# Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron

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ENCARNI MONTOYA,[1,2]* VALENTI RULL,[1] NATHAN D. STANSELL,[3] BROXTON W. BIRD,[3]
SANDRA NOGUÉ,[1,4] TERESA VEGAS-VILARRÚBIA,[5] MARK B. ABBOTT[6] and WILMER A. DÍAZ[7]

[1]Palynology and Palaeoecology Lab, Botanical Institute of Barcelona, Barcelona, Spain
[2]Department of Animal Biology, Plant Biology and Ecology, Autonomous University of Barcelona, Campus Bellaterra, 08193 Barcelona, Spain
[3]Byrd Polar Research Center, The Ohio State University, Columbus, OH, USA
[4]Oxford Long Term Ecology Lab, Biodiversity Institute, Department of Zoology, South Parks Road, Oxford, UK
[5]Department of Ecology, University of Barcelona, Barcelona, Spain
[6]Department of Geology and Planetary Science, University of Pittsburgh, Pittsburgh, PA, USA
[7]CIEG – UNEG, Puerto Ordaz, estado Bolivar, Venezuela

ABSTRACT: The occurrence of the Younger Dryas cold reversal in northern South America midlands and lowlands remains controversial. We present a palaeoecological analysis of a Late Glacial lacustrine section from a midland lake (Lake Chonita, 4.6501 °N, 61.0157 °W, 884 m elevation) located in the Venezuelan Gran Sabana, based on physical and biological proxies. The sediments were mostly barren from ~15.3 to 12.7 k cal a BP, probably due to poor preservation. A ligneous community with no clear modern analogues was dominant from 12.7 to 11.7 k cal a BP (Younger Dryas chronozone). At present, similar shrublands are situated around 200 m elevation above the lake, suggesting a cooling-driven downward shift in vegetation during that period. The interval from 11.7 to 10.6 k cal a BP is marked by a dramatic replacement of the shrubland by savannas and a conspicuous increase in fire incidence. The intensification of local and regional fires at this interval could have played a role in the vegetation shift. A change to wetter, and probably warmer, conditions is deduced after 11.7 k cal a BP, coinciding with the early Holocene warming. These results support the hypothesis of a mixed origin (climate and fire) of the Gran Sabana savannas, and highlight the climatic instability of the Neotropics during the Late Glacial. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: Fire; Late Glacial; Neotropics; vegetation change; Younger Dryas.

## Introduction

A relevant objective in palaeoecological research is the study of biotic responses to climatic changes (Huntley, 1990). Recently, emphasis has been placed on vegetation changes linked to rapid climate shifts, which has been useful in proposing future scenarios of climate change (Solomon *et al.*, 2007; Willis *et al.*, 2007). The Younger Dryas (YD) was an abrupt cooling recorded between about 12.85 and 11.65 k cal a BP, between the Bølling/Allerød (B/A) interstadial and the period of early Holocene warming (EHW) in the Northern Hemisphere (Rasmussen *et al.*, 2006). One of the more accepted causes for the YD cooling is a decrease in the Atlantic thermohaline circulation, which caused a reduction in heat transport from the tropics to the North Atlantic, although other hypotheses have been proposed (Firestone *et al.*, 2007). This may have been produced by a decrease in North Atlantic water density caused by the rapid release of meltwater from the Laurentide ice sheet of North America (Alley, 2000). Most evidence for the YD has been found in the North Atlantic region and adjacent locations under its influence, giving raise to the hypothesis that the YD may not be a global phenomenon (Bennett *et al.*, 2000). The lack of YD cooling and drying signals at some locations in southern South America and Australasia, on both sides of the Pacific Ocean, seems to support this view (Bennett *et al.*, 2000; Rodbell, 2000; Barrows *et al.*, 2007; Williams *et al.*, 2009).

There is a general lack of sufficient age control between 14 and 10 k cal a BP in most palaeoecological records within the Neotropical region to allow for clear identification of YD

