1   **An 8700-year record of the interplay of environmental and human drivers**

2   **in the development of the southern Gran Sabana landscape, SE Venezuela**

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22

23   Abstract

24   The vegetation of the southern Gran Sabana (SE Venezuela) consists primarily

25   of a treeless savanna with *morichales* (*Mauritia flexuosa* palm stands), despite

26   the prevailing climate being more favorable for the development of extensive

27   rainforests. Here we discus the results of our 8700-year palaeoecological

28   reconstruction from Lake Encantada based on analysis of pollen, algal remains,

29   charcoal and geochemical proxies. We use the findings to assess a number of

30   hypotheses that seek to explain the dominance of savanna vegetation and

31   consider the relative importance of factors such as climate, fire and erosion on

32   the landscape. The reconstruction of vegetation changes suggests the following

33   trends: open savanna with scattered forest patches (8700-6700 yr BP), forest-

34   savanna mosaic (6700-5400 yr BP), open savanna with forest patches (5400-

35   1700 yr BP) and treeless savanna with *morichales* (1700 yr BP-present). We

36   conclude that the interplay between climate and fire and the positive feedback

37   between the presence of grasses and increased fire frequency played a major

38   role in the vegetation dynamics from the early to middle Holocene (8700-6700

39   yr BP). The synergistic action between reduced fires and wetter conditions

40   appears to be a determinant in the development of rainforest around 6700 yr

41   BP. Despite higher available moisture at ~5400 yr BP, the savanna expanded

42   with the increased frequency of fire, potentially driven by human land-use

43   practices. We also propose that the interplay between fire and erosion created

44   forest instability during the middle and late Holocene. The current southern

45   Gran Sabana landscape is the result of the complex interplay between climate,

46   fire, erosion and vegetation.

47

48   Keywords

49   Environmental drivers, Feedbacks, Vegetation dynamics, Savanna expansion,

50   Land-use practices, Neotropics.

51

52   1. Introduction

53   Savanna is one of the most extensive tropical ecosystems, covering

54   approximately 20% of the Earth's land surface, and occurring over a broad

55   range of climatic, edaphic and topographic conditions. Fire frequency is high in

56   Savanna ecosystems from both natural and anthropogenic causes. This biome

57   occurs in areas showing annual precipitation values between 300 to 1800 mm;

58   values above 600 to 820 mm/yr correspond to humid ecosystems (Accatino and

59   De Michele, 2013). The presence of savanna in this high-rainfall areas suggests

60   that climate alone is not responsible for the distribution of this biome (Murphy

61   and Bowman, 2012). Instead, the interplay of environmental drivers such as

62   climate, soil development, geomorphology, land use and fire frequency are

63   important factors that influence the presence of savanna in areas that could be

64   covered by tropical rainforest. Despite an increased understanding of how these

65   drivers influence the evolution of savanna (Jeltsch et al., 2000; Murphy and

66   Bowman, 2012), the underlying ecological processes and interactions that

67   maintain this ecosystem are not well understood. Probably multiple factors

68   operate at different spatial and temporal scales (Jeltsch et al., 2000), and their

69   feedbacks with vegetation and soils contribute to the establishment and

70   maintenance of the savanna physiognomy (Beckage et al., 2009; Hoffmann et

71   al., 2012a,b). Savanna areas have experienced remarkable expansions in the

72   last millennia (Behling and Hooghiemstra, 1999; Breman et al., 2011; Montoya

73   and Rull, 2011) largely caused by the increased occurrence of human caused

74   fires. In order to prevent further expansion, an improved understanding of the

75   interplay between human and environmental drivers is needed.

76

77   The Venezuelan Gran Sabana (GS) region is an upland savanna located in

78   southeastern Venezuela (Figure 1a) and is situated within the extensive

79   Guayanan and Amazon rainforests (Barbosa and Campos, 2011). Even though

80   the regional climate is suitable for the development of rainforest vegetation, the

81   vegetation of the GS is savanna and has persisted since the beginning of the

82   Holocene (Montoya et al., 2011a; Rull, 2007). Three hypotheses have been

83   proposed to explain the long-term presence of savanna vegetation in the GS.

84   First, the climatic hypothesis suggests that the GS savannas are the relicts of

85   larger savanna extensions that originated in drier and/or colder epochs (e.g,

86   Last Glacial Maximum) (Eden, 1974). Second, the fire hypothesis presumes

87   that frequent burning, potentially from anthropogenic sources, formed and

88   maintained the savanna ecosystem. The more recent savanna expansion (~

89   2000 yr BP to present) appears to have been caused by human-induced forest

90   clearing through burning (Montoya et al., 2011b, c). The absence of

91   archaeological studies to date in the GS currently limits our knowledge of the

92   timing of human occupancy, as well as the associated land-use practices. Third,

93   the edaphic hypothesis suggests that unfavorable soil conditions in the GS,

94   such as low nutrient concentrations, low water retention and a shallow soil

95   profiles suppress forest growth resulting in Savanna development (Dezzeo et

96   al., 2004; Fölster et al., 2001). Modern short-term studies limited to the last

97   several decades highlight the negative impacts of soil stress on vegetation and

98   the landscape (Dezzeo et al., 2004; Fölster et al., 2001), although there are no

99   studies to date that have focused on the influence of soil development on

100   vegetation over longer timescales (centuries to millennia). A study of the long-

101 term vegetation dynamics is required in order to assess these hypotheses and

102 determine the interplay between climate, vegetation, fire ecology, soil related

103 factors and the associated feedback processes.

104

105 In this work, we present a multiproxy investigation of a lacustrine sediment

106 record recovered from a region in the southern GS covering the last 8700 yr.

107 We integrated pollen, spores, algal remains, charcoal and geochemical

108 analyses to generate a detailed reconstruction of the environmental changes in

109 the region, with a specific focus on the interplay and synergies between the

110 environmental drivers (climate and fire), soil erosion and vegetation.

111

112 [insert Figure 1]

113

114 2. Present-day environmental setting

115

116 2.1. Regional features

117 The GS is an extended region (~10,800 km^2) located in the Venezuelan

118 Guyana, in southeastern Venezuela (Bolívar state). This region lies in northeast

119 of the Precambrian Guiana Shield, and between the Orinoco and Amazon

120 basins (4º36' to 6º37'N and 61º4' to 74º2'W) (Figure 1a). The climate of the GS

121   has been described as submesothermic tropophilous, with annual average

122   temperatures of approximately 18–22 ºC and precipitation of 1600–2000 mm/yr.

123   The GS is a high, undulating erosion surface that forms an *Altiplano* inclined

124   from north (1450 m asl) to south (750 m asl). The GS is situated on quartzite

125   and sandstone bedrock, known as the Roraima group. These rocks have been

126   subject to long weathering processes and produce iron- and aluminum-oxide-

127   rich soils (Huber, 1995a), which have poor nutrient content, with low

128   concentrations of phosphorous, calcium and nitrogen (Huber, 1995a). The soil-

129   chemical stress caused by the calcium deficiency and aluminum toxicity

130   combined with the thin profile render the soils incapable of supporting certain

131   types of vegetation, especially forests (Fölster et al., 2001). This reduces the

132   capacity of the soil to withstand external and internal impacts such as burning

133   and drought (Fölster et al., 2001;Schubert and Huber, 1989).

134

135   In the Venezuelan Guayana region, the principal vegetation types are

136   evergreen montane and gallery forest, but the majority of the GS is covered by

137   savanna. Three primary types of savanna occur in this area (Huber, 1995b): (1)

138   open treeless savannas, (2) shrubs savannas and (3) open savannas with

139   *morichales*, which are mostly monospecific dense stands of the Arecaceae

140   *Mauritia flexuosa* (locally known as *moriche*). The stands of *morichales* grow

141 along river courses and around lakes on poorly drained soils with high clay

142 content (Rull, 1999). This type of gallery forest is an important vegetation

143 component occurring in the central and southern regions of the GS at elevations

144 lower than 1000 m asl (Huber, 1995b). Other vegetation types in the GS

145 landscape that form patchy mosaics in the savanna (Huber, 1986) are

146 montane rain forests (800-1500 m asl; Huber, 1995b; Hernández, 1999),

147 shrublands, secondary woody communities and *helechales* (dense fern

148 communities). Generally *helechales* establish after repeated burning, as part of

149 successional trend (Huber, 1986). A more detailed description of the vegetation

150 composition is provided in previous studies (Huber 1995b). For the main taxa,

151 refer to Supplementary material.

