in the case of spores (Fig. 5). The OSIC method provided a subdivision of the pollen diagram into three significant zones:

Pollen Zone APK I (197-125 cm; 8225-5335 cal yr BP; 18 samples). This zone was dominated by *Myrica* and Poaceae, both over 20% of the pollen sum, followed by *Cyrilla* and *Ilex* (~10% each); less important elements (<5%) are *Weinmannia*, *Podocarpus* and *Chimantaea*. Amongst spores, *Isoëtes* is the more abundant, with percentages over 40% of the pollen sum, and other characteristic components (~5%) are *Lycopodiella cernua*, *Pterozonium* and *Cyathea (psilate)*. A modern analog for this pollen assemblage has not been found in previous studies on any tepuian summit (Rull, 2005c; Rull et al., 2013; Safont et al., 2016). The main difference with modern assemblages is the abundance of *Myrica*, which is absent in today’s vegetation and also in modern pollen assemblages from the coring site and surroundings. The high abundance of *Isoëtes* spores is also unparalleled in studies developed so far in the tepuian summits. In the Chimantá massif, this genus is represented by *Isoëtes killippi*, growing in flooded sites such as pools, streams and waterfalls, from 1900 to 2800 m elevation (Huber, 1992). The whole picture suggests the occurrence of a *Myrica* forest in a swampy/marshy environment, which contrasts with all present-day vegetation types found around the coring site. The presence of gyttja and clay layers (Fig. 4) supports this interpretation and suggests the occurrence of a shallow water body.

Pollen Zone APK II (125-62 cm; 5335-2720 cal yr BP; 17 samples). A dramatic reduction of *Myrica* and *Isoëtes* occurred at the beginning of this zone and these pollen/spore types never
recovered their ancient values. *Podocarpus, Weinmannia, Chimantaea, Lycopodiella cernua* and *Pterozonium* also declined. This zone was dominated by herbs, notably Poaceae (~40%), *Cyperaceae* and *Xyris* (~10% each), with *Cyrilla* as the more abundant shrub (10-20%). These changes suggest a significant vegetation change towards tepuian meadows and *Cyrilla* shrublands in a non-flooded environment. Likely, *Chimantaea* shrublands did not occur around the coring site, as this pollen was very scarce or absent during the whole zone. The replacement of the *Myrica* forests by the tepuian meadows was gradual, starting at ~150 cm (~5830 cal yr BP) and ending at ~115 cm (4830 cal yr BP). Contrarily, the disappearance of the shallow lake, as indicated by the decrease of *Isoëtes*, was more abrupt and occurred around the boundary of zones APK I and APK II (125 cm; 5330 cal yr BP). The boundary between zones APK I and APK II coincided with a relevant drop in accumulation rates and a significant lithological change from clayey sediments to black peat.

**Pollen Zone APK III** (62-0 cm; 2720-0 cal yr BP; 32 samples). This zone followed the general trends of zone APK II with some difference. The more important is the increase of *Chimantaea, Weinmannia* and *Brocchinia*, and the slight decline of *Cyrilla*, Poaceae and Xyris. Pteridophytes were generally low with no significant differences, except for *Hymenophyllum/Trichomanes*. This assemblage is characteristic of the modern *Chimantaea* shrublands (Rull, 2005c), hence, the site was likely covered by this type of vegetation, as it is nowadays, since about 2720 cal yr BP. The significant increase of *Chimantaea* between 57 and 50 cm suggests that these shrublands were denser than present day between 2540 and 2290 cal yr BP. The nearby forests were composed mainly of *Weinmannia* and *Cyrilla*, as it occurs today. The increase of *Hymenophyllum/Trichomanes*, two genera of lithophilous ferns (Huber, 1992), indicates that the pioneer vegetation of rocky outcrops was developed to a greater degree. As in the former zone, there were no signs of flooding, although the increase of *Brocchinia* and the nature of sediments suggest the occurrence of tepuian peat bogs where this tubular Bromeliaceae is characteristic (Huber, 1992, 1995c).
3.3. Statistical analysis

