

1 **Holocene vegetation dynamics on the Apakar summit of the**
2 **neotropical Guayana Highlands and potential environmental**
3 **drivers**

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27 **Abstract**

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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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55 **1. Introduction**

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57 The Guayana Highlands (GH), situated between the Orinoco and the Amazon basins in northern
58 South America (Fig. 1A), have been considered a natural laboratory to study the origin of
59 neotropical biotic patterns in terms of the influencing ecological and evolutionary processes
60 and mechanisms, as well as the environmental drivers involved (Rull, 2010). Relevant general
61 aspects that have been studied since the early 20th century in the GH include (i) the classical
62 biogeographical debate between vicariance and dispersalism, (ii) the chronology, drivers and
63 mechanisms of neotropical diversification, (iii) the relative importance of Neogene vs.
64 Pleistocene speciation and extinction, (iv) the elevational biodiversity gradients and their
65 potential causes, (v) the eventual occurrence of Pleistocene glacial refugia in the tropics, (vi) the
66 robustness of the potential natural vegetation concept (vii) the expected extinction by habitat
67 loss under the effects of global warming or (viii) the more suitable biodiversity conservation
68 strategies, among others (e.g., Chapman, 1931; Tate, 1928, 1938a, b; Mayr and Phelps, 1967;
69 Maguire, 1970; Steyermark, 1979; Huber, 1988; Steyermark and Dunsterville, 1980; Gorzula,
70 1992; Mayr, 1999; Pérez-Hernández and Lew, 2001; Givnish *et al.*, 2000, 2004, 2011; Huber
71 and Foster, 2003; McDiarmid and Donnelly, 2005; Noonan and Gaucher, 2005, 2006; Rull,
72 2004a, 2005a, 2006, 2007, 2008, 2010, 2011a, b, 2015; Rull and Vegas-Vilarrúbia, 2006, 2008;
73 Rull and Nogué, 2007; Hopper, 2009; Nogué *et al.*, 2009a,b, 2013; Bernard *et al.*, 2011;
74 Vegas-Vilarrúbia *et al.*, 2011, 2012; Rull *et al.*, 2009, 2013, 2016; Safont *et al.*, 2012, 2014;
75 Salerno *et al.*, 2012; Leite *et al.*, 2015). In spite of the amount and variety of ecological and
76 evolutionary studies conducted to date in the GH, there are still many questions that remain
77 open and demand more research. In this paper, we focus on a relevant ecological topic as is the
78 long-term vegetation dynamics in relation to the potential external and internal drivers of
79 ecological change.

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81 The flat summits of the table mountains, locally called “tepui”, of the GH hold unique biomes
82 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 km² 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).

104

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

111 them revealed significant vegetation shifts likely linked to climatic changes and fire. The Churí
112 record, from the same massif as the Apakará summit (Fig. 1B), documented a Late Holocene
113 upward displacement of a characteristic ecotone that was interpreted in terms of a gentle
114 warming (Rull, 2004a, b, c). The Uei record is the only case documented so far where
115 anthropogenic fires have likely affected the tepuian vegetation in the past. According to Safont
116 *et al.* (2016), fires which originated in the nearby savanna uplands in the mid-18th century
117 spread to the summit of the Uei and significantly reduced forests and meadows, favoring
118 colonization by invader shrubs.

119

120 The apparent discrepancy between long-term vegetation constancy and change atop the tepuian
121 summits during the Holocene was tentatively explained in terms of climatic change intensity
122 and site sensitivity. On the one hand, it was suggested that the extremely high humidity (over
123 2500 mm per year) of the GH acted as a buffer preventing moderate climate shifts to
124 significantly affect vegetation. On the other hand, it was proposed that coring sites near an
125 altitudinal vegetation ecotone, as is the case of the Churí record, would be better suited to record
126 vegetation changes than those situated within the elevational range of a given formation (Rull,
127 2005b). A preliminary paleoecological study from the Apakará summit seemed to support the
128 hypothesis of site sensitivity (Rull *et al.*, 2011). A significant vegetation shift was recorded
129 around the middle Holocene, which was tentatively linked to the end of the Holocene Thermal
130 Maximum and the incoming of cooler and more unstable climates, in terms of precipitation, as
131 documented in the Cariaco records (Haug *et al.*, 2001) (Fig. 1A). However, this study was of
132 very low resolution (barely one sample per millennium) and it was recommended to increase the
133 resolution by intensifying sampling density.

