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

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27   **Abstract**

28

29   The Guayana Highlands (GH) are natural laboratories to study the influence of environmental

30   drivers on neotropical ecosystems. The GH summits have been characterized by constant

31   vegetation patterns during the Holocene, except for a few sites close to altitudinal ecotones.

32   Here, we report a new pollen record showing two significant vegetation shifts, from *Myrica*

33   forests to tepuian meadows (5340 cal yr BP) and then to *Chimantaea* shrublands (2720 cal yr

34   BP). These changes are analyzed in terms of potential forcing factors such as regional climate

35   changes, fire and autogenic succession. The first shift occurred shortly after the Holocene

36   Thermal Maximum and the onset of a cooling/drying trend. A charcoal peak was coeval with

37   this change suggesting some potential influence of fire. Autogenic processes related to lake

38   infilling might have also been involved. The second vegetation shift took place during a phase

39   of increased precipitation variability due to a ENSO intensification. The establishment of

40   *Chimantaea* shrublands started at the end of this phase coinciding with another charcoal peak

41   (2300 cal yr BP). These results support the idea of relevant ecological changes in the GH during

42   the Holocene, the apparent vegetation constancy recorded in other GH summits could be due to

43   site insensitivity.

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45   **Keywords:** Palynology, paleoecology, vegetation history, paleoclimates, Holocene, Neotropics

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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 yrnd 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 yrnd 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

83   definition of the Pantepui biogeographical province, within the Neotropical realm. Pantepui

84   comprises the assemblage of the ~60 flat summits that constitute the GH, with a total surface of

85   ~6000 km^2 and an elevation of 1500 to ~3000 m (Huber, 1994; Berry *et al.*, 1995). Though

86   systematic exploration is far from complete (Huber 1995b), almost 2500 vascular plant species

87   (belonging to 630 genera and around 160 families) have been described, of which 62% are

88   endemic to the Guayana Region, 42% are endemic to the Pantepui province, and around 25%

89   are endemic to a single tepui (Berry and Riina, 2005). Local endemism can reach 60% in some

90   tepuis, which is comparable to most oceanic islands (Rull, 2009). Vegetation types and

91   ecosystems atop the tepuis are also unique, not only as compared to other Guayana landscapes

92   but also in a global context (Huber, 1992, 1995c, 2005, 2006). The GH summits are virtually

93   pristine. No mineral resources to exploit have been found, the soils are not appropriate for

94   agriculture and there are no grasslands suitable for cattle raising. Indigenous people living in the

95   surrounding lowlands and uplands do not visit the tepui summits because they are considered to

96   be sacred and forbidden to humans. Tourism and scientific exploration are the only activities

97   that have been developed on Pantepui, using mainly helicopters as transportation (Gorzula and

98   Huber, 1992; Huber 1995d). There is no tourist infrastructure atop the tepuis to facilitate

99   visitation, which maintains the lack of human impact on the summit. The GH are protected by

100   several designations including national parks and a biosphere reserve (Huber, 1995d). In spite of

101   this, some localized but immediate threats linked to uncontrolled tourism have been identified

102   and should be urgently addressed to prevent their further expansion across the GH (Rull *et al.*,

103   2016).

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105   The biotic uniqueness and pristine nature of the GH summits and their biota make them

106   especially suitable for the study of long-term vegetation dynamics under natural forcing,

107   without the direct influence of human activities. To date, this type of studies has been conducted

108   on a number of tepuian summits, which has allowed the main Holocene vegetation trends to be

109   reconstructed (Rull, 2004b, 2005a, b; Nogué *et al.*, 2009a; Safont *et al.*, 2016). Most of these

110   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

139 Holocene vegetation dynamics atop the tepuis. It should be stressed that this study is not aimed

140 to investigate the response of the Apakará vegetation to regional climatic shifts but to

141 reconstruct the Holocene vegetation dynamics of this summit and discuss the potential drivers

142 involved, especially climatic changes, fire and autogenic successional processes. Climate

143 dynamics is also beyond the scope of this study, which is essentially ecological.

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145 **2. Material and methods**

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147 *2.1. Study site*

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149 The Apakará summit is part of the Chimantá massif, one of the largest tepuian complexes of the

150 GH with a total surface area of >600 km^2 (Figs. 1B and 2A). Like the other table mountains of

151 the Guayana region, the Chimantá massif is formed by the Precambrian quartzites/sandstones of

152 the Roraima Group, overlying the igneous/metamorphic Guayana Shield (Fig. 1A). The flat

153 summits of this massif range from 2200 to 2600 m elevation at their tops (Huber, 1995a). The

154 coring site was located at 5º 19' 22" N and 62º 13' 34" W, at 2170 m elevation. There is no

155 weather station near the site but it is known that, at these elevations, the GH have mesothermic

156 ombrophilous climates with average annual temperatures between 12 and 18 ºC and a total

157 annual precipitation ranging from 2500 to 3500 mm, with low seasonality. Additional moisture

158 is provided by dense mists, which are frequent in these summits. Winds and thunderstorms are

159 also common, especially when the Intertropical Convergence Zone (ITCZ), which seasonal

160 latitudinal displacement controls the seasonal precipitation regime in northern South America, is

161 close to the region (March to November) (Huber, 1995a). Inter-annual climatic variability is

162 controlled by the El Niño Southern Oscillation (ENSO) of 4-year periodicity, in average, which

163 is responsible for the intensification of land-sea temperature contrasts, which strongly affects

164 the evolution of trade winds and the intensity and distribution of precipitation (Poveda et al.,

165 2006). A common sequel is the occurrence of wetter or drier than average rainy seasons.