events (van't Veer *et al.*, 2000). In Central America, there are two records from Guatemala and Costa Rica which show a clear relationship with the onset of the YD, but the transition to the Holocene remains poorly dated (van't Veer *et al.*, 2000). For example, in a well-dated record from northern Guatemala, Hodell *et al.* (2008) observed a gypsum deposit was formed at 12.8 k cal a BP, indicating the onset of dry conditions. In Costa Rica, a cold reversal termed the La Chonta stadial was recorded, characterized by a downward migration of mountain forest by 300–400 m, which equates to a decrease of 2–3 °C (Islebe *et al.*, 1995). In South America, most YD evidence has been restricted to the Andes. However, reconstructions at different Andean sites have led to conflicting results (Rodbell *et al.*, 2009). For instance, Thompson *et al.* (1998) documented a cold and wet reversal during the YD from Bolivian ice cores. Others have used glacial deposits to identify the YD as a period of increased aridity in the Peruvian Andes associated with glacial retreat (Rodbell and Seltzer, 2000; Seltzer *et al.*, 2000). North of the equator, one of the more convincing Andean YD equivalents is the El Abra stadial, recorded in Colombia since 11.2 k [14]C a BP (13.1 k cal a BP), for which a temperature decrease of 1–3 °C below present has been estimated (van der Hammen and Hooghiemstra, 1995; van't Veer *et al.*, 2000). In the Venezuelan Andes, the Mucubají Cold Humid phase, between 11.7 and 9.4 k [14]C a BP (13.5–10.6 k cal a BP), was characterized by a temperature decrease of 2–3 °C below present (Salgado-Labouriau, 1989), although dating lacks the required precision. Other studies in nearby locations show decreases in pollen forest around 12.6 k cal a BP, but clear evidence of vegetation and climate change has not been found (Rull *et al.*, 2005, 2008). Mahaney *et al.* (2008) provided evidence of several peat layers and wood fragments within postglacial moraines and sediments dated between 18.8 and 12.4 k cal a BP, some of which might correspond to potential YD glacial advances. Recently, Stansell *et al.* (2010)

*Correspondence: E. Montoya, Department of Animal Biology, Plant Biology and Ecology, Autonomous University of Barcelona, Campus Bellaterra, 08193 Barcelona, Spain.
E-mail: Encarni.Montoya@uab.cat

documented a decrease in average temperatures of 2.2–2.9 °C between 12.85 and 11.75 k cal a BP, with a downward vegetation displacement of 400–500 m (Rull *et al.*, 2010b). Other evidence has been found in marine cores from the Cariaco Basin (Fig. 1), where the YD appears as a cold and dry event, attributed to the combined action of changes in both the Atlantic Ocean circulation and the position of the Intertropical Convergence Zone (ITCZ) (Peterson *et al.*, 2000; Werne *et al.*, 2000; Haug *et al.*, 2001; Lea *et al.*, 2003; Hughen *et al.*, 2004). Therefore, the bulk of the evidence for the potential occurrence of the YD in the northern South America Neotropics comes from high mountain and marine records, and there is a manifest lack of information at low and mid altitudes (Heine, 2000; van't Veer *et al.*, 2000).

Here we present a palaeoecological study of a lake core from the Gran Sabana (a mid-altitude plateau situated between the Orinoco and the Amazon basins, Fig. 1), based on pollen and spore analysis, and supported by charcoal, diatoms, magnetic susceptibility (MS), bulk density (BD) and organic matter analyses. The aim is to reconstruct the Late Glacial vegetation dynamics from ~15.3 to 10.6 k cal a BP, as well as to derive potential palaeoclimatic and palaeoecological inferences. The study is focused on the potential changes that occurred around the YD chron, and was prompted by the lack of Late Glacial palaeoecological studies in the region and the unknown responses of its unique ecosystems to potential environmental changes.

## Study area

The Gran Sabana (GS) is a vast region of about 18 000 km² located in south-east Venezuela (4.6089–6.6331 °N, 61.0679–74.0478 °W, Fig. 1). It is part of an undulating erosion surface developed on the Precambrian Roraima quartzites and sandstones, and forms an altiplano slightly inclined to the south, ranging from about 750 to 1450 m elevation (Briceño and Schubert, 1990; Huber, 1995a). The climate has been described as submesothermic ombrophilous, with annual average temperatures of around 18–22 °C and precipitation of 1600–2000 mm a⁻¹, with a dry season (<60 mm month⁻¹) from December to March (Huber and Febres, 2000). The GS is a huge island of savanna within the normally forested Guayanan landscape. These savannas form wide, and more or less continuous, treeless grasslands or in some places they are intermingled with forests, thus developing the typical forest–savanna mosaics (Huber, 1994). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b) has led to several hypotheses: (i) the savannas are favoured by poor edaphic (hydrology, nutritional status) conditions (Fölster, 1986; Fölster *et al.*, 2001); (ii) they are relicts of larger savanna extensions, originated in colder and drier epochs (e.g. the Last Glacial Maximum, LGM) (Eden, 1974); (iii) the savannas are the consequence of deforestation by frequent and extensive fires (Dezzeo *et al.*, 2004); or (iv) the present savannas derive from former smaller and scattered savanna patches, the extension of which has been favoured by both climate change and fire (Rull, 1999; Huber, 2006).