152

153 Fire currently plays a significant role in the landscape dynamics of the GS, with

154 a fire frequency between 5000 and 10,000 fires per year (Gómez et al., 2000).

155 Nearly 70% of detected fires start in savanna areas, but some fires cross the

156 savanna-forest boundary (Bilbao et al., 2010), causing forest degradation

157 (Dezzeo et al., 2004; Fölster, 1986; Fölster et al., 2001). The vast majority of

158 these fires are of anthropogenic origin (Bilbao et al., 2010). Fire is a key

159 element of the *Pemón* culture. This indigenous group currently inhabits the GS,

160 and belongs to the Carib-speaking ethnic group. They use fire daily to burn wide

161   extensions of treeless open savanna (Kingsbury, 2001). Fires in savanna-forest

162   borders are scarcely controlled and cause concern about further savanna

163   expansion. The anthropogenic fires have caused an impoverishment of tree

164   species, a drastic reduction of biomass in terms of basal area, a strong change

165   in the floristic composition and the loss of the organic-rich soil surface layer,

166   which negatively impacts on soil fertility (Dezzeo et al., 2004). Therefore, the

167   forest recovery may be strongly impaired by fire. To prevent further land

168   degradation, studies and strategies for fire management in the GS are currently

169   under investigation (Bilbao et al., 2009, 2010).

170

171   2.2. Study site

172   Lake Encantada (4º42'37. 44" N to 61º05'03. 29" W; 857 m asl; Figure 1a) is

173   located near the town of Santa Elena de Uairén on a private farm named "Hato

174   Santa Teresa". Lake Encantada is shallow with a maximum water depth of 2.6

175   m (measured in January 2007). The lake surface is <1km^2 and its watershed is

176   also small, both of which suggest that the sediment record contains a local

177   vegetation history (Mayle and Iriarte, 2012). Treeless savanna and scattered

178   *morichales* patches currently surround the Lake Encantada (Figure 1b).

179   Therefore, pollen signal of *M. flexuosa* may indicate the local occurrence of

180   *morichales* around the shores of the lake. However, wind-transported pollen

181 taxa (e.g., Urticales pollen grains) might have been sourced extra-locally from

182 neighboring forests (Jones et al., 2011).

183

184 3. Methodology

185 3.1. Core recovery and radiocarbon dating

186 The core discussed here, (PATAM4 C-07; 2.13 m-long), was obtained in January 2007

187 and was taken from the deepest part of the lake using a modified Livingstone squared-

188 rod piston (Wright et al., 1984). Four samples were taken along the core for AMS

189 radiocarbon dating, which was carried out at the Radiocarbon Laboratory of the

190 University of California, Irvine (UCI) and Beta Analytic (Beta). Three samples were

191 produced from a pollen residue (Table 1), due to the absence/insufficiency of suitable

192 macrofossil material. These samples were processed using a simplification of standard

193 palynological techniques (KOH, HCl and HF digestions). The radiocarbon dates were

194 calibrated with the CALIB 6.0.1 and the IntCal09.14c database

195 (http://calib.qub.ac.uk./calib/, last accessed on October 2012). The age-depth model

196 was produced with the Clam R statistical package (Blaauw, 2010).

197 3.2. Magnetic, physical and chemical analyses

198 Magnetic susceptibility (MS) was measured on half-core sections at 5 mm intervals with

199   a Bartington Susceptibility Meter. Bulk density (BD) was measured on 1 cm^3 samples

200   that were taken every 5 cm down the core and dried at 60 ºC for 24 h. The organic

201   matter and inorganic carbon content of the sediments were determined for each sample

202   by loss on ignition (LOI) at 550 ºC and 1000 ºC, respectively (Bengtsson and Enell,

203   1986; Heiri et al., 2001). Elemental determinations were performed with an ITRAX X-

204   Ray Fluorescence (XRF) core scanner at the Large Lakes Observatory of the University

205   of Minnesota, Duluth. Measurements were made at 1 cm intervals during 60 seconds of

206   exposure time. The elements are expressed as counts per second (cps), and those over

207   1500 cps were selected (Si, K, Ti, Mn, Fe, Co, Ni, Zn, As, Se, Br, Rb, Sr and Zr),

208   because they are usually considered to be statistically significant. Excluding Fe, Co and

209   Br, the remaining elements are considered a terrigenous-sourced group. Total Organic

210   Carbon (TOC) and Nitrogen (TN) and δ^{13}C and δ^{15}N were measured after acid pre-

211   treatment using an elemental analyzer coupled with a Finnigan Delta-plus mass

212   spectrometer. The isotope sample reproducibility was ± 0.2‰. Carbon and nitrogen

213   isotope ratios are reported in δ-notation, with δ= ([Rsample/Rstandard] -1) x 1000 and R

214   =^{13}C /^{12}C or ^{15}N/^{14}N. The isotopes are expressed per mil (‰) relative to the following

215   international standards: Vienna Peedee Belmnite (VPDB) for carbon and air (VAIR) for

216   nitrogen.

217   3.3. Pollen analysis

218   Forty-three volumetric samples (2 cm^3) were taken at 5 cm intervals. The samples were

219   processed using standard palynological techniques (KOH, HCl, acetolysis, HF digestion

220   and dehydration). *Lycopodium* tablets were added as exotic markers (batch 177745,

221   average of 18584 ± 1853 spores/tablet). The slides were mounted in silicone oil without

222   sealing and stored in the same mounting medium. Counts were conducted until a

223   minimum of 300 terrestrial pollen grains was attained. Pollen count was performed until

224   diversity saturation was reached (Rull, 1987). Identified pollen and pteridophyte spores

225   were classified according to the vegetation types previously described for the region

226   (Huber, 1995b). The pollen sum included pollen from trees, shrubs and herbs and

227   excluded pollen from aquatic (e.g., *Utricularia*, *Ludwigia*) and semi-aquatic plants (e.g.,

228   Cyperaceae, *Sagittaria*). The identification of pollen and spores was based on Burn and

229   Mayle (2008), Colinvaux et al (1999), Herrera & Urrego (1996), Leal et al (2011), Roubik

230   & Moreno (1991) and Rull (2003). Pollen diagrams were plotted with *PSIMPOLL 4.26*.

231   The zonation for the pollen diagrams was performed using the optimal splitting by

232   information content (OSIC) method, and the number of significant zones was

233   determined by the broken-stick model test (Bennett, 1996). Only pollen types exceeding

234   1% abundance were used for zonation. Sample PATAM4C 07_D3/50 at 213 cm was

235   excluded because of methodological problems, so pollen diagrams up to 208 cm were

236   created. Algal remains (e.g., *Botryococcus*, *Spirogyra*, *Mougeotia*) were counted on

237   pollen slides and, together with aquatic plants, were plotted in terms of percentages

238   based on pollen sum. The identification of the assemblages was based on comparison

239   with modern pollen samples from previous studies (Leal et al., 2013; Rull, 1999) and

240   the known autoecology of the taxa (Burn and Mayle, 2008; Burn et al., 2010; Marchant

241   et al., 2002). Charcoal counts were carried out using the same pollen slides and were

242   classified according to the two size classes defined by Rull (1999) for this study area:

243   Type I (smaller microcharcoal particles of 5–100 µm) consists of windborne charcoal

244   dispersed over long distances and represents regional fire events (Clark, 1998;

245   Blackford, 2000), and Type II (larger microcharcoal particles >100 µm) is indicative of

246   local fire events because it is not transported far from the fire source (Clark, 1998).

247   Influx values (unit-cm^{-2}*yr^{-1}) were obtained using concentration values (unit-cm^{-3}) and

248   accumulation rates (cm*y^{-1}) for charcoal particles and main taxa. Additionally, we

249   measured the woody: non-woody ratio after classifying the taxa into woody (trees and

250   shrubs) and non-woody (herbs and sedges) types. This ratio is indicative of the

251   vegetation cover (Bhagwat et al., 2012) and can be used to differentiate between

252   forested and savanna vegetation.

253   3.4. Silicobiolith analysis

254   Diatoms and sponge spicules were considered as silicobioliths, which are sediment

255   from the remains of living organisms formed by amorphous silica. Forty-three samples

256   taken at 5 cm intervals (1 cm^3) were digested according to their organic matter content

257   with either a mixture of sulphuric acid and potassium dichromate or hydrogen peroxide.