Pollen trends were analyzed in a more synthetic manner using Principal Component Analysis (PCA). The first three components explained >97% of the total variance (Table 3). PC1 is heavily influenced by Poaceae, PC2 by Myrica and PC3 by Chimantaea, which implies that these three taxa are the most responsible for the variance of the whole data set. Other important, though less relevant, associations are with Cyperaceae and Cyrilla (PC1), Ilex (PC2) and Brocchinia (PC3). The stratigraphic arrangement of these three PC is shown in Fig. 6, where it can be realized that PC1 maximized at Zone APK II, PC2 defines Zone APK I and PC3 characterizes Zone APK III. According to the interpretation of the pollen zones, PC1 represents the tepuian meadows, PC2 the Myrica forests and PC3 the Chimantaea shrublands. In this way, the trends of Fig. 6 may be considered a graphical representation of the dynamics of these three vegetation types during the last ~8000 cal yr BP, in the coring site.

3.4. Charcoal

Virtually all charcoal particles were smaller than 100 μm, most of them were below 50 μm. The stratigraphic distribution of these particles showed a pattern consistent with pollen zonation (Fig. 6). Charcoal particles increased in Zone APK1 peaking at the boundary with APK2 (ca. 5340 cal yr BP), where they started to decrease. The charcoal peak coincided with the decline of Myrica forests and the expansion of tepuian meadows. Slightly above the boundary between zones APK2 and APK3, charcoal particles experienced a sudden increase (ca. 2540 cal yr BP) and a further rapid decrease (ca. 2290 cal yr BP) coinciding with the same trend in Chimantaea shrublands. A third smaller charcoal peak occurred during the last centuries (AD 1700-1800) does not coincide with any relevant vegetation shift in the Apakará summit.
4. Discussion and conclusions

The vegetation of the Apakará coring site and surroundings has experienced two successive replacements, from a *Myrica* forest close to a shallow lake to tepuian meadows in non-flooded environments and, finally, a *Chimantaea* shrubland, which is the vegetation that grows in the area nowadays. The potential drivers of this ecological dynamics are discussed in this section, with emphasis on climate changes, fire and local ontogenetic features. Climate changes should be derived from evidence independent of pollen and spores, in order to avoid circularity. Unfortunately, no physico-chemical proxies are available for core PATAM9 A07. The same is true for most of the cores obtained to date atop the tepuis (Nogué et al., 2009a; Rull et al., 2010; Safont et al., 2016). Therefore, we will compare the vegetation dynamics of the Apakará summit with the Holocene climatic trends as reconstructed from the Cariaco Basin records, at the north of the GH (Fig. 1A), which have been considered to represent regional trends across northern South America, mostly in terms of temperature and precipitation (Haug et al., 2001; Rull et al., 2010). It should be noted that the current knowledge on the GH climatic history and their forcing factors is still insufficient to establish reliable cause-effect relationships between past climatic changes and vegetation shifts. The conservative approach used here is to highlight the chronological coincidences between past climatic and vegetation shifts, especially in the intervals of conspicuous vegetation change (i.e., the boundaries between pollen zones). We propose some potential climate-vegetation relationships as working hypotheses, in the hope that future studies will confirm, or not, the existence of causal links and will eventually reveal the involved processes and mechanisms. The same is true for fire and autogenic successional processes.

The Apakará record started during the Holocene Thermal Maximum (HTM), a global event occurred between ca. 9 and 6 cal ka BP as the culmination of the, also global, Early Holocene Warming (EHW) (Renssen et al., 2012). During those times, the component representing *Myrica* forests (PC2) experienced an increase until its maximum, which was attained at the end
of the HTM (Fig. 7). The tepuian meadows, represented by PC1, underwent an inverse trend.

During the HTM, climates in northern South America attained maximum temperature and moisture values (Haug et al., 2001) (Fig. 7). The situation changed drastically shortly after the HTM, when PC2 started a sustained decline until minimum scores at ca. 4 ka BP and PC2 increased until its maximum by the same date. This replacement of Myrica forests by tepuian meadows coincided with a cooling and drying trend, suggesting that these vegetation types might be sensitive to temperature and precipitation changes. The only species of Myrica present in the Guayana region is M. rotundata, which grows on the forested slopes of the Chimantá massif and in some Bonnetia forests between 1900 and 2200 m elevation (Miller, 2001). This species was not found around the coring site probably because its elevation (2170 m) is very close to its current upper distribution boundary of the species. It is possible that, during the HTM, warmer and wetter climates would have favored upslope migration of Myrica forests to higher elevations, which could explain their dominance around the coring site. The ensuing post-HTM cooling would have returned Myrica to lower elevations favoring the local expansion of meadows. HTM climatic conditions never recovered during the Holocene and Myrica remained at lower elevations until today. There are no records of this age from other tepuian summits at similar elevations for comparison, neither in the Chimantá massif nor in any other tepuian district. In the Guaiquinima summit, situated ~150 km W-NW, the interval 8-4.5 cal ka BP was characterized by Stegolepis meadows of a different composition to the present ones (Rull, 2005b). But this record was obtained at 1350 m elevation, where environmental and ecological conditions, as well as floristic features, are very different from the Chimantá summits and are not comparable.