The GS savannas are dominated by grasses of the genera *Axonopus* and *Trachypogon* and sedges such as *Bulbostylis* and *Rhyncospora*; woody elements are scarce and rarely emerge above the herb layer (Huber, 1995b). Most GS forests are considered to fall within the category of lower montane forests, because of their intermediate position between lowland and highland forests (Hernández, 1999). Common genera include *Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabeuia* (Bignoniaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chryso-balanaceae), *Clathrotropis* (Fabaceae), *Aspidosperma* (Apocynaceae), *Caraipa* (Clusiaceae), *Dimorphandra* (Caesalpinaceae) and *Byrsonima* (Malpighiaceae), and their composition varies with elevation (Huber, 1995b). The GS shrublands usually occur between 800 and 1500 m elevation and are more frequent at the northern area than at the southern part (Huber, 1995b), where our study site is located. Given the significance of these vegetation types in the present palaeoecological
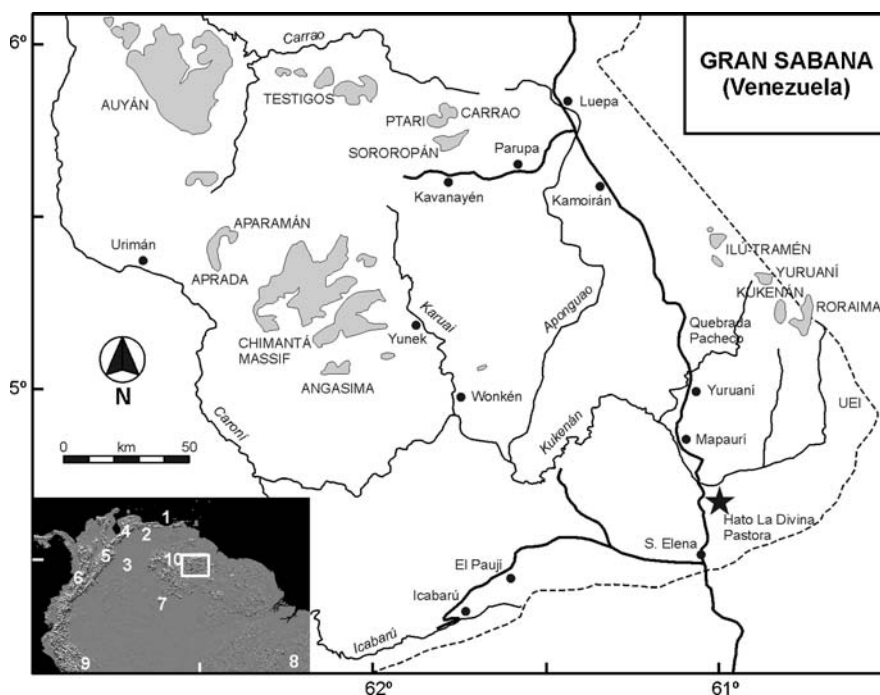


**Figure 1.** Location of the study area and its position within northern South America; radar image courtesy of NASA/JPL-Caltech. The coring site is indicated by a star. Numbers indicate sites with palaeoecological information mentioned in the text: 1, Cariaco Basin (Venezuela); 2, Lake Valencia (Venezuela); 3, Colombian Llanos; 4, Venezuelan Andes; 5, Colombian Andes; 6, Colombian midlands (Cauca Valley); 7, northern Amazon Basin; 8, northern Brazil; 9, Peruvian Andes foothills; 10, Canaima.

reconstruction, a more detailed description is pertinent. The GS shrublands have been classified into four main types, because of the strong dependence on the substrate type (Huber, 1994, 1995b):

1. *Shrublands on rocky soils.* Growing on low to moderately inclined sandstone outcrops. The shrub layer is very dense, and is distributed following a density gradient along the rock slope. The herb layer is irregularly and fragmentarily distributed. Dominant taxa are: *Clusia* (Clusiaceae), *Humiria* and *Sacoglottis* (Humiriaceae), *Euceraea* (Flacourtiaceae), *Euphronia* (Euphroniaceae), *Macairea* (Melastomataceae), *Pagamea* (Rubiaceae), and *Notopora* and *Thibaudia* (Ericaceae) (see Supporting information, Table S1).
2. *Shrublands on sandy soils.* On isolated patches of white sand. The shrub layer is scattered, forming islands in a matrix of bare soil. The herb layer is less developed as in shrublands on rocky soils. Dominant taxa include: *Pera* (Euphorbiaceae), *Emmotum* (Icacinaceae), *Matayba* (Sapindaceae), *Simarouba* (Simaroubaceae), *Gongylolepis* (Asteraceae), *Ternstroemia* (Theaceae) and *Befaria* (Ericaceae) (see supporting Table S2).
3. *Shrublands on ferruginous soils.* Located upon ferruginous duricrust (millimetric or centimetric, hard and iron-rich layer on top of the soil). A peculiar and isolated shrubland type only found north of GS, north-east of the Yuruaní catchment (Fig. 1: Quebrada Pacheco). Both diversity and taxa abundance show great differences with former shrubland types. This formation is organized into three different strata: herbaceous, shrubby and emergent layers. Dominant taxa are: *Bonnetia* (Theaceae), *Phyllantus* (Euphorbiaceae), *Cyrillopsis* (Ixonanthaceae), *Roupala* (Proteaceae) and *Bonyunia* (Loganiaceae) (see supporting Table S3).
4. *Shrublands on peaty soils.* Located also north of GS, between 1000 and 1300 m elevation, showing more similarities with shrublands from the Guayana Highlands (1500–3000 m elevation) than with other GS shrublands. Dominant taxa are: *Bonnetia* (Theaceae), *Chalepophyllum* and *Pagameopsis* (Rubiaceae), *Digomphia* (Bignoniaceae) and *Meriania* (Melastomataceae) (see supporting Table S4).