166

167   The vegetation of the Chimantá massif has been subdivided into four main categories, namely

168   forests, shrublands, meadows and pioneer vegetation. The more characteristic forests are gallery

169   forests dominated by *Bonnetia roraimae* (Bonnetiaceae) growing along water courses (Fig. 2B).

170   Among shrublands, the more representative are the so called "paramoid" shrublands –owing to

171   their physiognomic resemblance with the Andean páramo vegetation- dominated by several

172   species of the endemic genus *Chimantaea* (Asteraceae) (Fig. 3). Broad-leaved meadows

173   dominated by *Stegolepis ligutata* (Rapateaceae), endemic to the Chimantá, are the more

174   extended. Grassy meadows are rare. Pioneer vegetation grows on sandstone outcrops and is

175   composed of a variety of species from other formations, lichens and mosses are also frequent in

176   these rocky environments (Huber, 1992, 1995c). The coring site was in the margin of a large

177   paramoid shrubland (Fig. 3) patch dominated by *Chimantaea mirabilis* (Asteraceae) and the

178   bambusoid grass *Myriocladus steyermarkii*, surrounded by meadows, with gallery forests along

179   the nearby river and scattered shrub stands on sandstone outcrops (Rull *et al.*, 2011). The more

180   relevant components of the paramoid shrubland and the surrounding vegetation are listed in

181   Table 1. The site is close to the upper limit of the tepuian meadows dominated by *Stegolepis*

182   *ligulata*, which is around 2200-2300 m (Huber, 1992). The *Chimantaea mirabilis* shrublands

183   occur between 1900 and 2500 m elevation (Huber, 1995c; Pruski, 1997).

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185   *2.2. Methods*

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187   The peat core analyzed in this paper (PATAM9-A07; 2 m depth) was obtained with a Russian

188   corer in February 2007. Radiocarbon dating of nine plant macrofossil samples was conducted

189   by Beta Analytic and the Kek Carbon facility of the University of California (Table 2). The age-

190   depth model was performed with clam.R, version 2.2 (Blaauw, 2010), using the calibration of

191   Reimer *et al.* (2013). Samples for pollen analysis were processed using standard methods

192   including KOH, HCl and HF digestions, acetolysis and mounting/storing in silicone oil (Bennett

193   and Willis, 2001). *Lycopodium* tablets (batch nº 177745; 18,584 spores/tablet) were added

194   before chemical processing. Counting was conducted until a minimum of 300 pollen and spores

195   and the saturation of diversity (Rull, 1987). The pollen sum included all pollen types with the

196   exception of aquatic plants (Alismataceae, Onagraceae). Identification was based on local

197   pollen and spore morphological studies (Salgado-Labouriau and Villar, 1992; Rull, 2003; Leal

198   *et al.*, 2011; López-Martínez *et al.*, 2010) and other regional floras and atlases (e.g. Roubick

199   and Moreno, 1991; Tryon and Lugardon, 1991; Colinvaux *et al.*, 1999; Bush and Weng, 2006).

200   Charcoal particles were identified and counted in the same palynological samples, only particles

201   >5μm were considered. Pollen diagrams were plotted and zoned with psimpoll 4.27 using the

202   Optimal Splitting by Information Content (OSIC) method (Bennett, 1996). Statistical yrnalyses

203   were performed with MVSP 3.22. The interpretation of the pollen diagram in terms of

204   vegetation succession was based on previous studies of modern pollen sedimentation in relation

205   to the vegetation types (Rull, 2005c).

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207   **3. Results**

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209   *3.1. Lithology and age-depth model*

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211   Lithologically, core PATAM09-A07 was composed mainly of dark-brown peat, except for two

212   layers (190-200 cm and 140-145 cm) of clayey peat and a layer (170-190 cm) of gyttja (Fig. 4).

213   Regarding chronology, the best fit (GOF = 14.09) was obtained with a linear interpolation

214   model (Fig. 4). According to this model, the core encompasses the last ~8500 years (8556 to

215   268 cal yr BP). The base of the section exhibits extremely low accumulation rates (0.030 mm a^-

216   ^{1}) coinciding with the basal clayey peat. The change to gyttja was accompanied by a huge

217   increase in accumulation rates, which increased by >30 times starting slightly before 6000 cal yr

218   BP. This situation lasted until about 5800 cal yr BP, when accumulation rates declined to

219   moderate levels (0.209 mm a^{-1}).

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223   *3.2. Pollen zones and vegetation succession*

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225   A total of 97 pollen and spore types were identified, excluding those which were unidentifiable

226   owing to mechanical deformation or bad preservation (unknown). Types above 0.2% were

227   depicted in the percentage diagram individually whereas the others (<0.2%) were included in

228   the category called "other dicots", in the case of pollen, and "other pteridophytes", in the case of

229   spores (Fig. 5). The OSIC method provided a subdivision of the pollen diagram into three

230   significant zones:

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232   Pollen Zone APK I (197-125 cm; 8225-5335 cal yr BP; 18 samples). This zone was dominated

233   by *Myrica* and Poaceae, both over 20% of the pollen sum, followed by *Cyrilla* and *Ilex* (~10%

234   each); less important elements (<5%) are *Weinmannia*, *Podocarpus* and *Chimantaea*. Amongst

235   spores, *Isoëtes* is the more abundant, with percentages over 40% of the pollen sum, and other

236   characteristic components (~5%) are *Lycopodiella cernua*, *Pterozonium* and *Cyathea (psilate)*.