134

135 Here, we report the results of a multidecadal to centennial-scale study of the same core aimed at
136 (i) reconstructing the detailed long-term ecological dynamics of the Apakará vegetation, (ii)
137 documenting eventual regime shifts and identifying the potential environmental drivers
138 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 Apakar 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*

148

149 The Apakar summit is part of the Chimant massif, one of the largest tepuian complexes of the
150 GH with a total surface area of >600 km² (Figs. 1B and 2A). Like the other table mountains of
151 the Guayana region, the Chimant 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 5° 19' 22" N and 62° 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 °C 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 Nio 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 ligulata* (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).

184

185 2.2. Methods

186

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 n° 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 $>5\mu\text{m}$ 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 analyses
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).

206

207 **3. Results**

208

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^{-1})
216 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:

231

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.

248

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 *Isoetes*, 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.

263

264 Pollen Zone APK III (62-0 cm; 2720-0 cal yr BP; 32 samples). 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).

278

279 3.3. Statistical analysis

280

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.

292

293 3.4. Charcoal

294

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 peaking 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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307 **4. Discussion and conclusions**

308

309 The vegetation of the Apakar coring site and surroundings has experienced two successive
310 replacements, from a *Myrica* forest close to a shallow lake to tepuian meadows in non-flooded
311 environments and, finally, a *Chimantaea* shrubland, which is the vegetation that grows in the
312 area nowadays. The potential drivers of this ecological dynamics are discussed in this section,
313 with emphasis on climate changes, fire and local ontogenetic features. Climate changes should
314 be derived from evidence independent of pollen and spores, in order to avoid circularity.
315 Unfortunately, no physico-chemical proxies are available for core PATAM9 A07. The same is
316 true for most of the cores obtained to date atop the tepuis (Nogu *et al.*, 2009a; Rull *et al.*,
317 2010; Safont *et al.*, 2016). Therefore, we will compare the vegetation dynamics of the Apakar
318 summit with the Holocene climatic trends as reconstructed from the Cariaco Basin records, at
319 the north of the GH (Fig. 1A), which have been considered to represent regional trends across
320 northern South America, mostly in terms of temperature and precipitation (Haug *et al.*, 2001;
321 Rull *et al.*, 2010). It should be noted that the current knowledge on the GH climatic history and
322 their forcing factors is still insufficient to establish reliable cause-effect relationships between
323 past climatic changes and vegetation shifts. The conservative approach used here is to highlight
324 the chronological coincidences between past climatic and vegetation shifts, especially in the
325 intervals of conspicuous vegetation change (i.e., the boundaries between pollen zones). We
326 propose some potential climate-vegetation relationships as working hypotheses, in the hope that
327 future studies will confirm, or not, the existence of causal links and will eventually reveal the
328 involved processes and mechanisms. The same is true for fire and autogenic successional
329 processes.

330

331 The Apakar record started during the Holocene Thermal Maximum (HTM), a global event
332 occurred between ca. 9 and 6 cal ka BP as the culmination of the, also global, Early Holocene
333 Warming (EHW) (Renssen *et al.*, 2012). During those times, the component representing
334 *Myrica* forests (PC2) experienced an increase until its maximum, which was attained at the end

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.

357

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 Apakara
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 Chimanta massif (Acopan, Amurı, Churı, Eruoda and Torono) (Fig. 1B). Some of these
378 summits (Acopan and Amurı) 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 (Nogue *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 (Nogue *et al.*, 2009a). In Churı, 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 Amurı (Rull, 2005c), and an increase in available
390 moisture observed in some lakes of the surroundings Gran Sabana uplands (Rull, 1992), coeval