The GS region is the homeland of the Pemón indigenous group, from the Carib-speaking family. Today they are sedentary, living in small villages usually in open savannas. The Pemón seem to have reached GS very recently, probably around 300 years ago (Thomas, 1982; Colson, 1985). However, there is some archaeological evidence in closer regions with pre-Hispanic remains of ages around 9 k cal a BP (Gassón, 2002). A definitive assessment on the age of settlement of these groups on the GS it is not yet possible with the scarce available evidence. Fire is a key component of the Pemón culture as they use it every day to burn wide extensions of savannas and, occasionally, forests (Kingsbury, 2001). The reasons for the extent and frequency of these fires are related to activities such as cooking, hunting, fire prevention, communication and magic (Rodríguez, 2004, 2007). The Pemón people do not utilize extensive agriculture or livestock, which is typical for cultures strongly linked to fire (Rodríguez, 2004).

## Materials and methods

The study site (4.6501 °N, 61.0157 °W, 884 m elevation) is located within a private farm called 'Hato Divina Pastora' near Santa Elena de Uairén, south of the GS region (Fig. 1). The annual precipitation in Santa Elena, at 910 m altitude, is about 1700 mm, with a weak dry season from December to March (Huber, 1995a). The study lake lies within a treeless savanna landscape, surrounded by scattered palms of *Mauritia flexuosa* forming small stands locally known as 'morichales'. In the absence of a local name for the lake, it is here termed Lake Chonita. The core studied (PATAM1 B07; 4.67 m long) was obtained in the deepest part of the lake (3.13 m water depth), using a modified Livingstone squared-rod piston core (Wright *et al.*, 1984). The present study is focused on the detailed analysis and palaeoecological interpretation of the Late Glacial to early Holocene interval, ranging from 2.97 to 4.67 m. Nine samples were taken along the whole core for radiocarbon dating, four of them falling within the interval discussed here. Samples were pretreated using standard acid-base-acid procedures (Abbott and Stafford, 1996) and measured at the AMS Radiocarbon Laboratory of the University of California (UCI) and at Beta Analytic (Beta). Calibration was made with CALIB 6.0.1 and the IntCal09.14c database (http://calib.qub.ac.uk./calib/, last accessed June 2010).

Thirty-five volumetric samples (2 $cm^3$) were taken in the section studied, at 5-cm intervals, for pollen and diatom analyses. Pollen samples were processed using standard palynological techniques (Bennett and Willis, 2001), with some modifications that have shown to be efficient for Neotropical lake sediments (Rull *et al.*, 2010b), after spiking with *Lycopodium* tablets (batch 177745, average 18 584 ± 1853 spores per tablet). The slides were mounted in silicone oil without sealing. Pollen and spore identification was made according to Hooghiemstra (1984), Moore *et al.* (1991), Roubik and Moreno (1991), Tryon and Lugardon (1991), Herrera and Urrego (1996), Rull and Vegas-Vilarrúbia (1997), Rull (1998, 2003) and Colinvaux *et al.* (1999). Counts were conducted until a minimum of 300 pollen grains and spores were tabulated (excluding Cyperaceae and aquatic plants: *Myriophyllum*, *Sagittaria* and *Utricularia*), but counting continued until the saturation of diversity was reached (Rull, 1987). Final counts averaged 576 grains per sample (excluding barren and very poor samples). Pollen taxa were grouped according to the vegetation types previously described (Huber, 1986, 1989, 1994, 1995b; Huber and Febres, 2000). All pollen taxa identified were included in the pollen sum, except for Cyperaceae and the aquatic plants mentioned above. Pollen diagrams were plotted with PSIMPOLL 4.26, using a time scale derived from an age–depth model based on radiocarbon dating, developed with the clam.R statistical package (Blaauw, 2010). The zonation was performed by Optimal Splitting by Information Content, and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Only pollen types comprising more than 0.35% of the total were considered for zonation. Interpretation was based on comparison with modern samples from previous studies (Rull, 1992, 1999) and the known autoecology of taxa found (Marchant *et al.*, 2002; Rull, 2003). Correspondence analysis (CA) was made with MVSP v.3.13. Charcoal counts were carried out using the same pollen slides, considering two size classes (Rull, 1999): (i) Type I (5–100 μm): used as a proxy for mostly regional fires, because of their easy dispersion by wind; and (ii) Type II (>100 μm): used as a proxy for local fires.