258   Most samples were barren of silicobioliths. In the remaining samples, because of the

259   extremely low number of valves and spicules in different stages of preservation (e.g.,

260   0.2 valves/field on average), counting was stopped after approximately 500 fields and

261   the results were expressed as "traces". Diatoms were identified using specialized

262   literature (Krammer & Lange-Bertalot, 1986). The identified spicules correspond to adult

263   oxas type, so their taxonomic identification was not possible (Frost et al., 2001).

264   3.5. Statistical analysis

265   Canonical Correspondence Analysis (CCA) was performed with the Multivariate

266   Statistical Package (MVSP) v.3.13 software using all physico-chemical data and the

267   influx of charcoal and algae as environmental variables. All data were root-square

268   transformed and rare pollen taxa were down weighted. Six samples (3, 123, 128, 138,

269   143 and 173 cm) were excluded because of a lack of physico-chemical data. The

270   interval 213-173 cm was also excluded because it is barren of biological proxies.

271 Additionally, correlation analysis was carried out between the environmental variables

272 and the main pollen taxa by using influx values calculated according to the Pearson

273 product-moment correlation coefficient (r) and its corresponding significance (p-value).

274 4. Results

275 4.1. Stratigraphy and chronology

276 The Encantada lacustrine sequence was characterized by three lithological units from

277 bottom to top (Figure 2). The first unit is from 213 to 173 cm and is characterized by

278 homogeneous, well-sorted and fine white sands. The second unit is from 173 to 113 cm

279 and is made up of homogeneous, yellowish-white clays, but between 150 and 131 cm, a

280 yellowish-brown clay layer is present. The third lithological unit is present from 113 cm

281 to the top and consists of massive, brown clay sediments.

282 [insert Figure 2]

283 The results of AMS radiocarbon dating (Table 1) were used to build the age-depth

284 model for the sequence. The best fit was obtained with a smooth-spline model (Blaauw,

285 2010) (Figure 2). Sedimentation rates fluctuated between 0.04 and 0.02 cm yr^{-1} and

286 progressively decreased from the bottom to the top. The sequence encompassed most

287   of the Holocene (ca. 9700 cal yr BP to the present), and the time interval between

288   consecutive samples ranged from approximately 100 to 300 yr (centennial to multi-

289   centennial resolution). We focused on the last 8700 yr for the palaeoecological analysis

290   because of the absence of biological proxies prior this time (see section 4.3.1).

291   **Table 1.**

292   AMS radiocarbon dates used of the age-depth model.

293

Laboratory number	Sample	Depth (cm)	Material	Age (yr ^{14}C BP)	Age (cal yr BP) 2σ	Age (cal yr BP) estimation*
UCI-43538	PATAM4C07_D1/40	40	Wood	2260±60	2154-2272	2309
Beta-287338	PATAM4C07_D2/19	100	Pollen residue	5030±40	5705-5896	5763
Beta-287340	PATAM4C07_D2/72	152	Pollen residue	7300±40	8019-8180	8043
Beta-287339	PATAM4C07_D3/47	207	Pollen residue	8530±50	9453-9556	9543

294   * Weighted average of the probability distribution function. This method is

295   recommended as the best central-point estimate

296

297

298   4.2. Geochemical proxies

299   Figure 3 shows the results of the geochemical analyses. According to variations along

300   the entire sequence, three intervals (listed below) were identified that coincide with

301   those based on the sediment description.

302   4.2.1. Interval A (213 to 173 cm)

303   This interval corresponds to the oldest described lithological unit. All

304   geochemical elements had values that were low to very low and roughly

305   constant, except Si (up to 8,330 cps) and BD (ranging between 1.3 to 1.5

306   g/cm^3), which exhibited the highest values of the entire record.

307

308   4.2.2. Interval B (173 to 113 cm)

309   Most physico-chemical proxies displayed high variability related to the

310   lithological changes present in this interval, which allowed three sub-intervals to

311   be defined: B-1, B-2 and B-3. B-1 and B-3 coincided with the yellowish-white

312   clay layers, whereas B-2 corresponded to the intermediate yellowish-brown

313   clays of lithological unit 2 (Figure 3). B-1 and B-3 were characterized by a high

314   cps of K, Ti, Mn, Se, Sr and Zr; these chemical elements abruptly dropped in B-

315   2, whereas Fe ($22.9*10^5$ cps) and Co ($13.6*10^3$ cps) were found at their

316   maximum values. MS (up to $240*10^{-6}$ S.I), δ^{13}C (1.3 ‰), C/N (191) and TOC

317   (ca. 10 %) peaked in B-2. δ^{15}N reached minimum values in B-2 (up to 1‰).

318

319   4.2.3. Interval C (113 to 0 cm)

320   Most of the elements showed medium to low values in interval C in comparison

321   with values from two previous intervals, but Br displayed the highest ones (up to

322   1,737 cps) of the entire record. TOC (from 8 to 31%), TN (ranging between 0.5

323   and 2.1 %) progressively increased upwards, and δ^{15}N decreased (varying from

324   0.8 to -1.3 ‰).

325   [Insert Figure 3]

326

327   4.3. Biological proxies

328   The stratigraphic variations of pollen assemblages allowed us to subdivide the

329   pollen diagram into four zones. Because silicobioliths were only found in trace

330   amounts, they could not be plotted in a taxa percentage diagram; however,

331   these results were included in the diagram of aquatics and expressed

332   qualitatively.

333

334   4.3.1. ENC-BZ (208 to 173 cm, 8 samples).

335   Palynomorphs were absent (Figs. 4 and 5) and therefore this zone was

336   considered barren (BZ). Charcoal particles remained at low abundances but

337   exhibited a pronounced increase at the boundary with the upper zone (ENC-I).

338

339   4.3.2. ENC-I (173 to 120.5 cm, 11 samples)

340   ENC-I coincides both with the physico-chemical interval B and with the second

341   lithological unit (Figure 2). The pollen assemblage was dominated by

342   herbaceous elements, with Poaceae as the most important taxa. The

343   percentage of herb pollen (ca. 50-80%) decreased towards the top of the zone

344   and was synchronous with an increase in tree pollen, which can also be

345   observed in the vegetation cover ratio (Figure 4). Woody elements were

346   represented primarily by *Brosimum* (the most abundant), Ochnaceae, *Miconia*,

347   *Solanum*. section *Pachyphylla*, *Cecropia* and Urticales (others). Pteridophyte

348   spores were primarily dominated by psilate monoletes and psilate triletes

349   (Figure 5), which showed two peaks at approximately 158-153 cm and 128-123

350   cm, that co-occurred with the peaks of *Miconia* (Figure. 4) and maximum

351   abundances of Cyperaceae (at 158-153 cm; Figure 5). *Mougeotia* appeared in

352   the lower half of the zone, whereas *Sagittaria*, *Botryococcus* and *Spirogyra*

353   appeared for the first time at the top of the zone (Figure 5). Charcoal particles

354   showed the highest values of the entire record at the base of the zone (Figure

355   4). Regarding the influx values, Poaceae displayed an abrupt maximum at 143

356   cm, which coincided with a charcoal peak (Figure 6). These values occurred in

357   the lithological/stratigraphical sub-interval B-2.

358   [insert Figure 4]

359   [insert Figure 5]

360

361   4.3.3. ENC-II (120.5 to 30.5 cm, 18 samples)

362   The ENC-II zone is represented by marked increase in forest elements,

363   primarily Urticales 3-4p, in its lower half. Vegetation cover ratios (in average

364   1.33) showed the same trend. *Cecropia* was more abundant (2-3%) towards the

365   bottom and the top of the zone. In the lower half of the zone Urticales reached

366   its highest proportion (>40%) and influx (> $5*10^2$ grains*$cm^{-2}yr^{-1}$) (Figs. 4 and 6).

367   Among the aquatic elements, *Sagittaria* was nearly constant along the zone and

368   increased slightly near the top (⌣1.5%). *Spirogyra* was abundant in the lower

369   half (3-4%), while *Botryococcus* was the dominant aquatic element in the upper

370   region of the zone (5-6.5%, Figure 5). Total algal remains had the highest

371   values in the upper half (up to 110 elements*$cm^{-2}yr^{-1}$; Figure 6). From 103 cm

372   upwards, the presence of sponge spicules was almost constant (Figure 5).