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 Apakar vegetation change that occurred between zones APK II and APK III. The
394 whole picture indicates that the main Holocene vegetation trends of the Apakar 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 Apakar 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 Amur summit of the Chimant 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). Nogu *et al.* (2009a) reported the occurrence of a
411 background signal of small charcoal particles atop the neighbor Eruoda summit (Chimant
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 Apakar 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 Apakar, 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 Apakar 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 Apakar 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 Apakar summits. Third, if the charcoal recorded on the Apakar 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 Apakar (Fig. 7).
454 The small charcoal peak corresponding to the LIA was recorded in both the Eruoda and the
455 Apakar 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 Apakar 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 Apakar
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

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497

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502

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780 **Table 1.** Main plant species present around the Apakar 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	<i>Chimantaea mirabilis</i>	Asteraceae	S
	<i>Notopora cardonae</i>	Ericaceae	S
	<i>Mycerinus chimantensis</i>	Ericaceae	S
	<i>Tepuia venusta</i>	Ericaceae	S
	<i>Weinmannia laxiramea</i>	Cunoniaceae	S
	<i>Rhamnus chimantensis</i>	Rhamnaceae	S
	<i>Ilex retusa</i>	Aquifoliaceae	S
	<i>Drymis roraimensis</i>	Winteraceae	S
	<i>Cyrilla racemiflora</i>	Cyrillaceae	S
	<i>Myriocladus steyermarkii</i>	Poaceae	H
	<i>Lindmannia</i> sp	Bromeliaceae	H
	<i>Everardia angusta</i>	Cyperaceae	H
	<i>Heliamphora minor</i>	Sarraceniaceae	H
Meadows	<i>Panicum eligulatum</i>	Poaceae	H
	<i>Stegolepis ligulata</i>	Rapateaceae	H
	<i>Xyris frondosa</i>	Xyridaceae	H
	<i>Everardia angusta</i>	Cyperaceae	H
	<i>Rhondonanthus acopaensis</i>	Eriocaulaceae	H
	<i>Paepalanthus chimantensis</i>	Eriocaulaceae	H
	<i>Sphagnum</i> sp	Sphagnaceae	M
Gallery forests	<i>Schefflera cf. clavigera</i>	Araliaceae	T
	<i>Cyrilla racemiflora</i>	Cyrillaceae	T/S
	<i>Drymis winteri</i>	Winteraceae	T/S
	<i>Weinmannia laraximea</i>	Cunoniaceae	T/S
	<i>Podocarpus bucholzii</i>	Podocarpaceae	T

	<i>Gaiadendron punctatum</i>	Loranthaceae	S
Rock outcrops	<i>Mallophyton chimantense</i>	Melastomataceae	S
	<i>Adenanthe bicarpellata</i>	Ochnaceae	S
	<i>Bonnetia roraimae</i>	Bonnetiaceae	S
	<i>Quelchia bracteata</i>	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 (2σ)
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
<i>Adenanthe</i>	0.025	-0.019	0.050
<i>Brocchinia</i>	0.067	-0.051	0.173
<i>Chimantaea</i>	0.095	-0.008	0.880
CYPERACEAE	0.217	-0.259	0.167
<i>Cyrilla</i>	0.318	0.043	-0.160
ERICACEAE	0.041	0.021	0.107
<i>Ilex</i>	0.128	0.253	0.068
MELASTOMATACEAE	0.051	0.030	0.071
<i>Myrica</i>	0.148	0.905	0.004
<i>Myrsine</i>	0.016	-0.005	0.069
POACEAE	0.873	-0.132	-0.152
<i>Podocarpus</i>	0.031	0.093	0.038
<i>Psychotria</i>	0.031	-0.004	0.037
<i>Schefflera</i>	0.026	0.023	0.022
<i>Stegolepis</i>	0.020	-0.004	0.039
URTICALES	0.011	0.011	0.056
<i>Weinmannia</i>	0.110	0.052	0.286
<i>Xyris</i>	0.130	-0.118	-0.023
Cumulative variance (%)	89.450	95.760	97.374