A phase of increased precipitation variability was recorded between ca. 4 and 2.5 cal ka BP that was attributed to a general intensification of the ENSO (El Niño-Southern Oscillation) variability across northern South America (Haug et al., 2001) (Fig. 7). Tepuian meadows (PC1) dominated until the middle of this phase (ca. 3 cal ka BP), when they started to decrease at the same time that Chimantaea shrublands (PC3) underwent a gentle increase that became abrupt
since ca. 2.5 cal ka BP. The maximum of these shrublands was recorded at the end of the phase of precipitation variability and was followed by an equally abrupt decline after barely ~300 years. In general, the vegetation seems not to have been affected significantly by the regional precipitation variability until the end of this phase, which supports the hypothesis that the extremely high humidity of the GH would have acted as a climatic buffer. The sudden response of the vegetation close to the end of this unstable climatic phase is noteworthy but the evidence is still insufficient for a sound interpretation. The subsequent climatic stabilization returned the vegetation to former conditions. Unfortunately, the lack of studies on the ecological requirements of the taxa and vegetation types involved prevents sound interpretations in this sense. The last climatic shift recorded during the Holocene, i.e. the cooler-drier phase corresponding to the Little Ice Age (LIA), did not show evident effects on the Apakará vegetation, but this could be due to the lack of resolution to resolve this phase properly.

Millennial-scale Middle to Late Holocene records are available for other summits of the Chimantá massif (Acopán, Amurí, Churí, Eruoda and Toronó) (Fig. 1B). Some of these summits (Acopán and Amurí) did not show significant changes in vegetation likely due to the insensitivity of coring sites (Rull 2005c). In Eruoda, proxies independent of pollen (peat accumulation rates, algae remains) suggested a phase of drier conditions between 4 and 2.7 cal ka BP, coinciding with the intensification of the ENSO activity reported in Cariaco (Nogué et al., 2009a) and also with the onset of a lowstand phase in Lake Valencia, which was related to a shift in the mean position of the Intertropical Convergence Zone (ITCZ) (Curtis et al., 1999). In spite of these environmental shifts, the vegetation of the Euroda summit remained unchanged, possibly due to the low intensity of change or to the buffering capacity of the hyper-humid tepuian climates, or both (Nogué et al., 2009a). In Churí, a phase slightly colder than today was suggested to have occurred before 2.5 cal ka BP, when a shift towards climates similar to today or possibly warmer established (Rull, 2004b). This coincided with the expansion of gallery forests in other tepuis, as for example the Amurí (Rull, 2005c), and an increase in available moisture observed in some lakes of the surroundings Gran Sabana uplands (Rull, 1992), coeval
with the end of the Cariaco unstable phase (Fig. 7). Therefore, a general, albeit low, increase in both temperature and precipitation was suggested by ca. 2.5 cal ka BP, which roughly coincided with the Apakará vegetation change that occurred between zones APK II and APK III. The whole picture indicates that the main Holocene vegetation trends of the Apakará summit coincided with the main climatic trends of northern South America, at the resolution used in this study. A causal relationship remains to be demonstrated but, with the available knowledge, it would be reasonable to accept that regional Holocene climatic shifts may have affected the Apakará summit vegetation.