237   A modern analog for this pollen assemblage has not been found in previous studies on any

238   tepuian summit (Rull, 2005c; Rull *et al.*, 2013; Safont *et al.*, 2016). The main difference with

239   modern assemblages is the abundance of *Myrica*, which is absent in today's vegetation and also

240   in modern pollen assemblages from the coring site and surroundings. The high abundance of

241   *Isoëtes* spores is also unparalleled in studies developed so far in the tepuian summits. In the

242   Chimantá massif, this genus is represented by *Isoëtes killippi*, growing in flooded sites such as

243   pools, streams and waterfalls, from 1900 to 2800 m elevation (Huber, 1992). The whole picture

244   suggests the occurrence of a *Myrica* forest in a swampy/marshy environment, which contrasts

245   with all present-day vegetation types found around the coring site. The presence of gyttja and

246   clay layers (Fig. 4) supports this interpretation and suggests the occurrence of a shallow water

247   body.

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249   Pollen Zone APK II (125-62 cm; 5335-2720 cal yr BP; 17 samples). A dramatic reduction of

250   *Myrica* and *Isoëtes* occurred at the beginning of this zone and these pollen/spore types never

251 recovered their ancient values. *Podocarpus*, *Weinmannia*, *Chimantaea*, *Lycopodiella cernua*

252 and *Pterozonium* also declined. This zone was dominated by herbs, notably Poaceae (~40%),

253 Cyperaceae and *Xyris* (~10% each), with *Cyrilla* as the more abundant shrub (10-20%). These

254 changes suggest a significant vegetation change towards tepuian meadows and *Cyrilla*

255 shrublands in a non-flooded environment. Likely, *Chimantaea* shrublands did not occur around

256 the coring site, as this pollen was very scarce or absent during the whole zone. The replacement

257 of the *Myrica* forests by the tepuian meadows was gradual, starting at ~150 cm (~5830 cal yr

258 BP) and ending at ~115 cm (4830 cal yr BP). Contrarily, the disappearance of the shallow lake,

259 as indicated by the decrease of *Isoëtes*, was more abrupt and occurred around the boundary of

260 zones APK I and APK II (125 cm; 5330 cal yr BP). The boundary between zones APK I and

261 APK II coincided with a relevant drop in accumulation rates and a significant lithological

262 change from clayey sediments to black peat.

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264 <u>Pollen Zone APK III (62-0 cm; 2720-0 cal yr BP; 32 samples).</u> This zone followed the general

265 trends of zone APK II with some difference. The more important is the increase of *Chimantaea*,

266 *Weinmannia* and *Brocchinia*, and the slight decline of *Cyrilla*, Poaceae and Xyris. Pteridophytes

267 were generally low with no significant differences, except for *Hymenophyllum/Trichomanes*.

268 This assemblage is characteristic of the modern *Chimantaea* shrublands (Rull, 2005c), hence,

269 the site was likely covered by this type of vegetation, as it is nowadays, since about 2720 cal yr

270 BP. The significant increase of *Chimantaea* between 57 and 50 cm suggests that these

271 shrublands were denser than present day between 2540 and 2290 cal yr BP. The nearby forests

272 were composed mainly of *Weinmannia* and *Cyrilla*, as it occurs today. The increase of

273 *Hymenophyllum/Trichomanes*, two genera of lithophilous ferns (Huber, 1992), indicates that the

274 pioneer vegetation of rocky outcrops was developed to a greater degree. As in the former zone,

275 there were no signs of flooding, although the increase of *Brocchinia* and the nature of sediments

276 suggest the occurrence of tepuian peat bogs where this tubular Bromeliaceae is characteristic

277 (Huber, 1992, 1995c).

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279   *3.3. Statistical yrnalysis*

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281   Pollen trends were analyzed in a more synthetic manner using Principal Component Analysis

282   (PCA). The first three components explained >97% of the total variance (Table 3). PC1 is

283   heavily influenced by Poaceae, PC2 by *Myrica* and PC3 by *Chimantaea*, which implies that

284   these three taxa are the most responsible for the variance of the whole data set. Other important,

285   though less relevant, associations are with Cyperaceae and *Cyrilla* (PC1), *Ilex* (PC2) and

286   *Brocchinia* (PC3). The stratigraphic arrangement of these three PC is shown in Fig. 6, where it

287   can be realized that PC1 maximized at Zone APK II, PC2 defines Zone APK I and PC3

288   characterizes Zone APK III. According to the interpretation of the pollen zones, PC1 represents

289   the tepuian meadows, PC2 the *Myrica* forests and PC3 the *Chimantaea* shrublands. In this way,

290   the trends of Fig. 6 may be considered a graphical representation of the dynamics of these three

291   vegetation types during the last ~8000 cal yr BP, in the coring site.