BD was measured on 1-$cm^3$ samples, taken every 5 cm down-core. The samples were weighed wet, and again after drying in a 60 °C oven for 24 h. Total organic matter was measured every 5 cm by loss-on-ignition (LOI) at 550 °C (Dean, 1974). There is no measurable calcium carbonate in the sediments, based on LOI measurements made after burning at 1000 °C. MS was measured at 0.5-cm intervals using a Tamiscan high-resolution surface scanning sensor connected

to a Bartington susceptibility meter at the University of Pittsburgh.

Diatoms were extracted from 1 g of wet sediment. Organic matter was oxidized with a mixture of concentrated sulphuric acid and potassium dichromate. Specimens were mounted in Naphrax and analysed at $1000 \times$ under interferential phase contrast with a Polyvar microscope. Valve concentrations per unit weight of wet sediment were estimated using plastic microspheres (Battarbee and Kneen, 1982). At least 300 valves were counted whenever possible (Flower, 1993; Battarbee et al., 2001; Abrantes et al., 2005). In poorer quality samples, counting was stopped after counting around 1000 microspheres and the results were expressed as traces. Dominant species were identified using specialized literature (Krammer and Lange-Bertalot, 1986–1991; Krammer, 1997; Metzeltin and Lange-Bertalot, 1998; Rumrich et al., 2000; Lange-Bertalot, 2001). Only species comprising >3% of the total abundance were represented individually in the corresponding diatom diagram, the remaining species being included in 'other diatoms'.

## Results and interpretation

### Chronology

The results of accelerator mass spectrometry (AMS) radiocarbon dating (Table 1) were used to produce an age–depth model for the whole sequence. The best fit was obtained with a smooth-spline model (Blaauw, 2010), and is represented in Fig. 2 for the interval of interest. According to this model, sedimentation rates ranged from 0.03 to 0.16 cm a$^{-1}$, and the mean resolution of our analyses was between 31 and 165 years per sampling interval.

### Zonation

The pollen diagram is dominated alternatively by pollen assemblages from two different plant formations: a ligneous community of shrubs, lianas and small trees; and a savanna grassland (Fig. 3). The more abundant pteridophyte spores were Lycopodium cernuum and psilate triletes, with two prominent peaks around the middle of the diagram (Fig. 4). The stratigraphic variations of the pollen and spore assemblages allowed its subdivision into three zones, which are described below for the different proxies analysed.

### CHO-I (4.67–4.00 m, 15.3–12.7 k cal a BP, 14 samples)

This was characterized by grey clay and mottled grey clay with desiccation features. MS values were the highest of the whole section under study, with a slight decrease in the upper part. The dry BD values were high (0.8–1.3 g cm$^{-3}$) and the concentration of organic matter was low (<20%) through-

out this zone (Fig. 2). This section was generally barren for palynomorphs and diatoms, except for several isolated samples with scattered and mostly degraded specimens. At the end of the zone, there was a sudden increase in Lycopodium cernuun (Fig. 4).

The presence of mottled clay may indicate the existence of an intermittent pond, and the absence of palynomorphs and organic material is probably caused by subaerial exposure leading to poor biological preservation. The absence of diatom and other algae remains suggests that the lake did not exist yet, at least in its present condition. The organic matter data support the interpretation based on the pollen evidence of a watershed that was mostly barren of vegetation. This zone probably represents a period of high clastic sedimentation and low plant cover. The sudden increase of Lycopodium cernuun, which in the Guayana region is a common colonizer of open wet areas between 100 and 2200 m elevation (Øllgaard, 1995), at the end of this zone and the beginning of the next one could be indicative of the first colonization steps of the site by terrestrial plants.

### CHO-II (4.00–3.75 m, 12.7–11.7 k cal a BP, five samples)

This intermediate zone is characterized by a shift from grey clay to black peat sediments at the top, a decreasing trend of MS and dry BD values, and increasing amounts of organic matter (Fig. 2). The continuous presence of palynomorphs begins in this zone, around 12.7 k cal a BP, and is marked by a sudden increase of L. cernuum followed by high percentages of pollen from ligneous taxa such as Bonyunia, Protium, Weinmannia, Cyrilla, Miconia, Myrsine, Odontadenia-type and Marcgraviaceae. Poaceae is also present at low concentrations, but increases at the top. Non-identified types show a sudden increase at the beginning of the zone, and are present at low concentrations at the upper part (Fig. 3). L. cernuun peaks at the base and suddenly decreases until it almost disappears. There is a low frequency of algae and Cyperaceae, while diatom valves are almost absent, except for a single sample at the top showing traces of diatoms (Fig. 4). Smaller microcharcoal particles (5–100 μm) are present throughout this section at low concentration, but dramatically increase at the top, together with a slight increase of larger particles (>100 μm) (Fig. 3). Simultaneously, there is a noticeable increase in psilate triletes (Fig. 4) and a change to dark lacustrine sediments (Fig. 2). Pollen and spore influx are high in this interval.