373   Charcoal particles presented the lowest values of all the sequences at the base

374   of the zone but exhibited a subsequent increase. Excluding the upper region,

375   this zone broadly coincided with interval *C*.

376

377   4.3.4. ENC-III (30.5 to 3 cm, 6 samples)

378   The pollen assemblage of the ENC-III zone showed an abrupt change in

379   composition. *M. flexuosa* increased dramatically from 1.5% to 27.7%, while

380   pollen of woody taxa underwent a drastic reduction from >40% to 3% (Figure 4).

381   From 23 to 18 cm, *M. flexuosa* declined whereas a tree pollen recovery (32%)

382   was observed, synchronous with a subtle decrease in charcoal particles (Types

383   I and II). A return to former *Mauritia* values was recorded shortly thereafter and

384   was coeval with a severe reduction of pollen of woody taxa to ca. 3%. Urticales

385   and *M. flexuosa* influx values followed similar trends with their respective

386   relative abundances, confirming the trends inferred from the percentage values

387   (Figure 6). In the upper region, Poaceae dominated the pollen assemblage,

388   reaching almost 70% of the pollen sum. Pteridophyte spores were common but

389   occurred in low percentages (Figure 5). Aquatic elements remained at low

390   abundances (< 2%, Figure 5). Charcoal particles showed values that were

391   roughly similar to those of the previous zone ($\backsim$ 16*10^3 particles*cm^{-2}yr^{-1}).

392   [insert Figure 6]

393

394   4.4. Statistical analysis

395   Figure 7 shows the results of the CCA along the biplot of the first two axes,

396   which explain 47.88% of the total variance (Axis 1=28.42%, Axis 2= 19.46%).

397   Positive values on axis 1 are represented by TN and, to a lesser extent, by

398   TOC, the inc/coh ratio (indicator of the organic matter content of the sample;

399   see Croudace et al., 2006, Sáez et al., 2009, Ziegler et al., 2008), Co and Fe,

400   whereas negative values are represented by Ti, Zn and Zr and, to a lesser

401   extent, by As, Ni, Rb, K, Mn, Si, Sr and BD. Charcoal and MS represent the

402   positive values on axis 2, whereas algae and Br have more influence on the

403   negative values.

404

405   Within the space defined by these two axes, samples are clustered according to

406   the previously defined pollen zones. Pollen zone ENC-I falls on the negative

407   side of axis 1 and the positive side of axis 2, which is linked to a suite of

408   elements (As, Ni, Rb, K, Mn, Si, Sr and BD). Pollen zone ENC-II is situated in

409   the middle of axis 1 and the negative side of axis 2, showing a widespread

410   arrangement of samples that are linked to a variety of elements (such as TOC,

411   TN, $\delta^{13}C$, $\delta^{15}N$ and algae). Zone ENC-III is located on the positive sides of both

412   axes, showing no relationship with physico-chemical proxies.

413

414   Charcoal and *M. flexuosa* showed no significant relationship when considering

415   the whole diagram; however, when only zone ENC-III is taken into account

416   (*Mauritia* is absent from the other pollen zones), the linear correlation between

417   charcoal and *M. flexuosa* is positive and significant (r= 0.68; p= 0.015).

418   Charcoal also shows a strong positive relationship with psilate spores (r= 0.66;

419   *p*-value < 0.001) and these are highly associated with *Miconia* (*r*= 0.70; *p*-value

420   < 0.001).

421   [insert Figure 7]

422

423   5. Reconstruction of environmental changes

424   The environmental variations in the sediments of Lake Encantada allowed us to

425   differentiate four periods.

426

427   5.1. *Period 1:* 9700 to 8700 cal yr BP (from 213 to 173 cm)

428   The presence of well-rounded and sorted siliclastic sediments together with the

429   highest sedimentation rates (0.04 cm yr^{-1}) suggests that these sediments were

430   likely deposited in a fluvial environment. We believe that flowing waters would

431   have prevented the deposition and/or preservation of most biological proxies.

432

433   5.2. *Period 2*: 8700 to 6700 cal yr BP (from 173 to 120 cm)

434   Pollen analysis suggests that during this period the landscape was covered by

435   open savanna with scattered small forest patches. Regional fires peaked and

436   decreased several times, and when fires decreased the forest patches

437   expanded. This expansion is indicated by the wind-pollinated taxa of the

438   Moraceae family (Figure 4; Burn et al., 2010) (ca. from 8500 to 8000 cal yr BP,

439   and ca. from 7500 to 7000 cal yr BP). After more intense burning events,

440   *Miconia* increased in parallel to a significant increase in psilate-fern spores.

441   Both *Miconia* and pteridophytes with psilate spores are colonizers of burnt

442   areas during early stages of succession (Berry et al., 1995; Hernández and

443   Fölster, 1994; Marchant et al., 2002). In the GS, a similar assemblage formed

444   by *helechales* (fern communities), intermingled with patches of shrubs

445   (*matorrales*), is considered to be a degrading successional stage after

446   secondary forest burning (Fölster et al., 2001; Rull, 1999). Conversely, when

447   regional fires increased, the forest and *helechales-matorrales* retreated and the

448   savanna expanded (ca. from 8000 to 7500 cal yr BP). Around ca. 7700 cal yr

449   BP, higher δ^{13}C values (indicative of C_4-land plants; Meyers and Lallier-Vergés,

450   1999), higher C/N ratios (Figure 3) and greater Poaceae-influx values coincided

451   with the enhancement of fires (Figure 6). According to modern plant surveys

452   (see Supplementary material), most herbs in GS have C_4-photosynthetic

453   pathway. This evidence confirms the dominance of expanding open vegetation

454   when fires were more intense. Other paleorecords from the area indicate that

455   this period was dry across the greater region (*Llanos Orientales*: Behling and

456   Hooghiemstra, 1998; Amazonia: Mayle and Power, 2008) which is also

457   consistent with a previous work in the GS (Montoya et al., 2011a) and the

458   evidence presented here.

459

460   At the beginning of the period, the abrupt change from clastic sediments to

461   yellowish-white clays (interval B-1) might indicate the change from fluvial to

462   lacustrine conditions. Most geochemical (TOC and TN) and biological (algal

463   influx) proxies suggest that the aquatic productivity was negligible or not

464   preserved in the sediments (Figs. 3 and 6). During the periods from 8700 to

465   8000 cal yr BP and from 7200 to 6700 cal yr BP yellowish-white clays (intervals

466   B-1 and B-3) were deposited (Figure 3). The change in sediments combined

467   with higher terrigenous inputs (Figure 3) indicates the disconnection with the

468   fluvial system (Figure 3). Based on the analysis of biological proxies, we believe

469   these intervals represented wetter conditions. Conversely, during the period

470   from 8000 to 7200 cal yr BP the lithological change to brown clays (interval B-2)

471   suggests the deepening of the water body. However, based on palynological

472   results we suggest that during this interval the conditions were drier. According

473   to the MS results (Figure 3) and axis 2 of the CCA (Figure 7), the intense

474   erosional events may be interpreted as soil instability caused by fires (see a

475   detailed explanation in section 5.5) instead of being driven by enhanced rainfall,

476   which commonly occurs in tropical regions (Warrier and Shankar, 2009).

477   Evidence may be indicating a temporal connection with the fluvial system. Thus,

478   the interplay of fires, open landscape and long-distance transport of terrigenous

479 elements (Figure 7) might have promoted high erosion events. Poaceae pollen

480 grains are airborne and waterborne transported (Brown et al., 2007), and hence

481 can be transported a long distance. So the high amount of Poaceae pollen

482 grains during interval B-2 (Figure 6) would have been locally and extra-locally

483 sourced. On other hand, the decrease in the $\delta15N$ values (<0‰) suggests the

484 lake primary productivity might be ruled by nitrogen-fixing bacteria (Figure 3). In

485 summary, this period might be considered as highly variable, with an alternation

486 of drier and wetter intervals. We tentatively suggest that disconnection-

487 connection dynamics with the fluvial system could have been driven by

488 variations in the river's drainage pattern.