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293   *3.4. Charcoal*

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295   Virtually all charcoal particles were smaller than 100 μm, most of them were below 50 μm. The

296   stratigraphic distribution of these particles showed a pattern consistent with pollen zonation

297   (Fig. 6). Charcoal particles increased in Zone APK1 peacking at the boundary with APK2 (ca.

298   5340 cal yr BP), where they started to decrease. The charcoal peak coincided with the decline of

299   *Myrica* forests and the expansion of tepuian meadows. Slightly above the boundary between

300   zones APK2 and APK3, charcoal particles experienced a sudden increase (ca. 2540 cal yr BP)

301   and a further rapid decrease (ca. 2290 cal yr BP) coinciding with the same trend in *Chimantaea*

302   shrublands. A third smaller charcoal peak occurred during the last centuries (AD 1700-1800)

303   does not coincide with any relevant vegetation shift in the Apakará summit.

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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

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335   of the HTM (Fig. 7). The tepuian meadows, represented by PC1, underwent an inverse trend.

336   During the HTM, climates in northern South America attained maximum temperature and

337   moisture values (Haug *et al.*, 2001) (Fig. 7). The situation changed drastically shortly after the

338   HTM, when PC2 started a sustained decline until minimum scores at ca. 4 ka BP and PC2

339   increased until its maximum by the same date. This replacement of *Myrica* forests by tepuian

340   meadows coincided with a cooling and drying trend, suggesting that these vegetation types

341   might be sensitive to temperature and precipitation changes. The only species of *Myrica* present

342   in the Guayana region is *M. rotundata*, which grows on the forested slopes of the Chimantá

343   massif and in some *Bonnetia* forests between 1900 and 2200 m elevation (Miller, 2001). This

344   species was not found around the coring site probably because its elevation (2170 m) is very

345   close to its current upper distribution boundary of the species. It is possible that, during the

346   HTM, warmer and wetter climates would have favored upslope migration of *Myrica* forests to

347   higher elevations, which could explain their dominance around the coring site. The ensuing

348   post-HTM cooling would have returned *Myrica* to lower elevations favoring the local expansion

349   of meadows. HTM climatic conditions never recovered during the Holocene and *Myrica*

350   remained at lower elevations until today. There are no records of this age from other tepuian

351   summits at similar elevations for comparison, neither in the Chimantá massif nor in any other

352   tepuian district. In the Guaiquinima summit, situated ~150 km W-NW, the interval 8-4.5 cal ka

353   BP was characterized by *Stegolepis* meadows of a different composition to the present ones

354   (Rull, 2005b). But this record was obtained at 1350 m elevation, where environmental and

355   ecological conditions, as well as floristic features, are very different from the Chimantá summits

356   and are not comparable.

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358   A phase of increased precipitation variability was recorded between ca. 4 and 2.5 cal ka BP that

359   was attributed to a general intensification of the ENSO (El Niño-Southern Oscillation)

360   variability across northern South America (Haug *et al.*, 2001) (Fig. 7). Tepuian meadows (PC1)

361   dominated until the middle of this phase (ca. 3 cal ka BP), when they started to decrease at the

362   same time that *Chimantaea* shrublands (PC3) underwent a gentle increase that became abrupt

363 since ca. 2.5 cal ka BP. The maximum of these shrublands was recorded at the end of the phase

364 of precipitation variability and was followed by an equally abrupt decline after barely ~300

365 years. In general, the vegetation seems not to have been affected significantly by the regional

366 precipitation variability until the end of this phase, which supports the hypothesis that the

367 extremely high humidity of the GH would have acted as a climatic buffer. The sudden response

368 of the vegetation close to the end of this unstable climatic phase is noteworthy but the evidence

369 is still insufficient for a sound interpretation. The subsequent climatic stabilization returned the

370 vegetation to former conditions. Unfortunately, the lack of studies on the ecological

371 requirements of the taxa and vegetation types involved prevents sound interpretations in this

372 sense. The last climatic shift recorded during the Holocene, i.e. the cooler-drier phase

373 corresponding to the Little Ice Age (LIA), did not show evident effects on the Apakará

374 vegetation, but this could be due to the lack of resolution to resolve this phase properly.

375

376 Millennial-scale Middle to Late Holocene records are available for other summits of the

377 Chimantá massif (Acopán, Amurí, Churí, Eruoda and Toronó) (Fig. 1B). Some of these

378 summits (Acopán and Amurí) did not show significant changes in vegetation likely due to the

379 insensitivity of coring sites (Rull 2005c). In Eruoda, proxies independent of pollen (peat

380 accumulation rates, algae remains) suggested a phase of drier conditions between 4 and 2.7 cal

381 ka BP, coinciding with the intensification of the ENSO activity reported in Cariaco (Nogué *et*

382 *al.*, 2009a) and also with the onset of a lowstand phase in Lake Valencia, which was related to a

383 shift in the mean position of the Intertropical Convergence Zone (ITCZ) (Curtis *et al.*, 1999). In

384 spite of these environmental shifts, the vegetation of the Euroda summit remained unchanged,

385 possibly due to the low intensity of change or to the buffering capacity of the hyper-humid

386 tepuian climates, or both (Nogué *et al.*, 2009a). In Churí, a phase slightly colder than today was