The pollen assemblage suggests a more or less diverse ligneous community, probably a shrubland or a low forest. The composition of this inferred community shows similarities to and differences from present-day GS forests and shrublands. Indeed, most elements (Bonyunia, Protium, Cyrilla, Miconia and Myrsine) are indicative of a shrubland community, but

**Table 1.** AMS radiocarbon dates used for the age–depth model for the whole record.

| Laboratory | Sample no. | Depth (cm) | Sample type | Age (C$^{14}$ a BP) | Age (cal a BP), 2σ | Age (cal a BP) estimation[†] |
|---|---|---|---|---|---|---|
| Beta - 279600 | 3 | 13 | Pollen extract | 890±40 | 731–915 | 803 |
| Beta - 277185 | 11 | 51 | Pollen extract | 2850±40 | 2855–3078 | 2732 |
| Beta - 277184 | 22 | 98 | Pollen extract | 3340±40 | 3471–3643 | 3658 |
| UCI - 43705 | 32 | 144 | Wood | 4080±40 | 4497–4655 | 4642 |
| UCI - 43706 | 49 | 212 | Wood | 6465±25 | 7323–7403 | 7383 |
| Beta - 277186[*] | 70 | 298 | Pollen extract | 9590±60 | 10 738–11 164 | 10 685 |
| UCI - 43537[*] | 87 | 362 | Wood | 9720±70 | 11 063–11 251 | 11 384 |
| Beta - 247284[*] | 93 | 392 | Wood | 10 440±40 | 12 128–12 530 | 12 342 |
| UCI - 43614[*] | 99 | 402 | Wood | 11 005±45 | 12 699–13 078 | 12 736 |

[*]Dates included in the interval under study. [†]Weighed average.
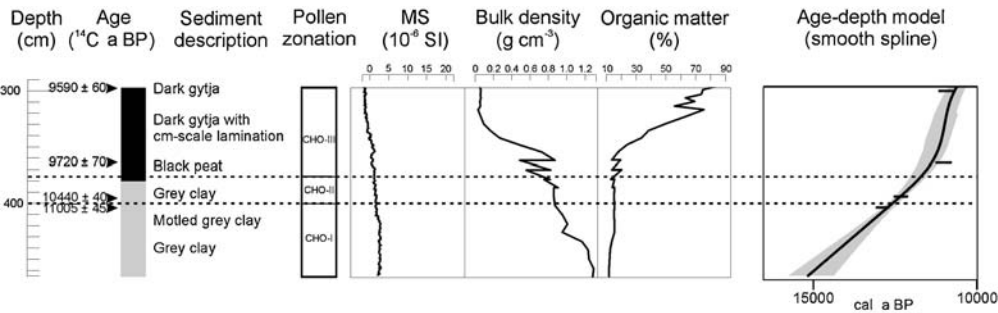
**Figure 2.** Core stratigraphy, with radiocarbon ages and sediment description; pollen zonation; physical parameter curves; and age–depth model of the interval analysed. MS, magnetic susceptibility.