489

490

491 5.3. *Period 3:* 6700 to 1700 cal yr BP (from 120 to 30 cm)

492 The pollen assemblage showed a remarkable compositional and structural

493 change in plant communities during this period. The vegetation shifted to

494 patches of dense rainforest within savanna from 6700 to 5400 cal yr BP. As

495 noted by modern ecological studies (Leal et al., 2013; Rull, 1999), the

496 percentages of herbs and tree pollen would indicate the occurrence of a forest-

497 savanna mosaic during this period. Forest was highly dominated by Urticales

498 with 3-4p pollen grains, *Brosimum*, Sapotaceae, *Cecropia*, *Pourouma* and

499   *Hyeronima*. Urticales values suggest that an evergreen tropical forest with a

500   closed-canopy was established nearby or patchily distributed in the location

501   (Gosling et al., 2009). An additional local environmental reconstruction for the

502   area was provided by a peat core extracted from the shore of Lake Encantada

503   (Montoya et al., 2009). This sequence also showed a notable development of

504   forest roughly at the same time interval. Hence, it seems to indicate that dense

505   forest patches expanded locally. However, the palynological signal of some

506   regional forest expansion expressed by the arrival of some wind-borne pollen

507   grains to the sampling location cannot be disregarded. The rainforest

508   development occurred when fires (regional and local) declined dramatically,

509   which enabled *Cecropia,* as a pioneer tree, to colonize the land cleared by the

510   fire disturbances (Burn et al., 2010; Marchant et al., 2002) and subsequently

511   rainforest expanded. Because of the humidity requirements of rainforests and

512   the higher abundances of *Spirogyra*, we consider this to be a period of higher

513   available moisture during forest development.

514

515   In the upper half of this period, a clear shift to more open vegetation occurred.

516   The region near Lake Encantada was dominated by either open savanna with

517   forest patches or reduced forest-savanna mosaic, under higher fire intensity and

518   moisture availability and than before 5400 cal BP. This is supported by

519   maximum values of aquatic elements (e.g., *Botryococcus*, deeper water

520   inhabitant; Figure 5). Similar forest development and wetter climates during the

521   middle to late Holocene are supported by similar studies from other locations in

522   the GS (Montoya et al., 2011b; Rull, 1992), and in the neighbouring savannas of

523   Colombia *Llanos Orientales* and northern Amazonia (Behling and

524   Hooghiemstra, 2000; Pessenda et al., 2010; Figure 1a). This increase in humid

525   conditions was the opposite of the trend toward drier conditions that occurred in

526   the northernmost South American Andes (Vélez et al., 2003). Thus, the wet

527   climate inferred in our study fits with regional climatic trends recorded in

528   localities north of the Amazon basin, which would have been strongly influenced

529   by moisture coming from the basin.

530

531   The sedimentological change to brown clays and the pronounced increase in

532   Br, TOC and TN (Figure 3) occurred at the base of the interval C. Probably the

533   lake became more productive.

534

535

536   5.4. *Period 4:* 1700 cal yr BP to present (30 to 3 cm)

537   In the period from 1700 cal yr BP to present, the vegetation experienced an

538   abrupt change towards the establishment of treeless savanna with *morichales*

539   stands (*Mauritia* palm), that is, the modern-day landscape. The continuous

540   presence of small *helechales* indicates a network dynamic of fern patches. Rull

541   (1999) interpreted these communities as a transitional stage from open

542   secondary forest cleared by fires to open savanna with *morichales* (Rull, 1999).

543   The high percentage of *M. flexuosa* pollen in sediments indicates the local

544   occurrence of *morichales* (Rull, 1999). According to its ecology, this palm

545   seems to be opportunistic and able to colonize new habitats created by fire and

546   poorly drained soils resulting from wet conditions (Rull, 1999). Although fire

547   evidence is not conclusive with regard to the initial establishment of the

548   *morichales* (Figs. 4 and 7), the correlation analysis (r=0.68; p=0.015) indicates

549   some level of fire influence on this plant community, which is also suggested by

550   several former studies (Montoya et al., 2009, 2011c; Rull, 1999). On the other

551   hand, the marked rise in TOC and slight rise in TN indicate an increase in

552   primary lake productivity, which occurred in synchrony with decreased $\delta^{15}N$

553   values and algae scarcity. These results suggest that aquatic productivity was

554   almost entirely dominated by nitrogen-fixing bacteria. The scarcity of algal

555   remains and predominance of bacteria might indicate drier conditions and/or

556   nutrient-limited conditions.

557

558   5.5. Interpretation of the environmental gradients: Canonical

559   Correspondence Analysis (CCA)

560

561   Chemical elements such as Ti, Zr and Zn are usually associated with

562   terrigenous inputs of sediments to the lake, whereas total nitrogen (TN) and

563   total organic carbon (TOC) commonly reflects variations in the organic

564   productivity of the lake (Cohen, 2003). A careful analysis of the sample

565   distribution in the plane defined by the two first CCA axes reveals that they are

566   stratigraphically ordered, with the deepest elements located on the left side of

567   the graph (sandy lithological unit 1) and the uppermost elements located on the

568   right side (clayish lithological unit 3). Therefore, the first axis could be related to

569   the suggested progressive change from a fluvial sedimentary environment to a

570   lacustrine one.

571

572   Despite absence of archaeological evidence, previous palaeoecological studies

573   in the southern GS suggest that the consistent presence and abundance of

574   charcoal (fire proxy) could be related to land highly managed and altered by

575   humans for at least the last two millennia (Montoya & Rull, 2011; Montoya et al.,

576   2011c). Thus, axis 2 might reflect changes in the anthropogenic management of

577   the catchment. The presence of charcoal particles associated with MS at the

578   positive end of axis 2 suggests that the burning of vegetal cover could initiate or

579 enhance the erosion of the soils. When fires were reduced and *Cecropia*

580 established (Figure 4), the development of middle to late successional rainforest

581 might have been favored, as indicated by the presence of Urticales (Burn and

582 Mayle, 2008; Gosling et al., 2009) on the negative side of axis 2. The algae

583 were located parallel to Urticales 3-4p, suggesting a positive relationship with

584 forest expansion and a negative relationship with fire frequency.

585

586 6. Discussion and conclusions:

587

588 6.1.The role of environmental drivers in the SE Gran Sabana

589

590 6.1.1. Interplay between climate and fire

591 Climate alone was not the determining factor affecting the vegetation dynamics

592 during both dry (~8700 to 6700 cal yr BP) and wet (~6700 cal ky BP to present)

593 periods. The moisture content of a fuel source, which is determined by the

594 preceding rainfall, affects how readily it will burn, thus acting as a regulator of

595 fire in tropical systems (Cochrane and Ryan, 2009). Thus, higher available

596 moisture restricted the incidence of fire (Figure 7). Hence, the predominance of

597 savanna during early to middle Holocene would be the result of the positive

598 feedback between dry conditions, fires and grassy vegetation. A similar

599   reinforcing feedback of open savanna occurred near Mapaurí record during

600   early Holocene (Rull, 2007; Figure 1a). When climate conditions turned wetter

601   ~6700 cal yr BP, fire ignition was reduced. After longer fire-free intervals, trees

602   would have reached a fire-suppression threshold through the development of a

603   sufficient canopy cover, which prevented the growth of grasses (Hoffmann et

604   al., 2012a). The synergistic action between reduced fires and a wetter climate

605   appears to be a determinant in the development of rainforest. Thus, we suggest

606   that during early to middle Holocene the fire regime may have been unaffected

607   by humans.

608

609   Despite the wetter conditions that occurred since ~5400 cal yr BP, the savanna

610   expansion would have been the result of forest burning, which could be caused

611   by fires set by humans (Montoya et al., 2011b). The coexistence of wetter

612   conditions, forest vegetation and fires might be explained by land-use practices

613   similar to those currently found in many neotropical forested landscapes (e.g.,

614   slash-and-burn), in which small forest spots are cleared and burned for shifting

615   agriculture (known locally as *conucos*). Shifting cultivation practices apparently

616   occurred in the El Paují region, south of Lake Encantada, from 7700-to 2700 cal

617   yr BP (Montoya et al., 2011b; Figure 1a). Considering a lag of about 2300 years

618   between the start of *conucos* in El Paují and Lake Encantada, palaeoecological

619   results might suggest that semi-nomadic and forest-like indigenous culture

620   migrated northward from the southernmost part of the GS. Fires increased after

621   6200 cal yr BP and since 5400 cal yr BP forest retreated gradually. The forest

622   communities in the GS have been considered low resilient to burning (Fölster et

623   al., 2001). However, this evidence might indicate that forest communities may

624   have been resilient and recurrent burns could have reduced their resilience.