387 suggested to have occurred before 2.5 cal ka BP, when a shift towards climates similar to today

388 or possibly warmer established (Rull, 2004b). This coincided with the expansion of gallery

389 forests in other tepuis, as for example the Amurí (Rull, 2005c), and an increase in available

390 moisture observed in some lakes of the surroundings Gran Sabana uplands (Rull, 1992), coeval

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391 with the end of the Cariaco unstable phase (Fig. 7). Therefore, a general, albeit low, increase in

392 both temperature and precipitation was suggested by ca. 2.5 cal ka BP, which roughly coincided

393 with the Apakará vegetation change that occurred between zones APK II and APK III. The

394 whole picture indicates that the main Holocene vegetation trends of the Apakará summit

395 coincided with the main climatic trends of northern South America, at the resolution used in this

396 study. A causal relationship remains to be demonstrated but, with the available knowledge, it

397 would be reasonable to accept that regional Holocene climatic shifts may have affected the

398 Apakará summit vegetation.

399

400 The coincidence of some vegetation changes with charcoal trends (Fig. 6) might suggest some

401 influence of fire on ecological shifts. However, the occurrence of fires on tepuian summits is a

402 controversial matter. Based on the occurrence of some plant traits interpreted as possible

403 adaptations to fire, Givnish *et al.* (1986) suggested that fires might be a regular feature on

404 tepuian summits. However, field observations do not support such hypothesis. Huber (1995d)

405 summarized these observations and concluded that signs of past fires have been observed only

406 in 10 tepuis, including the Amurí summit of the Chimantá massif (Fig. 1B). Most of these fires

407 were set in the surrounding lowlands and reached the summits by their slopes (e.g. Mayr and

408 Phelps, 1967; Safont *et al.*, 2016). Natural fires lighted on the tepui summits have not been

409 observed to date and only four summits show signs of recent burning, likely of human origin

410 and of accidental nature (Huber, 1995d). Nogué *et al.* (2009a) reported the occurrence of a

411 background signal of small charcoal particles atop the neighbor Eruoda summit (Chimantá

412 massif) (Fig. 1B) since the Middle Holocene with a conspicuous peak at ~4000 cal yr BP. Due

413 to the small size of the particles (<100 μm), this charcoal was considered to have originated

414 from fires in the surrounding Gran Sabana uplands and transported to the Eruoda summit by

415 upward winds. In the case of the Apakará discussed here, the particles were of similar size and

416 possibly of the same origin. Previous studies in the Gran Sabana showed that particles

417 originating from local fires were larger than 100 μm and those below this size originated from

418 regional fires (Rull, 1999; Leal *et al.*, 2013). In the Apakará, most particles are even smaller

419 (<50 μm), hence, the hypothesis of charcoal particles originating from regional Gran Sabana

420 fires is the most likely. The amount of charcoal also favors an allochthonous source, as local

421 fires usually produce particle concentrations some orders of magnitude higher than those

422 recorded at the Apakará coring site (Montoya and Rull, 2011). Whether these fires were natural

423 or anthropogenic cannot be deduced from our data but previous studies suggested that

424 anthropogenic Gran Sabana paleofires were scarce during the middle Holocene (Montoya and

425 Rull, 2011; Rull *et al.*, 2015). Therefore, the two charcoal peaks documented here, centered at

426 ca. 5340 and 2400 cal yr BP, were probably of natural origin. Savanna wildfires are usually

427 associated to climatic dryness, which drives positive feedbacks and exacerbates burning (Jacobs

428 *et al.*, 1999; Beerling and Osborne, 2006). Therefore, it would be interesting to compare fire

429 incidence with climatic trends. The first charcoal increase occurred at ca. 6000 cal yr BP, at the

430 end of the HTM, when regional precipitation was decreasing (Fig. 7). The first charcoal peak

431 was coeval with a precipitation minimum which occurred near 5000 cal yr BP. The second

432 significant charcoal increase was recorded at the end of the phase of ENSO intensification

433 coinciding with an outstanding precipitation decrease at ca. 2500 cal yr BP. Interestingly, these

434 two charcoal peaks roughly coincide with general peaks of biomass burning reported all over

435 the tropics (Marlon et al., 2016) suggesting that they might be the reflection of some supra-

436 regional phenomenon. Such phenomenon should not be necessarily climatic but could be linked

437 to fuel availability -that is, to biomass production- and/or increased flammability (Marlon et al.,

438 2008). A third charcoal peak was documented during the LIA, when precipitation also

439 experienced a significant decline. Therefore, it is possible that the Gran Sabana fires that

440 produced the charcoal recovered in the Apakará coring site were linked to regional dry climatic

441 phases.

442

443 However, our results are not incompatible with eventual Holocene fires in the tepuian summits

444 for several reasons. First, the small size of charcoal particles indicates that fire did not affect the

445 coring area, but the potential occurrence of fires in other summit areas cannot be dismissed.

446 Second, there is no evidence of significant fire events in the Gran Sabana during the middle

447   Holocene that could have been the source for the particles recovered on the Eruoda and the

448   Apakará summits. Third, if the charcoal recorded on the Apakará and the Eruoda summits was

449   originated from the Gran Sabana, it would be expected that charcoal peaks of these tepuis

450   coincided, as both tepuian summits are situated NW of the Gran Sabana (Fig. 1B) and, hence,

451   under the influence of the same wind patterns. However, charcoal peaks do not coincide.