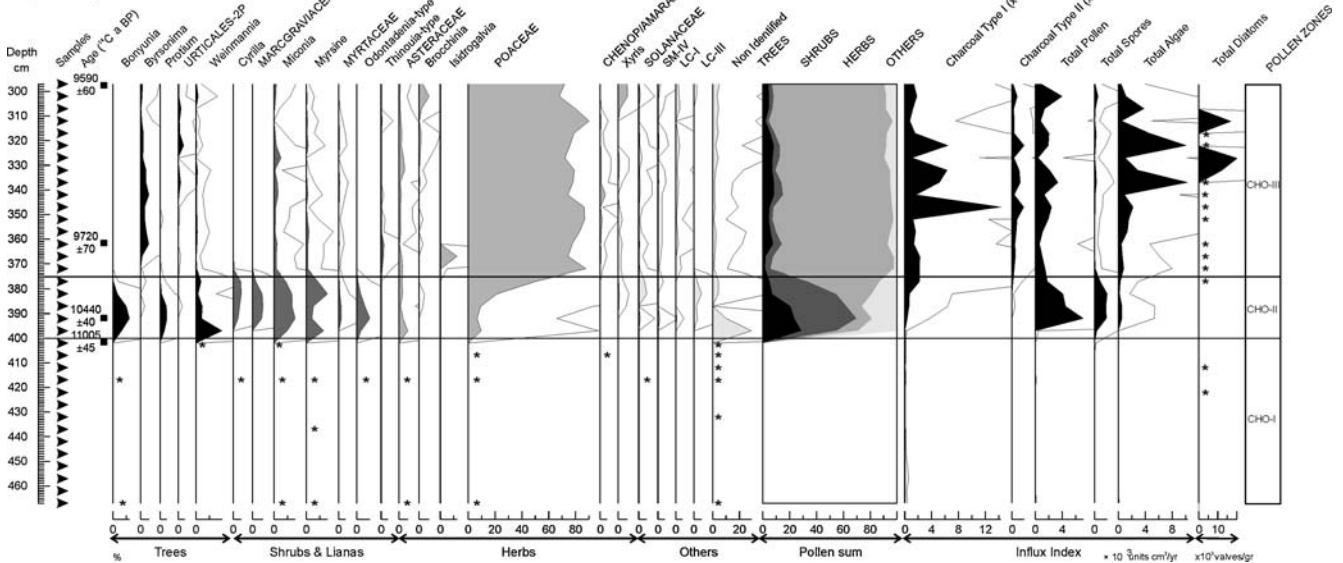**Figure 3.** General pollen diagram with abundance expressed as percentages. Solid lines represent × 10 exaggeration. *Low traces or very low (scattered) presence.
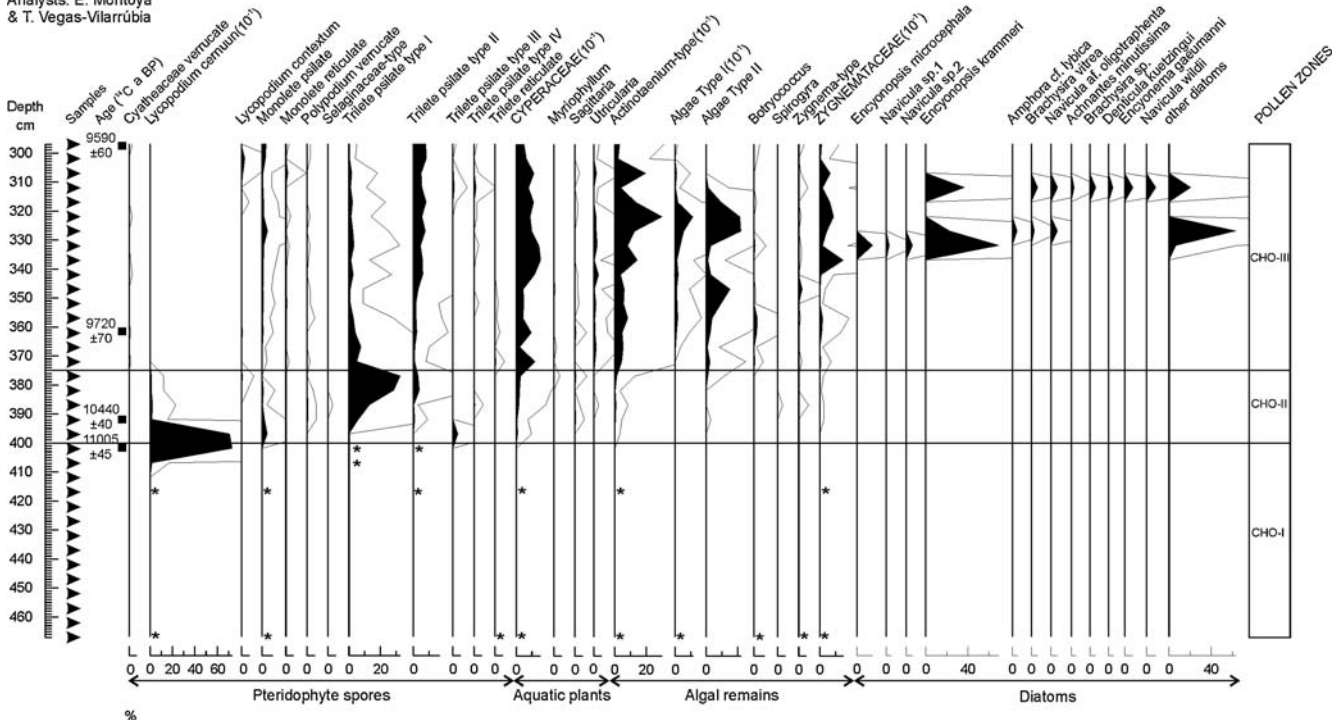


**Figure 4.** Diagram showing the elements outside the pollen sum (pteridophyte spores and aquatic elements). Percentages of pteridophyte spores, aquatic plants and algal remains are based on pollen sum. Percentages of diatoms are based on diatom sum. *Low traces or very low (scattered) presence.

the presence of lianas (such as Marcgraviaceae and *Odonta-denia*-type), common in GS forests, but scarce in the shrublands (Huber, 1994), is unexpected. It is interesting that *Bonyunia*, one of the main components of the pollen assemblage, is only reported as frequent or dominant in a particular and isolated type of shrubland, located at the north of the GS on ferruginous soils. Pollen from aquatic plants, diatoms and other algae taxa appear, but remain scarce probably because of continued subaerial exposure. There are no indications of a lake resembling the present one. The increase of smaller charcoal particles, as proxies for regional fires, is paralleled by a significant increase in psilate trilete spores which, in the GS, represent the earlier stages of secondary succession after fire (Rull, 1999). Local fires, represented by larger charcoal particles, probably started at the end of this zone, around 11.7 k cal a BP.