The coincidence of some vegetation changes with charcoal trends (Fig. 6) might suggest some influence of fire on ecological shifts. However, the occurrence of fires on tepuian summits is a controversial matter. Based on the occurrence of some plant traits interpreted as possible adaptations to fire, Givnish et al. (1986) suggested that fires might be a regular feature on tepuian summits. However, field observations do not support such hypothesis. Huber (1995d) summarized these observations and concluded that signs of past fires have been observed only in 10 tepuis, including the Amurí summit of the Chimantá massif (Fig. 1B). Most of these fires were set in the surrounding lowlands and reached the summits by their slopes (e.g. Mayr and Phelps, 1967; Safont et al., 2016). Natural fires lighted on the tepui summits have not been observed to date and only four summits show signs of recent burning, likely of human origin and of accidental nature (Huber, 1995d). Nogué et al. (2009a) reported the occurrence of a background signal of small charcoal particles atop the neighbor Eruoda summit (Chimantá massif) (Fig. 1B) since the Middle Holocene with a conspicuous peak at ~4000 cal yr BP. Due to the small size of the particles (<100 μm), this charcoal was considered to have originated from fires in the surrounding Gran Sabana uplands and transported to the Eruoda summit by upward winds. In the case of the Apakará discussed here, the particles were of similar size and possibly of the same origin. Previous studies in the Gran Sabana showed that particles originating from local fires were larger than 100 μm and those below this size originated from regional fires (Rull, 1999; Leal et al., 2013). In the Apakará, most particles are even smaller.
(<50 μm), hence, the hypothesis of charcoal particles originating from regional Gran Sabana fires is the most likely. The amount of charcoal also favors an allochthonous source, as local fires usually produce particle concentrations some orders of magnitude higher than those recorded at the Apakará coring site (Montoya and Rull, 2011). Whether these fires were natural or anthropogenic cannot be deduced from our data but previous studies suggested that anthropogenic Gran Sabana paleofires were scarce during the middle Holocene (Montoya and Rull, 2011; Rull et al., 2015). Therefore, the two charcoal peaks documented here, centered at ca. 5340 and 2400 cal yr BP, were probably of natural origin. Savanna wildfires are usually associated to climatic dryness, which drives positive feedbacks and exacerbates burning (Jacobs et al., 1999; Beerling and Osborne, 2006). Therefore, it would be interesting to compare fire incidence with climatic trends. The first charcoal increase occurred at ca. 6000 cal yr BP, at the end of the HTM, when regional precipitation was decreasing (Fig. 7). The first charcoal peak was coeval with a precipitation minimum which occurred near 5000 cal yr BP. The second significant charcoal increase was recorded at the end of the phase of ENSO intensification coinciding with an outstanding precipitation decrease at ca. 2500 cal yr BP. Interestingly, these two charcoal peaks roughly coincide with general peaks of biomass burning reported all over the tropics (Marlon et al., 2016) suggesting that they might be the reflection of some supra-regional phenomenon. Such phenomenon should not be necessarily climatic but could be linked to fuel availability -that is, to biomass production- and/or increased flammability (Marlon et al., 2008). A third charcoal peak was documented during the LIA, when precipitation also experienced a significant decline. Therefore, it is possible that the Gran Sabana fires that produced the charcoal recovered in the Apakará coring site were linked to regional dry climatic phases.

However, our results are not incompatible with eventual Holocene fires in the tepuian summits for several reasons. First, the small size of charcoal particles indicates that fire did not affect the coring area, but the potential occurrence of fires in other summit areas cannot be dismissed. Second, there is no evidence of significant fire events in the Gran Sabana during the middle
Holocene that could have been the source for the particles recovered on the Eruoda and the Apakará summits. Third, if the charcoal recorded on the Apakará and the Eruoda summits was originated from the Gran Sabana, it would be expected that charcoal peaks of these tepuis coincided, as both tepuian summits are situated NW of the Gran Sabana (Fig. 1B) and, hence, under the influence of the same wind patterns. However, charcoal peaks do not coincide. Indeed, the only significant charcoal acme recorded on the Eruoda summit took place at ca. 4000 cal yr BP, when a minimum in charcoal concentration was recorded in Apakará (Fig. 7). The small charcoal peak corresponding to the LIA was recorded in both the Eruoda and the Apakará summits, as well as in most Gran Sabana records, thus appearing as a regional phenomenon, which seems to be linked to both climate and humans and their corresponding feedbacks (Rull et al., 2013).