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829 **Figure captions**

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831 **1.** Location maps. A) Sketch-map of northern 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 an 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 rosettes 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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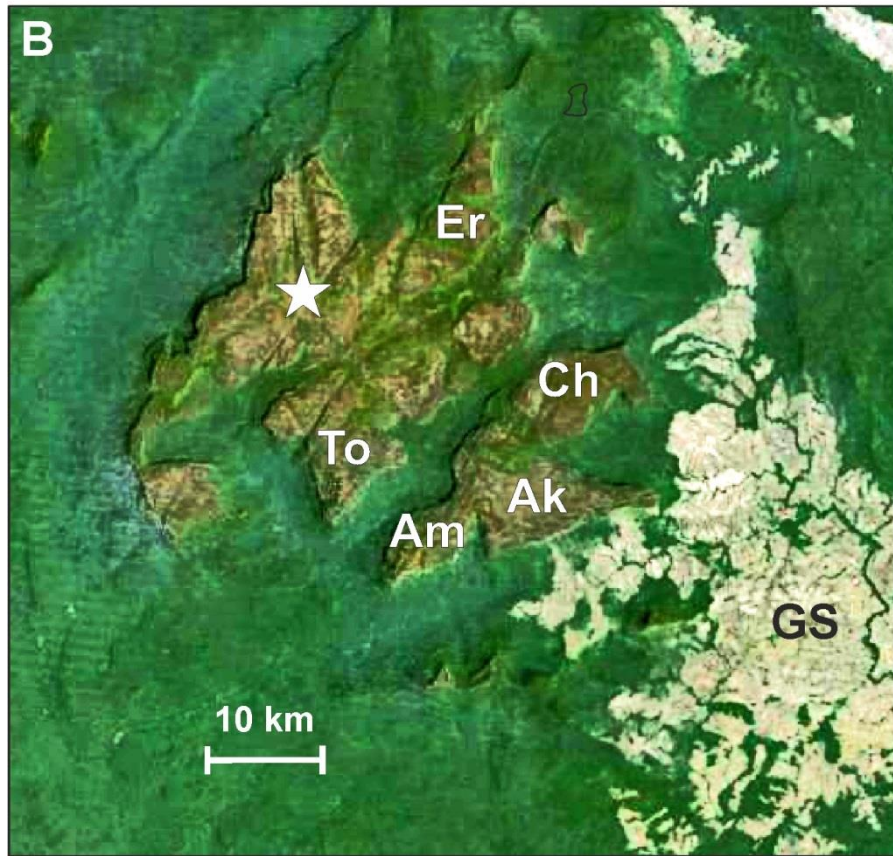
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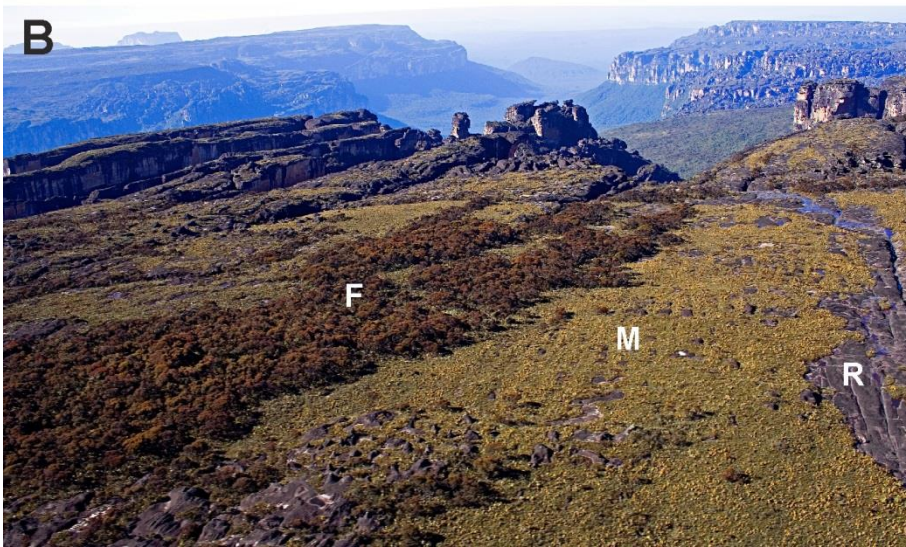
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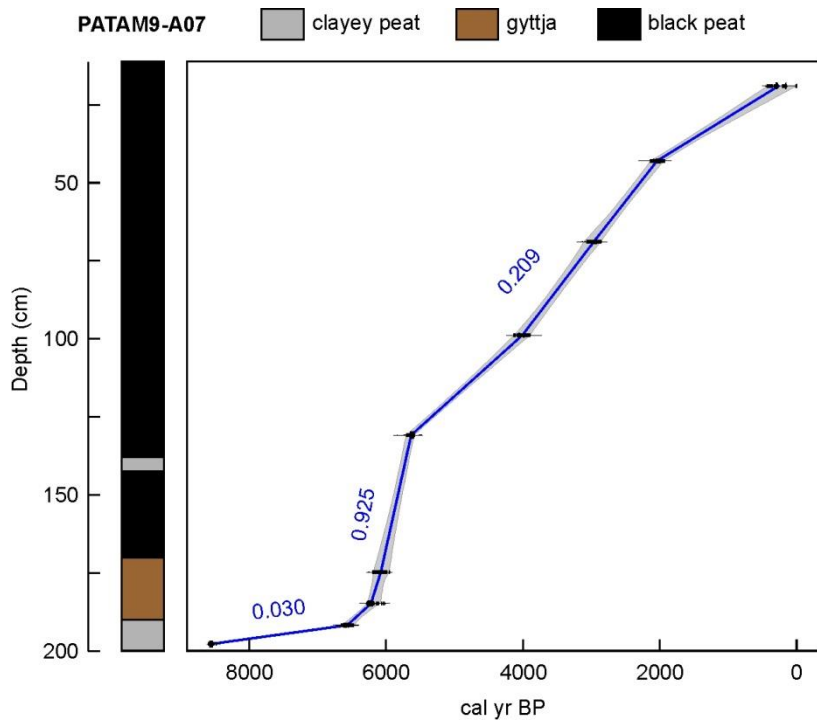