625   This ecological feature of GS forest communities needs further assessment. An

626   apparent shift in land-use practices towards more extensive use of fire in open

627   landscapes was recorded ~2000 years ago and continued to the present in

628   several of the GS localities (El Paují, Lake Chonita, Urué, Divina Pastora, Santa

629   Teresa; Montoya et al., 2009, 2011b,c; Rull 1992,1999; Figure 1a). In El Paují,

630   humans appear to have abandoned the study area around 2700 cal yr BP,

631   although the area could have been populated again from 1400 cal yr BP

632   onwards by a different culture (Montoya et al., 2011b). A change to a new-

633   savanna like culture could have also occurred near Lake Encantada around

634   1700 cal yr BP. Drier conditions may have been influential in the maintenance

635   of savanna vegetation and continuity of fires. Recurrent burns were required to

636   maintain the openness of the landscape and allowed the development of highly

637   flammable vegetation, which drove the ecosystem to a treeless savanna state

638   during the last two millennia (Montoya & Rull, 2011).

639

640   6.1. 2. Interplay between erosion and fire

641   In the GS, soil erosion is greatly enhanced when the organic-rich surface layer

642   is lost along with the forest vegetation (Fölster, 1986). Thus, the prolonged loss

643   of forests could be associated with the progressive loss of soil water and

644   nutrients, which could have subsequently hindered re-establishment of tree

645   species. Moreover, because of the shallow root system (Dezzeo et al., 2004),

646   calcium deficiency and limited water retention capacity of the soils, tree

647   mortality (Fölster et al., 2001) and drying of the soils might have been

648   significantly affected by fire. Therefore, the synergism between fire and erosion

649   could have resulted in forest instability, promoting an increase in soil erosion

650   and nutrient loss. This synergism would have favored the establishment of the

651   grass stratum. This process was likely triggered by fires, but maintained by

652   enduring soil-stress conditions. Rull (1992) suggested that the burning of the

653   GS forests has initiated a degenerative and irreversible process that when

654   coupled with soil degradation (Rull et al., 2013), results in the savanna

655   expansion (Rull, 1992,1999). The interplay between fire, erosion and the grass

656   vegetation was probably intensified around 5400 cal yr BP, enabling the

657   landscape change to open savanna with forest patches. That state remained

658   until ~2000 years ago, when the shift of land use practices allowed surpassing

659   the tipping point towards an irreversible expansion of savanna, reinforced by

660   drier climates. Thus, due to the opening of the landscape, the synergistic action

661   between fire and erosion appears to have increased during the last 2000 years.

662

663   The Lake Encantada record, combined with former paleoecological studies

664   (e.g., El Paují, Chonita, Urué), allows for the reconstruction of the regional

665   picture of environmental change and land-use patterns in the southern GS, and

666   for the assessment of competing hypotheses (climate, fire, soils) for explaining

667   the maintenance of the savanna.

668

669   6.2. Relationship between GS savannas and other moist savanna areas

670

671   Although the GS has different vegetation types, human history and lower

672   climatic variability than the Brazilian savannas (Cerrado biome), it shares a

673   long-history of fire regime, poor soil conditions (e.g., low pH, high aluminum

674   concentrations, poor nutrient availability) and climatic fluctuations during the

675   Holocene. Humid climate conditions would also favor the establishment of forest

676   instead of savanna (Oliveira-Filho and Ratter, 2002). It is widely accepted that

677   climate, soils and fire have been highly interactive in their effect on Cerrado

678   vegetation (Oliveira-Filho and Ratter, 2002). The complex interaction of these

679   factors in the GS was first assessed and recognized in this study. Climate alone

680   does not explain the current predominance of savannas in these two humid

681   regions. We consider that, as in Cerrado biome (Pinheiro and Monteiro, 2010),

682   climate has been the trigger of this assumed interaction in vegetation history of

683   the GS during the early Holocene. Seasonal and/or dry climate may have

684   produced conditions prone to fires (Oliveira-Filho and Ratter, 2002) in Cerrados,

685   and our evidence shows that that this also occurred in the GS. Recurrent fires

686   apparently tended to prevent forest recovery and caused soil impoverishment in

687   these two regions (Cerrados: Oliveira-Filho and Ratter, 2002). In some areas of

688   Cerrado, the transition from forest to savanna seems to have been related to

689   edaphic factors rather than to fire action (Pinheiro and Monteiro, 2010).

690   However, limited data in the GS (this study) suggests that fires would have

691   primarily driven this vegetation shift. Fires and soils have shown to be selective

692   agents of savanna vegetation (e.g., fire-adapted and fire-dependent species) in

693   the Brazilian savanas (Pinheiro and Monteiro, 2010), in which environmental

694   factors are better understood (Oliveira-Filho and Ratter, 2002). Therefore,

695   further assessment of the role played by fires and soils and the interplay

696   between these two drivers is required in the GS. Since the middle Holocene, the

697   failure of Cerrado (Ledru et al., 1998) and GS forests (Montoya et al., 2011b) to

698   expand into savanna may be largely caused by human-induced fires through

699   shifting cultivation (Pivello 2011), overriding the effect of wetter conditions

700   (Ledru, 1993; Montoya et al., 2011b). We believe that the interplay between

701   fires and soil conditions has played a role in the vegetation history in humid

702   Neotropical savanna areas and that humans may have largely influenced it.

703

704

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706

719

720 References

721

722 Accatino F and De Michele C (2013) Humid savanna-forest dynamics: Amatrix
723   model with vegetation-fire interactions and seasonality. *Ecological*
724   *Modelling* 265: 170-179
725 Barbosa RI and Campos C (2011) Detection and geographical distribution of
726   clearing areas in the savannas ('lavrado') of Roraima using Google
727   Earth web tool. *Journal of Geography and Regional Planning* 4: 122-
728   136.
729 Beckage B, Platt WJ, Gross LJ (2009) Vegetation, Fire, and Feedbacks:
730   A Disturbance‑Mediated Model of Savannas. *The American Naturalist*
731   174: 805–818.
732 Behling H and Hooghiemstra H (1998) Late Quaternary palaeoecology and
733   palaeoclimatology from pollen records of the savannas of the Llanos
734   Orientales in Colombia. *Palaeogeography,*
735   *Palaeoclimatology,Palaeoecology* 139: 251–267.
736 Behling H and Hooghiemstra H (1999) Environmental history of the Colombian
737   savannas of the Llanos Orientales since the LGM from El Piñal and
738   Carimagua. *Journal of Paleolimnology* 21: 461-476.
739 Behling H and Hooghiemstra H (2000) Holocene Amazon rainforest-savanna
740   dynamics and climatic implications: high-resolution pollen record from
741   Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science*
742   15: 687–695.
743 Bengtsson L and Enell M (1986) Chemical analysis. In: Berglund BE (eds).
744   Handbook of Holocene Palaeoecology and Palaeohydrology. John
745   Wiley & Sons Ltd. Chichester: pp. 423–451.
746 Bennett KD (1996) Determination of the number of zones in a
747   biostratigraphical sequence. *New Phytologist* 132: 155–170.
748 Berry PE, Yatskievych K, Holst BK (1995) Miconia. In: Steyemark, JA,
749   Berry PE, Holst BK (eds) Flora of the Venzuelan Guayana.
750   Volume 6. Missouri Bot. Gard. Press.St. Louis:
751   pp. 387-468.
752 Bhagwat SA, Nogué S, Willis KJ (2012) Resilience of an ancient tropical forest
753   landscape to 7500 years of environmental change. *Biological*
754   *Conservation* 153: 108–117.
755 Bilbao B, Leal A, Méndez C et al. (2009) The role of
756   fire in the vegetation dynamics of upland savannas of the Venezuelan

757   Guayana. In: Cochrane MA, Ryan KC (eds) Tropial fire

758   ecology: Climate Change, Land Use and Ecosystem Dynamics.

759   Springer, pp 451-476.

760   Bilbao BA, Leal AV, Méndez CL (2010) Indigenous Use of Fire and

761   Forest Loss in Canaima National Park, Venezuela. Assessment of and

762   Tools for Alternative Strategies of Fire Management in Pemón

763   Indigenous Lands. *Human Ecology* 38: 663–673.

764   Blaauw M (2010) Methods and code for "classical" age-modelling of

765   radiocarbon sequences. *Quaternary Geochronology* 5:512–518.