Besides external environmental and anthropogenic drivers, the vegetation sequence observed in the Apakará summit would be explained, at least in part, by local ontogenetic processes leading to an autogenic ecological succession. The shift from an aquatic environment (zone APK I) to a peatland (zones APK II and III) might be interpreted in terms of lake infilling leading to vegetation changes by progressive edaphic modifications. However, the ensuing vegetation changes are difficult to explain with the available knowledge. The study of ecological successions on the tepuian summits is still in its infancy and any assessment would be speculative. A first attempt in this sense was done by Vareschi (1992), who proposed that the succession proceeded from the first phases of colonization of rock outcrops by algae and lichens to the “climacic” Bonnetia forests. However, this author based his conclusions on a few field observations and unwarranted comparisons with the Andean highland vegetation, under a Clementsian perspective. In the present state of knowledge, we cannot dismiss a potential influence of autogenic processes, at least for the basal part of the sequence, on the Apakará vegetation record, but more detailed and systematic studies of higher resolution are needed for a proper assessment.
The significant vegetation changes recorded in this paper and their potential relationship with local and regional environmental drivers reinforces the idea that the GH summits have been subjected to relevant ecological changes during the Holocene and the vegetation constancy documented in some summits could be due to the inability of these sites to record ecological shifts by pollen analysis (Rull, 2005b,c; 2015). Elevation seems to be a critical factor as most sites showing vegetation constancy were located around the center of the altitudinal range of the vegetation type where they lie, whereas sites exhibiting significant ecological shifts were close to the altitudinal ecotone between two different vegetation types. Therefore, the better suited sites for paleoecological study atop the tepuis are those situated close to altitudinal ecotones, as they are more sensitive to eventual vertical vegetation shifts driven by environmental changes (Rull et al., 2011; Rull, 2015).

This paper represents a new contribution to the Latin American Pollen Database (LAPD), which has been recently improved and updated (Flantua et al., 2015, 2016a, b) to optimize continental paleoenvironmental reconstructions. Also, charcoal data could contribute to fill a geographical gap in the charcoal database for the South American tropics. The present interest in global paleoclimatic and fire reconstructions and the ensuing biotic responses demands not only improved modelling techniques, but also more raw data from specific regions where the existing studies are still insufficient, as is the case of South America and Australia (Harrison et al., 2016).

Acknowledgements

This research was funded by the Spanish Ministry of Science and Innovation (projects CGL2006-00974/BOS and CGL2009-07069/BOS) and the Banco de Vizcaya Argentaria Foundation (project BIOCON 2004-90/05). Pollen samples were processed by Arantza Lara. English grammar was reviewed by Hayley F. Keen.
References


biomass burning from sediment-charcoal records to improve data-model comparisons.

Biogeosciences 13, 3225-3244.


Poveda, G., Waylen, P.R., Pulwarthy, R.S., 2006. Annual and inter-annual variability of the present climate in northern South America and southern South America. Palaeogeogr.

Palaeoclimatol. Palaeoecol. 234, 3-27.


Table 1. Main plant species present around the Apakará coring site (according to O. Huber, in Rull et al., 2011). T = Tree, S = Shrub, H = Herb, M = Moss.