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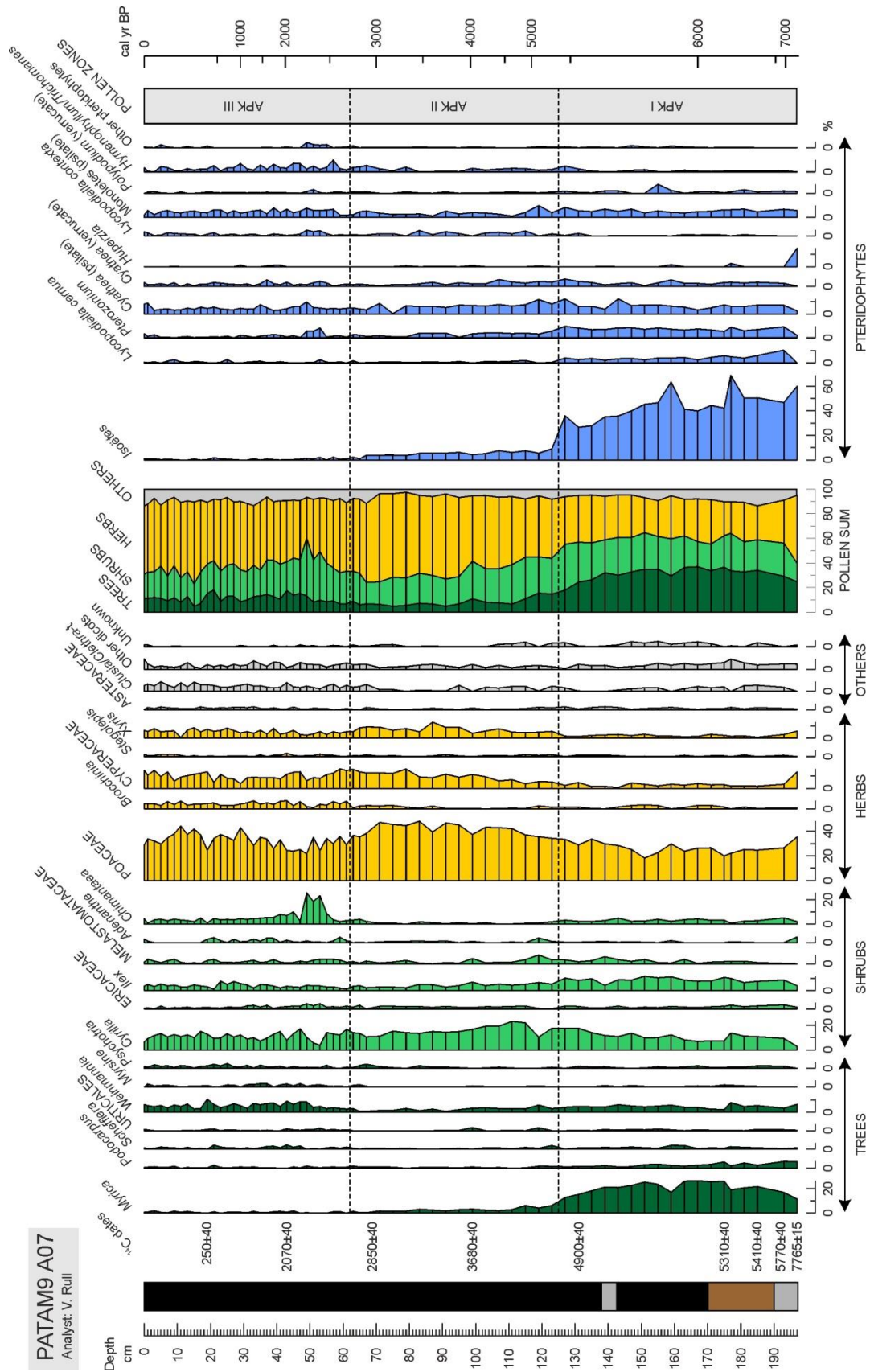
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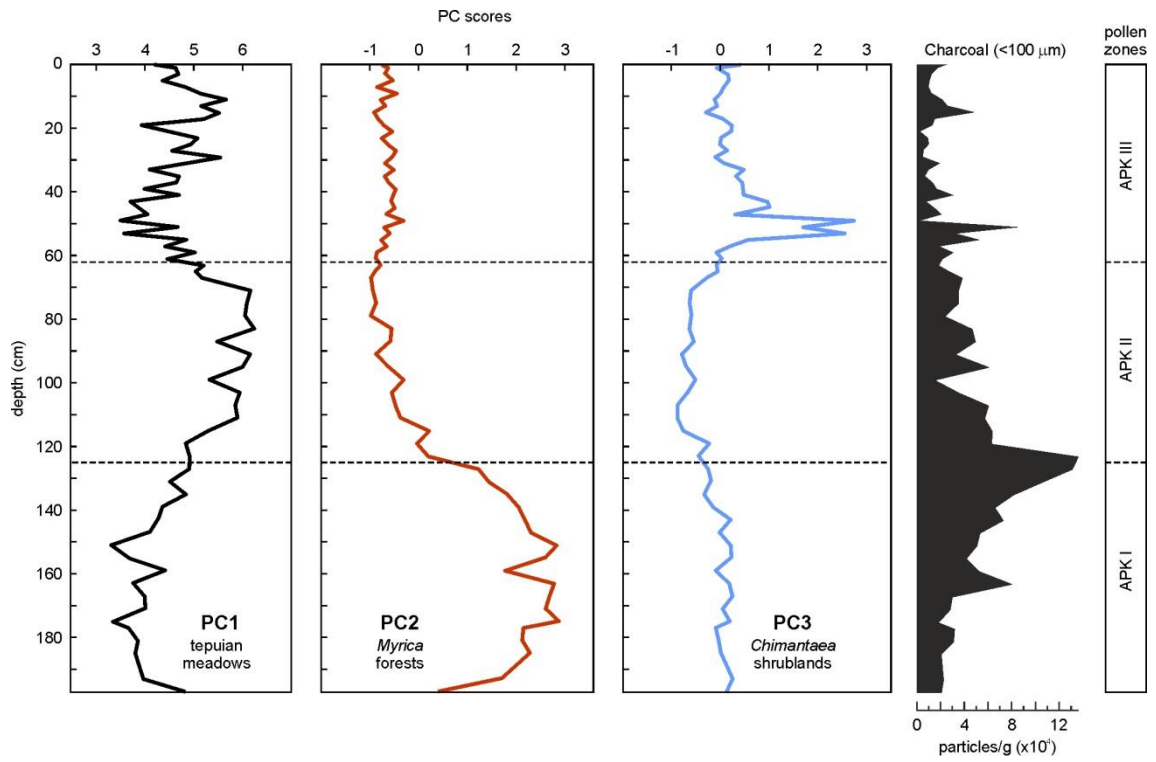
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937 Figure 5