766   Blackford J (2000) Palaeoclimatic records from peat bogs. *Trends in Ecology*

767   *& Evolution* 15: 193-198.

768   Breman E, Gillson L, Willis K (2011) How fire and climate shaped grass-

769   dominated vegetation and forest mosaics in northern South Africa

770   during past millennia. *The Holocene* 22: 1427–1439.

771   Brown AG, Carpenter RG, Walling DE (2007) Monitoring fluvial pollen transport,

772   its relationship to catchment vegetation and implications for

773   palaeoevironmental studies. *Review of Palaeobotany and Palynology*

774   147: 60–76

775   Burn MJ and Mayle FE (2008) Palynological differentiation between genera of

776   the Moraceae family and implications for Amazonian palaeoecology.

777   *Review of Palaeobotany and Palynology* 149: 187–201.

778   Burn MJ, Mayle FE, Killeen TJ (2010) Pollen-based differentiation of Amazonian

779   rainforest communities and implications for lowland palaeoecology in

780   tropical South America. *Palaeogeography,*

781   *Palaeoclimatology,Palaeoecology* 295: 1–18.

782   Clark JS, Lynch J, Stocks BJ et al. (1998) Relationships

783   between charcoal particles in air and sediments in west-central Siberia.

784   *The Holocene* 8: 19-29.

785   Cochrane MA and Ryan KC (2009) Fire and fire ecology: Concepts and

786   principles. In: Cochrane MA (eds) Tropial fire ecology: Climate

787   Change, Land Use and Ecosystem Dynamics. Springer, pp. 25-55.

788   Cohen AS (2003) Paleolimnology: The History and Evolution of Lake

789   Systems, Oxford University Press.

790   Colinvaux PA, De Oliveira PE, Moreno JE (1999) Amazon Pollen

791   Manual and Atlas, Harwood Academic Publishers, Amsterdam.

792   Croudace IW, Rindby A, Rothwell RG (2006) ITRAX: description and evaluation

793   of a new multi-function X-ray core scanner. In: Rothwell, R.G. (Ed.), New

794   Techniques in Sediment Core Analysis. The Geological Society of

795   London, London, pp. 51–63.

796   Dezzeo N, Chacón N, Sanoja E et al. (2004) Changes in soil

797   properties and vegetation characteristics along a forest-savanna
798   gradient in southern Venezuela. *Forest Ecology and Management* 200:
799   183–193.
800 Eden MJ (1974) Paleoclimatic influences and the development of savanna
801   in southern Venezuela. *Journal of Biogeography* 1: 95-109.
802 Fölster H (1986) Forest–savanna dynamics and desertification processes in
803   the Gran Sabana. *Interciencia* 11(6): 311–316.
804 Fölster H, Dezzeo N, Priess J (2001) Soil–vegetation relationship in base-
805   deficient premontane moist forest–savanna mosaics of the Venezuelan
806   Guayana. *Geoderma* 104: 95–113.
807 Frost TM (2001) Terrestrial, Algal, and Siliceous Indicators. In: Smol JP,
808   Birks HJ, Williams M (eds) Tracking Environmental Change Using
809   Lake Sediments. Volume 3. Kluwer Academic Publishers, pp.253-264.
810 Gómez E, Picón G, Bilbao B (2000) Los incendios forestales en Iberoamérica.
811   Caso Venezuela. In: Vélez-Muñoz R (eds) La defensa
812   contra incendios forestales, Fundamentos y experiencias.McGraw-Hill,
813   Madrid.
814 Gosling WD, Mayle FE, Tate NJ et al. (2009) Differentiation between
815   Neotropical rainforest, dry forest, and savannah ecosystems by their
816   modern pollen spectra and implications for the fossil pollen record.
817   *Review of Palaeobotany and Palynology* 153: 70–85.
818 Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for
819   estimating organic and carbonate content in sediments: reproducibility
820   and comparability of results. *Journal of Paleolimnology* 25: 101–110.
821 Hernández L and Fölster H (1994) Vegetación en transición. *Scientia*
822   *Guayanae* 4: 118-144.
823 Hernández L (1999) Fisionomía y estructura de bosques submesotérmicos y
824   mesotérmicos. In: Hernández L (eds) Ecología de la altiplanicie de la
825   Gran Sabana(Guayana Venezolana) II. Estructura, diversidad,
826   crecimiento y adaptación en bosques de las subcuencas de los ríos
827   Yuruaní y Alto Kukenán. Scientia Guayanae.Volume 9. Ediciones
828   Tamandúa. Caracas, pp. 5–34.
829 Herrera LF and Urrego, LE (1996) Atlas de polen de plantas útiles y cultivadas
830   de la Amazonia colombiana, Tropenbos Colombia, Colombia.
831 Hoffmann WA, Geiger EL, Gotsch SG et al. (2012a) Ecological thresholds at
832   the savanna-forest boundary: how plant traits, resources and fire
833   govern the distribution of tropical biomes. *Ecology Letters* 15: 759–768.
834 Hoffmann WA, Jaconis SY, Mckinley KL et al. (2012b) Fuels or microclimate?
835   Understanding the drivers of fire feedbacks at savanna-forest
836   boundaries: Flammability of savanna-forest boundary. *Austral Ecology*

837   37: 634–643.
838   Huber O (1986) La vegetación de la cuenca del río Caroní. *Interciencia*
839   11(6): 301–310.
840   Huber O (1995a) Geographical and physical features. In: Steyemark JA,
841   Berry PE, Holst BK (eds) Flora of the Venzuelan Guayana.
842   Volume 1. Introduction. Missouri Botanical Garden. Press. St. Louis, pp.
843   1-62.
844   Huber, O (1995b) Vegetation. In: Steyemark JA, Berry PE, Holst BK
845   (eds) Flora of the Venzuelan Guayana. Volume 1. Introduction.
846   Missouri Botanical Garden. Press. St. Louis, pp.97-160.
847   Jeltsch F, Weber GE, Grimm V (2000) Ecological buffering mechanisms
848   in savannas: A unifying theory of long-term tree-grass coexistence.
849   *Plant Ecology* 161: 161-171.
850   Jones HT, Mayle FE, Pennington RT, Killeen TJ (2011) Characterisation of
851   Bolivian savanna ecosystems by their modern pollen rain and
852   implications for fossil pollen records. *Review of Palaeobotany and*
853   *Palynology* 164: 223–237
854   Kingsbury D (2001) Impacts of land use and cultural change in a fragile
855   environment: indigenous acculturation and deforestation in kavanayén,
856   Gran Sabana, Venezuela. *Interciencia* 26: 327–336.
857   Krammer K, Lange-Bertalot H (1986–1991) Süsswasserßora von
858   Mitteleuropa, (4 volumes). Gustav Fischer Verlag: Stuttgart.
859   Leal A, Berrío JC, Raimúndez E et al. (2011) A pollen atlas of
860   premontane woody and herbaceous communities from the upland
861   savannas of Guayana, Venezuela. *Palynology* 35: 226–266.
862   Leal A, Bilbao B, Berrío JC (2013) A Contribution to Pollen Rain
863   Characterization in Forest-Savanna Mosaics of the Venezuelan Guayana
864   and Its Use in Vegetation Reconstructions from Sedimentary Records.
865   *American Journal of Plant Sciences* 4: 33–52.
866   Ledru MP (1993) Late Quaternary environmental and climatic changes in
867   central Brazil. *Quaternary Research* 39:90–98.
868   Ledru MP, Salgado-Labouriau ML, Lorscheitter ML (1998) Vegetation
869   dynamics in southern and central Brazil during the last 10,000 yr
870   BP. *Review of Palaeobotany and Palynolog*y 99:131–142.
871   Marchant R, Almeida L, Behling H et al. (2002) Distribution and ecology of
872   parent taxa of pollen lodged within the Latin American Pollen Database.
873   *Review of Palaeobotany and Palynology* 121: 1–75.
874   Mayle FE and Power MJ (2008) Impact of a drier Early-Mid-Holocene climate
875   upon Amazonian forests. *Philosophical Transactions of the Royal Society*
876   *B Biological Sciences* 363: 1829–1838.