452   Indeed, the only significant charcoal acme recorded on the Eruoda summit took place at ca.

453   4000 cal yr BP, when a minimum in charcoal concentration was recorded in Apakará (Fig. 7).

454   The small charcoal peak corresponding to the LIA was recorded in both the Eruoda and the

455   Apakará summits, as well as in most Gran Sabana records, thus appearing as a regional

456   phenomenon, which seems to be linked to both climate and humans and their corresponding

457   feedbacks (Rull *et al.*, 2013).

458

459   Besides external environmental and anthropogenic drivers, the vegetation sequence observed in

460   the Apakará summit would be explained, at least in part, by local ontogenetic processes leading

461   to an autogenic ecological succession. The shift from an aquatic environment (zone APK I) to a

462   peatland (zones APK II and III) might be interpreted in terms of lake infilling leading to

463   vegetation changes by progressive edaphic modifications. However, the ensuing vegetation

464   changes are difficult to explain with the available knowledge. The study of ecological

465   successions on the tepuian summits is still in its infancy and any assessment would be

466   speculative. A first attempt in this sense was done by Vareschi (1992), who proposed that the

467   succession proceeded from the first phases of colonization of rock outcrops by algae and lichens

468   to the "climacic" *Bonnetia* forests. However, this author based his conclusions on a few field

469   observations and unwarranted comparisons with the Andean highland vegetation, under a

470   Clementsian perspective. In the present state of knowledge, we cannot dismiss a potential

471   influence of autogenic processes, at least for the basal part of the sequence, on the Apakará

472   vegetation record, but more detailed and systematic studies of higher resolution are needed for a

473   proper assessment.

474

475   The significant vegetation changes recorded in this paper and their potential relationship with

476   local yrnd regional environmental drivers reinforces the idea that the GH summits have been

477   subjected to relevant ecological changes during the Holocene and the vegetation constancy

478   documented in some summits could be due to the inability of these sites to record ecological

479   shifts by pollen analysis (Rull, 2005b,c; 2015). Elevation seems to be a critical factor as most

480   sites showing vegetation constancy were located around the center of the altitudinal range of the

481   vegetation type where they lie, whereas sites exhibiting significant ecological shifts were close

482   to the altitudinal ecotone between two different vegetation types. Therefore, the better suited

483   sites for paleoecological study atop the tepuis are those situated close to altitudinal ecotones, as

484   they are more sensitive to eventual vertical vegetation shifts driven by environmental changes

485   (Rull et al., 2011; Rull, 2015).

486

487   This paper represents a new contribution to the Latin American Pollen Database (LAPD), which

488   has been recently improved and updated (Flantua *et al.*, 2015, 2016a, b) to optimize continental

489   paleoenvironmental reconstructions. Also, charcoal data could contribute to fill a geographical

490   gap in the charcoal database for the South American tropics. The present interest in global

491   paleoclimatic and fire reconstructions and the ensuing biotic responses demands not only

492   improved modelling techniques, but also more raw data from specific regions where the existing

493   studies are still insufficient, as is the case of South America and Australia (Harrison *et al.*,

494   2016).

495

502

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780   **Table 1.** Main plant species present around the Apakará coring site (according to O. Huber, in

781   Rull *et al.*, 2011). T = Tree, S = Shrub, H = Herb, M = Moss.

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Vegetation	Species	Family	Habit
Paramoid shrubland	*Chimantaea mirabilis*	Asteraceae	S
	Notopora cardonae	Ericaceae	S
	Mycerinus chimantensis	Ericaceae	S
	Tepuia venusta	Ericaceae	S
	Weinmannia laxiramea	Cunoniaceae	S
	Rhamnus chimantensis	Rhamnaceae	S
	Ilex retusa	Aquifoliaceae	S
	Drymis roraimensis	Winteraceae	S
	Cyrilla racemiflora	Cyrillaceae	S
	Myriocladus steyermarkii	Poaceae	H
	Lindmannia sp	Bromeliaceae	H
	Everardia angusta	Cyperaceae	H
	Heliamphora minor	Sarraceniaceae	H
Meadows	*Panicum eligulatum*	Poaceae	H
	Stegolepis ligulata	Rapateaceae	H
	Xyris frondosa	Xyridaceae	H
	Everardia angusta	Cyperaceae	H
	Rhondonanthus acopaensis	Eriocaulaceae	H
	Paepalanthus chimantensis	Eriocaulaceae	H
	Sphagnum sp	Sphagnaceae	M
Gallery forests	*Schefflera* cf. *clavigera*	Araliaceae	T
	Cyrilla racemiflora	Cyrillaceae	T/S
	Drymis winteri	Winteraceae	T/S
	Weinmannia laraximea	Cunoniaceae	T/S
	Podocarpus bucholzii	Podocarpaceae	T

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	Gaiadendron punctatum	Loranthaceae	S
Rock outcrops	Mallophyton chimantense	Melastomataceae	S
	Adenanthe bicarpellata	Ochnaceae	S
	Bonnetia roraimae	Bonnetiaceae	S
	Quelchia bracteata	Asteraceae	S

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804 **Table 2.** AMS radiocarbon dates of core PATAM9-A07. Beta – Beta Analytic Inc., UCI – Kek

805 Crabon Cycle AMS Laboratory (University of California, Irvine). Calibration after Reimer *et*

806 *al.* (2013) using CALIB 7.1.