<table>
<thead>
<tr>
<th>Vegetation</th>
<th>Species</th>
<th>Family</th>
<th>Habit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paramoid shrubland</td>
<td>Chimantaea mirabilis</td>
<td>Asteraceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Notopora cardonae</td>
<td>Ericaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Mycerinus chimantensis</td>
<td>Ericaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Tepuia venusta</td>
<td>Ericaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Weinmannia laxiramea</td>
<td>Cunoniaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Rhamnus chimantensis</td>
<td>Rhamnaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Ilex retusa</td>
<td>Aquifoliaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Drymis roraimensis</td>
<td>Winteraceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Cyrilla racemiflora</td>
<td>Cyrilliaceae</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Myriocladus steyermarkii</td>
<td>Poaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Lindmannia sp</td>
<td>Bromeliaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Everardia angusta</td>
<td>Cyperaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Heliamphora minor</td>
<td>Sarraceniaceae</td>
<td>H</td>
</tr>
<tr>
<td>Meadows</td>
<td>Panicum eligulatum</td>
<td>Poaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Stegolepis ligulata</td>
<td>Rapateaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Xyris frondosa</td>
<td>Xyridaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Everardia angusta</td>
<td>Cyperaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Rhondonanthus acopaensis</td>
<td>Eriocaulaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Paepalanthus chimantensis</td>
<td>Eriocaulaceae</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>Sphagnnum sp</td>
<td>Sphagnaceae</td>
<td>M</td>
</tr>
<tr>
<td>Gallery forests</td>
<td>Schefflera cf. clavigera</td>
<td>Araliaceae</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>Cyrilla racemiflora</td>
<td>Cyrilliaceae</td>
<td>T/S</td>
</tr>
<tr>
<td></td>
<td>Drymis winteri</td>
<td>Winteraceae</td>
<td>T/S</td>
</tr>
<tr>
<td></td>
<td>Weinmannia laraximea</td>
<td>Cunoniaceae</td>
<td>T/S</td>
</tr>
<tr>
<td></td>
<td>Podocarpus bucholzii</td>
<td>Podocarpaceae</td>
<td>T</td>
</tr>
<tr>
<td>Species</td>
<td>Family</td>
<td>Location</td>
<td>Note</td>
</tr>
<tr>
<td>----------------------</td>
<td>-------------------</td>
<td>-------------</td>
<td>------</td>
</tr>
<tr>
<td><em>Gaiadendron punctatum</em></td>
<td>Loranthaceae</td>
<td>Rock outcrops</td>
<td>S</td>
</tr>
<tr>
<td><em>Mallophyton chimantense</em></td>
<td>Melastomataceae</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td><em>Adenanthe bicarpellata</em></td>
<td>Ochnaceae</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td><em>Bonnetia roraimae</em></td>
<td>Bonnetiaceae</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td><em>Quelchia bracteata</em></td>
<td>Asteraceae</td>
<td></td>
<td>S</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth (cm)</th>
<th>Lab code</th>
<th>Material</th>
<th>^{14}C a BP</th>
<th>Cal yr BP (2 millennia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PATAM9_A07/10</td>
<td>18-20</td>
<td>Beta-242284</td>
<td>Plant macrofossils</td>
<td>250 ± 40</td>
<td>267-333</td>
</tr>
<tr>
<td>PATAM9_A07/22</td>
<td>42-44</td>
<td>Beta-269200</td>
<td>Plant macrofossils</td>
<td>2070 ± 40</td>
<td>1942-2143</td>
</tr>
<tr>
<td>PATAM9_A07/35</td>
<td>68-70</td>
<td>Beta-242285</td>
<td>Plant macrofossils</td>
<td>2850 ± 40</td>
<td>2854-3076</td>
</tr>
<tr>
<td>PATAM9_A07/50</td>
<td>98-100</td>
<td>Beta-269201</td>
<td>Plant macrofossils</td>
<td>3680 ± 40</td>
<td>3897-4096</td>
</tr>
<tr>
<td>PATAM9_A07/66</td>
<td>130-132</td>
<td>Beta-242286</td>
<td>Plant macrofossils</td>
<td>4900 ± 40</td>
<td>5587-5715</td>
</tr>
<tr>
<td>PATAM9_A07/88</td>
<td>174-176</td>
<td>Beta-242287</td>
<td>Plant macrofossils</td>
<td>5310 ± 40</td>
<td>5989-6206</td>
</tr>
<tr>
<td>PATAM9_A07/93</td>
<td>184-186</td>
<td>Beta-262202</td>
<td>Plant macrofossils</td>
<td>5410 ± 40</td>
<td>6175-6296</td>
</tr>
<tr>
<td>PATAM9_A07/97</td>
<td>192</td>
<td>Beta-277187</td>
<td>Plant macrofossils</td>
<td>5770 ± 40</td>
<td>6474-6665</td>
</tr>
<tr>
<td>PATAM9_A07/100</td>
<td>198</td>
<td>UCI-37505</td>
<td>Plant macrofossils</td>
<td>7765 ± 15</td>
<td>8517-8592</td>
</tr>
</tbody>
</table>
Table 3. PCA variable loadings and percentage of variance explained for the first three principal components. The more significant loadings are in bold.