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940 Figure 6

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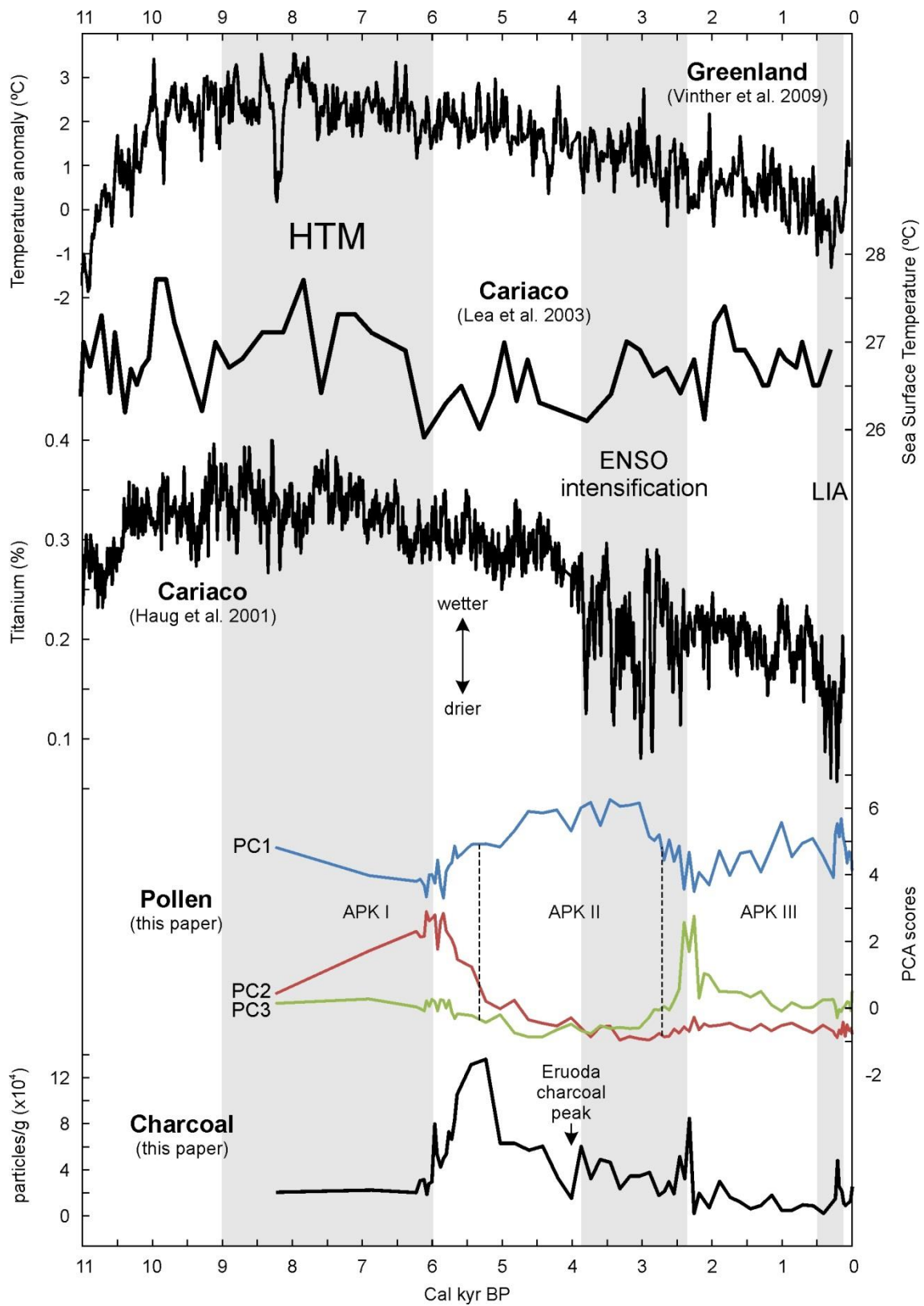
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957 Figure 7