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Sample	Depth (cm)	Lab code	Material	^{14}C a BP	Cal yr BP (2$\square$)
PATAM9_A07/10	18-20	Beta-242284	Plant macrofossils	250 ± 40	267-333
PATAM9_A07/22	42-44	Beta-269200	Plant macrofossils	2070 ± 40	1942-2143
PATAM9_A07/35	68-70	Beta-242285	Plant macrofossils	2850 ± 40	2854-3076
PATAM9_A07/50	98-100	Beta-269201	Plant macrofossils	3680 ± 40	3897-4096
PATAM9_A07/66	130-132	Beta-242286	Plant macrofossils	4900 ± 40	5587-5715
PATAM9_A07/88	174-176	Beta-242287	Plant macrofossils	5310 ± 40	5989-6206
PATAM9_A07/93	184-186	Beta-262202	Plant macrofossils	5410 ± 40	6175-6296
PATAM9_A07/97	192	Beta-277187	Plant macrofossils	5770 ± 40	6474-6665
PATAM9_A07/100	198	UCI-37505	Plant macrofossils	7765 ± 15	8517-8592

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822   **Table 3.** PCA variable loadings and percentage of variance explained for the first three

823   principal components. The more significant loadings are in bold.

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Pollen taxa	PC1	PC2	PC3
Adenanthe	0.025	-0.019	0.050
Brocchinia	0.067	-0.051	**0.173**
Chimantaea	0.095	-0.008	**0.880**
CYPERACEAE	**0.217**	-0.259	0.167
Cyrilla	**0.318**	0.043	-0.160
ERICACEAE	0.041	0.021	0.107
Ilex	0.128	**0.253**	0.068
MELASTOMATACEAE	0.051	0.030	0.071
Myrica	0.148	**0.905**	0.004
Myrsine	0.016	-0.005	0.069
POACEAE	**0.873**	-0.132	-0.152
Podocarpus	0.031	0.093	0.038
Psychotria	0.031	-0.004	0.037
Schefflera	0.026	0.023	0.022
Stegolepis	0.020	-0.004	0.039
URTICALES	0.011	0.011	0.056
Weinmannia	0.110	0.052	0.286
Xyris	0.130	-0.118	-0.023
Cumulative variance (%)	89.450	95.760	97.374

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Figure captions

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831   **1.** Location maps. A) Sketch-map of northen South America indicating the approximate

832   extension of the Guayana Highlands (GH) (encircled) and the situation of the Chimantá massif

833   (red box). The Guayana Shield is indicated by a gray area. CB = Cariaco Basin, LV = Lake

834   Valencia. B). GoogleEarth image of the Chimantá massif summits (brown areas) indicating the

835   coring site (PATAM9-A07, white star) and the other summits with published paleoecological

836   studies (Ak = Akopán, Am = Amurí, Ch = Churí, Er = Eruoda, To = Toronó). Green areas are

837   slope and lowland rainforests and light-yellow areas represent the savannas of the Gran Sabana

838   (GS) uplands.

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840   **2.** The Chimantá massif. A) Aerial view of a inner valley of the Chimantá massif with some of

841   its tepuian summits at both sides. B) Aerial view of the center of the massif, close to the

842   Apakará summit, showing the summit vegetation (F = Gallery forests, M = Meadows, R =

843   Rocks outcrops). Photos: V. Rull.

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845   **3.** General view of the paramoid shrubland of the Apakará summit, close to the coring site, with

846   the columnar rossettes of *Chimantaea mirabilis*, which can attain >3 m high. Photo: V. Rull.

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848   **4.** Best-fit (linear interpolation) age-depth model for core PATAM9-A07 using all dates from

849   Table 1. The gray band around the interpolated line represents the 95% confidence interval.

850   Blue numbers close to the curve are accumulation rates in mm/y.

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

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854   **6.** PC scores and charcoal concentration.

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856 **7.** Correlation panel showing the main global and regional Holocene climatic trends

857 (temperature and precipitation) and the results obtained in this paper concerning vegetation

858 shifts (represented by pollen assemblages) and fire incidence (charcoal). The charcoal peak