877 Mayle FE and Iriarte J (2012) Integrated palaeoecology and archaeology e a
878   powerful approach for understanding pre-Columbian Amazonia. *Journal*
879   *of Archaeological Science*, http://dx.doi.org/10.1016/j.jas.2012.08.038
880 Meyers PA and Lallier-Vergés E (1999) Lacustrine sedimentary organic matter
881   records of Late Quaternary paleoclimates. *Journal of Paleolimnology* 21:
882   345-372
883 Montoya E, Rull V, Nogué S et al. (2009) Paleoecología del Holoceno en la
884   Gran Sabana, SE Venezuela: Análisis preliminar de polen y
885   microcarbones en la Laguna Encantada. *Collectanea Botanica* 28: 65–
886   79.
887 Montoya E and Rull V (2011) Gran Sabana fires (SE Venezuela):
888   paleoecological perspective. *Quaternary Science Reviews* 30: 3430–
889   3444.
890 Montoya E, Rull V, Stansell ND et al. (2011a) Vegetation changes in the
891   Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron.
892   *Journal of Quaternary Science* 26: 207–218.
893 Montoya E, Rull V, Nogué S (2011b) Early human occupation and land
894   use changes near the boundary of the Orinoco and the Amazon basins
895   (SE Venezuela): Palynological evidence from El Paují record.
896   *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 413–426.
897 Montoya E, Rull V, Stansell ND et al. (2011c) Forest–savanna–morichal
898   dynamics in relation to fire and human occupation in the southern Gran
899   Sabana (SE Venezuela) during the last millennia. *Quaternary Research*
900   76: 335–344.
901 Murphy BP and Bowman DMJS (2012) What controls the distribution of tropical
902   forest and savanna?. *Ecology Letters* 15: 748–758.
903 Oliveira-Filho AT and Ratter JA (2002) Vegetation physiognomies and woody
904   flora of the Cerrado Biome. In: Paulo S. Oliveira; Robert J. Marquis.
905   (Org.). The Cerrados of Brazil: ecology and natural history of a
906   Neotropical savanna. New York: Columbia University Press. p. 91-120.
907 Pessenda LCR, Gouveia SEM, Ribeiro A et al. (2010) Late Pleistocene and
908   Holocene vegetation changes in northeastern Brazil determined from
909   carbon isotopes and charcoal records in soils. *Palaeogeography,*
910   *Palaeoclimatology, Palaeoecology* 297: 597–608.
911 Pinheiro MHO and Monteiro R (2010) Contribution of the discussions on the
912   origin of the cerrado biome: Brazilian savanna. *Brazilian Journal of*
913   *Biology* 70(1): 95-102.
914 Pivello VR (2011) The Use of Fire in the Cerrado and Amazonian Rainforests of
915   Brazil: Past and Present. *Fire Ecology* 7:1, 24-39.
916 Roubik DW and Moreno JE (1991) Pollen and Spores of Barro Colorado

917   Island, Missouri Botanical Garden, Missouri.

918 Rull V (1987) A note on pollen counting in palaeoecology. *Pollen et Spores*
919   29: 471–480.

920 Rull V (1992) Successional Patterns of the Gran Sabana (Southeastern
921   Venezuela) Vegetation During the Last 5000 Years, and Its Responses
922   to Climatic Fluctuations and Fire. *Journal of Biogeography* 19: 329-338.

923 Rull V (1999) A palynological record of a secondary succession after fire in the
924   Gran Sabana, Venezuela. *Journal of Quaternary Science* 14: 137–152.

925 Rull V (2003) An illlustrated key for the identification of pollen from Pantepui and
926   the Gran Sabana (eastern Venezuelan Guayana). *Palynology* 27: 99-
927   133.

928 Rull V (2007) Holocene global warming and the origin of the Neotropical
929   Gran Sabana in the Venezuelan Guayana. *Journal of Biogeography* 34:
930   279–288.

931 Rull V, Montoya E, Nogué S (2013) Ecological palaeoecology in the neotropical
932   Gran Sabana region: Long-term records of vegetation dynamics as a
933   basis for ecological hypothesis testing. *Perspectives in Plant Ecology,*
934   *Evolution and Systematics* 15(6): 338-359.

935 Sáez A, Valero-Garcés BL, Giralt S, Moreno A, Bao R, Pueyo JJ, Hernández,
936   A, Casas D (2009) Glacial to Holocene climate changesin the SE Pacific.
937   The Raraku Lake sedimentary record (Easter Island, 27º S). *Quaternary*
938   *Science Reviews* 28: 2743-2759.

939 Schubert C and Huber O (1989) The Gran Sabana: Panorama of a region.
940   Cuadernos LAGOVEN, Caracas.

941 Vélez MI, Hooghiemstra H, Metcalfe S et al. (2003) Pollen- and diatom based
942   environmental history since the Last Glacial Maximum from the Andean
943   core Fúquene-7, Colombia. *Journal of Quaternary Science* 18(1): 17-30.

944 Warrier AK and Shankar R (2009) Geochemical evidence for the use of
945   magnetic susceptibility as a paleorainfall proxy in the tropics. *Chemical*
946   *Geology* 265: 553–562.

947 Wright HE, Mann DH, Glaser PH (1984) Piston corers for peat and lake
948   sediments. *Ecology* 65: 657–659.

949 Ziegler M, Jilbert T, de Lange GJ, Lourens LJ, Reichart GJ (2008) Bromine
950   counts from XRF scanning as an estimate of the marine organic carbon
951   content of sediment cores. *Geochemistry, Geophysics, Geosystems*, 9,
952   Q05009, doi:10.1029/2007GC001932.

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957 Figure captions

958 Figure 1. A) Location of the study area and its position within northern South

959 America. The Gran Sabana is delimited by the white square. The coring site is

960 indicated by a star. Numbers indicate the sites with paleoecological information

961 mentioned in the text: 1 — Roraima savannas; 2 —*Llanos* (Llanos Orientales of

962 Colombia and Venezuelan Orinoco llanos); 3 — Northern Amazonia; 4 —

963 Northern Andes; 5 — Encantada peat-bog; 6 — Mapaurí; 7 — El Paují; 8 —

964 Lake Chonita; 9 — Urué; 10 — Divina Pastora); 11 — Santa Teresa. B) Lake

965 Encantada. *Morichales* bordering the lake shore. Regional open savanna

966 landscape. (Photo: V. Rull, 2007).

967

968 Figure 2. Core stratigraphy with radiocarbon ages, sediment description, age-

969 depth model of the sequence, pollen and lithological zones.

970

971 Figure 3. Elemental counts (Si, K, Ti, Mn, Fe, Co, Ni, Zn, As, Se, Br, Rb, Sr, Zr),

972 Inc/coh fraction, magnetic susceptibility (MS), bulk density (BD), Total inorganic

973 carbon (TIC), total organic carbon (TOC), total nitrogen (TN), nitrogen isotope

974 (δ15N), carbon isotope (δ13C) and C/N ratio in terms of depth. Calibrated ages

975 shown on the right side are based on the age depth model outputs

976

977   Figure 4. Diagram showing percentage of pollen taxa and influx of charcoal.

978   Solid lines represent ×10 exaggeration. Representation of the lithology: ■

979   Brown clays, □ Yellowish-white clays, ■ Yellowish-brown clays and ▨ White

980   sands.

981

982   Figure 5. Diagram showing the elements outside the pollen sum, such as the

983   aquatic and semi-aquatic plants, pteridophyte spores, algal remains, and

984   silicobioliths traces. The abundances are expressed in percentages with respect

985   to the pollen sum. Silicobioliths traces are expressed as barren (empty space)

986   and present (filled space). Diatoms taxa. C.c= *C. cylopuncta*, A.m=

987   *Achnanthidium minutissimum*, N.p= *Nitzschia palea*, N.c= *Nitzschia capitellata*,

988   S.p= *Sellaphora pupula*, A.p= *Amphora pediculus*, N.v1= *Navicula veneta*,

989   N.V2= *Navicula viridula* var.*rostellata,* A.V=*Amphora veneta*, C.p= *Cocconeis*

990   *placentula* var. *euglypta*, C= *Craticula sp*.

991

992   Figure 6. Diagram showing the influx values of the main taxa, total algae and

993   microcharcoal particles. Calibrated ages shown on the right side are based on

994   the age depth model outputs

995

996   Figure 7. Biplot of the canonical correspondence analysis (CCA). Numbers

997   correspond to the sample's core depth (cm). ENC-I, ENC-II and ENC-III

998   correspond to pollen zones. Barren zone ENC-BZ is not included.

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