<table>
<thead>
<tr>
<th>Pollen taxa</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adenanthe</td>
<td>0.025</td>
<td>-0.019</td>
<td>0.050</td>
</tr>
<tr>
<td>Brocchinia</td>
<td>0.067</td>
<td>-0.051</td>
<td>0.173</td>
</tr>
<tr>
<td>Chimantaea</td>
<td>0.095</td>
<td>-0.008</td>
<td>0.880</td>
</tr>
<tr>
<td>CYPERACEAE</td>
<td>0.217</td>
<td>-0.259</td>
<td>0.167</td>
</tr>
<tr>
<td>Cyrilla</td>
<td>0.318</td>
<td>0.043</td>
<td>-0.160</td>
</tr>
<tr>
<td>ERICACEAE</td>
<td>0.041</td>
<td>0.021</td>
<td>0.107</td>
</tr>
<tr>
<td>Ilex</td>
<td>0.128</td>
<td></td>
<td>0.253</td>
</tr>
<tr>
<td>MELASTOMATAEAE</td>
<td>0.051</td>
<td>0.030</td>
<td>0.071</td>
</tr>
<tr>
<td>Myrica</td>
<td>0.148</td>
<td>0.905</td>
<td>0.004</td>
</tr>
<tr>
<td>Myrsine</td>
<td>0.016</td>
<td>-0.005</td>
<td>0.069</td>
</tr>
<tr>
<td>POACEAE</td>
<td>0.873</td>
<td>-0.132</td>
<td>-0.152</td>
</tr>
<tr>
<td>Podocarpus</td>
<td>0.031</td>
<td>0.093</td>
<td>0.038</td>
</tr>
<tr>
<td>Psychotria</td>
<td>0.031</td>
<td>-0.004</td>
<td>0.037</td>
</tr>
<tr>
<td>Schefflera</td>
<td>0.026</td>
<td>0.023</td>
<td>0.022</td>
</tr>
<tr>
<td>Stegolepis</td>
<td>0.020</td>
<td>-0.004</td>
<td>0.039</td>
</tr>
<tr>
<td>URTICALES</td>
<td>0.011</td>
<td>0.011</td>
<td>0.056</td>
</tr>
<tr>
<td>Weimmannia</td>
<td>0.110</td>
<td>0.052</td>
<td>0.286</td>
</tr>
<tr>
<td>Xyris</td>
<td>0.130</td>
<td>-0.118</td>
<td>-0.023</td>
</tr>
<tr>
<td><strong>Cumulative variance (%)</strong></td>
<td>89.450</td>
<td>95.760</td>
<td>97.374</td>
</tr>
</tbody>
</table>
Figure captions

1. Location maps. A) Sketch-map of northern South America indicating the approximate extension of the Guayana Highlands (GH) (encircled) and the situation of the Chimantá massif (red box). The Guayana Shield is indicated by a gray area. CB = Cariaco Basin, LV = Lake Valencia. B). GoogleEarth image of the Chimantá massif summits (brown areas) indicating the coring site (PATAM9-A07, white star) and the other summits with published paleoecological studies (Ak = Akopán, Am = Amurí, Ch = Churí, Er = Eruoda, To = Toronó). Green areas are slope and lowland rainforests and light-yellow areas represent the savannas of the Gran Sabana (GS) uplands.

2. The Chimantá massif. A) Aerial view of a inner valley of the Chimantá massif with some of its tepuian summits at both sides. B) Aerial view of the center of the massif, close to the Apakará summit, showing the summit vegetation (F = Gallery forests, M = Meadows, R = Rocks outcrops). Photos: V. Rull.

3. General view of the paramoid shrubland of the Apakará summit, close to the coring site, with the columnar rosettes of Chimantaea mirabilis, which can attain >3 m high. Photo: V. Rull.

4. Best-fit (linear interpolation) age-depth model for core PATAM9-A07 using all dates from Table 1. The gray band around the interpolated line represents the 95% confidence interval. Blue numbers close to the curve are accumulation rates in mm/y.

5. Pollen percentage diagram from core PATAM9-A07. Lithology as in Figure 4.

6. PC scores and charcoal concentration.
7. Correlation panel showing the main global and regional Holocene climatic trends (temperature and precipitation) and the results obtained in this paper concerning vegetation shifts (represented by pollen assemblages) and fire incidence (charcoal). The charcoal peak recorded on the Eruoda summit (Nogué et al., 2009) is indicated by an arrow close to the charcoal curve.
Figure 1
Figure 2
Fig. 4
Figure 6
Figure 7