859 recorded on the Eruoda summit (Nogué *et al.*, 2009) is indicated by an arrow close to the
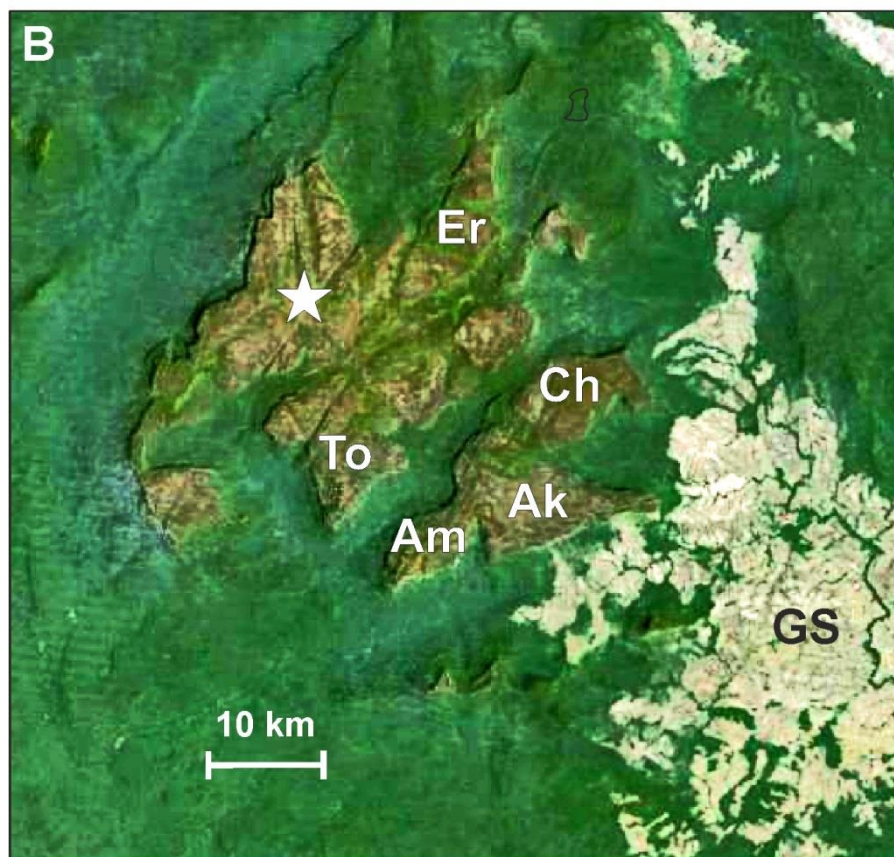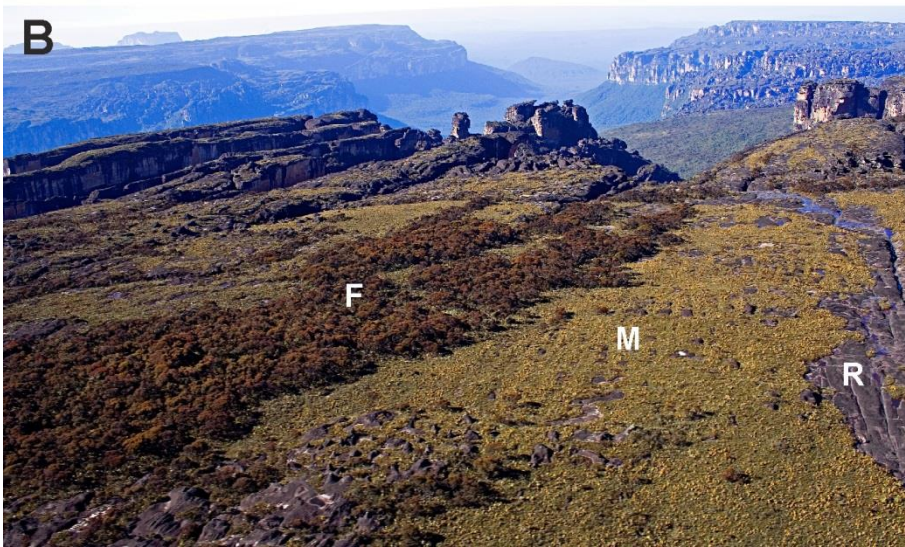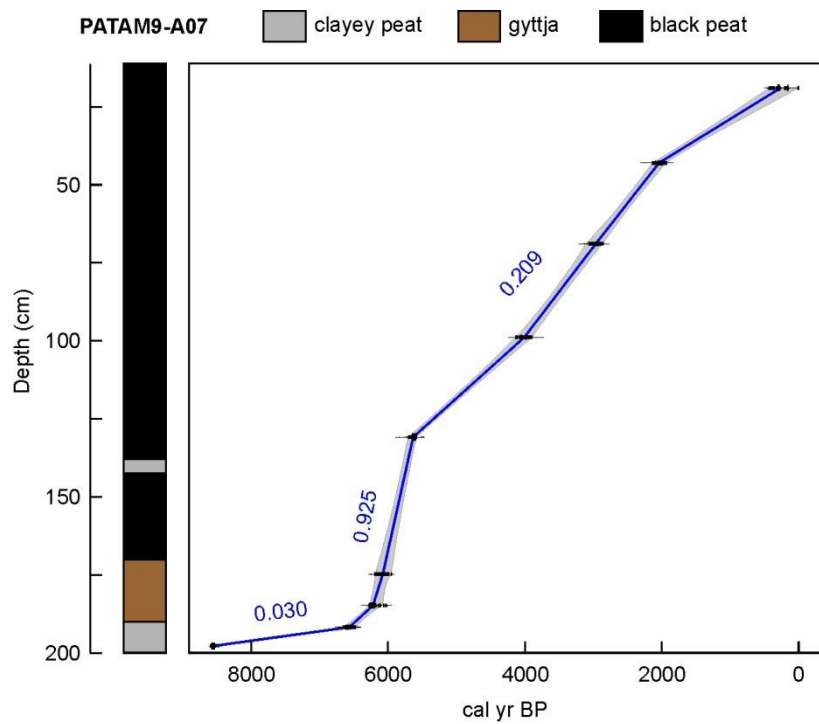
860 charcoal curve.

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957 Figure 7