In summary, between 12.7 and 11.7 k cal a BP, the site was probably covered by an incipient shallow lake surrounded by a shrubland or a low forest community with a composition different from present-day GS similar formations. Increasing concentrations of organic matter and lower BD values indicate a decreased influx of clastic sediments in the lake basin. Regional fires started to occur in this zone and reached the site around the end, but with low frequency/intensity.

### CHO-III (3.75–2.97 m, 11.7–10.6 k cal a BP, 16 samples)

The sediments of this interval are marked by the transition from black peat to dark organic-rich sediments with centimetre-scale lamination in the lower part; this interval has the lowest MS and BD values of the whole section. It also shows a strong increase in organic matter values, with the highest concentrations of the interval under study (Fig. 2). The zone represents a marked change in palynomorph assemblages. At the beginning, there is a sudden drop in all the dominant taxa from the previous zone, and a dramatic increase of Poaceae. Among ligneous elements, *Byrsonima* and, to a lesser extent, Urticales, *Miconia* and Asteraceae become more abundant. At the top of the section, an increase in other herbaceous elements, such as *Brocchinia* and *Xyris*, is recorded (Fig. 3). *L. cernuum* is absent and the psilate triletes of the former zone strongly decreases, while another type of psilate triletes slightly increase. Pollen from aquatics plants (Cyperaceae) increases at the beginning and remains at similar percentages through the whole zone. Diatoms and other algae show a similar trend, with a significant increase at the middle to upper part and a decrease at the top (Fig. 4). Proportions of both smaller and larger charcoal particles remain at the values attained at the end of the former zone (Fig. 3).

At the beginning of this zone, around 11.7 k cal a BP, a dramatic and complete replacement of the former ligneous community by a treeless savanna dominated by grasses is inferred. Diatom assemblages appear for the first time in the record, although valves are found in low quantities (Fig. 3). The most frequent diatom species are *Encynopsis krammeri* and *E. microcephala*, but species diversity is high and many species appear with abundances <3% (Fig. 4). The species found are commonly reported in peaty environments and suggest the existence of dystrophic and oligotrophic waters with a poor electrolyte content. Other algae (mostly *Actino-taenium*-type) appear regularly and markedly increase from 10.95 to 10.8 k cal a BP coinciding with laminations, and indicating higher water levels and probably an increase in the available moisture. The following decrease of algae remains and the disappearance of diatoms suggest that a shallower water body formed at this time. The increase of *Brocchinia* and *Xyris* and the characteristics of the sediment (disappearance of

laminations and a significant increase of peat) at the top support the existence of more peaty conditions in the site.

The replacement of a ligneous community by a treeless savanna (which is more adapted to drier and/or more seasonal climates) contrasts with the water balance inferred from aquatic elements. This suggests that fire could have played a role in the vegetation change. Local fires did not start until the ligneous community was already at its lowest values. However, the decreasing trend of this community, starting around 12.2 k cal a BP, coincides with the increase in regional fires.

### Correspondence analysis

To compare the ligneous community represented in zone CHO-II (hereafter CHO-II shrubland) with potentially similar present-day communities of the GS, CA was performed using presence/absence data (see Table 2 for CHO-II, and supporting Tables S1–S4 for data on present-day GS shrublands). A scatter plot using the first two CA axes, which account for 60% of the total variance, is shown in Fig. 5. The CHO-II shrubland shows no floristic relationship with the peat shrublands, but it does with the other three. It is most similar to the shrublands on ferruginous soils, situated to the north of the GS. However, this similarity is only partial, and a significant amount of the CHO-II taxa are not present in any of the GS shrublands studied to date.

## Discussion

The region around Lake Chonita experienced significant and abrupt vegetation changes during the Late Glacial and early Holocene. The basin probably remained largely unvegetated, or at least unable to preserve the organic remains until about 12.7 k cal a BP, when a shrubland with no known modern analogue was established and remained at the site for more than 1000 years. Around 11.7 k cal a BP, the shrubland was replaced by a treeless savanna, which was the dominant vegetation during the early Holocene, at least until 10.6 k cal a BP. These results do not support previous hypotheses, which considered the GS as a relict of more extensive glacial savannas (Eden, 1974), or proposed an almost barren post-glacial landscape due to an arid or semi-arid climate until about 8.0 k $^{14}$C a BP (Schubert and Fritz, 1985; Schubert *et al.*, 1986). The following sections discuss the palaeoecological sequence in detail, in a Neotropical context, and the contribution of these results to our understanding of the origin of the GS.

### Palaeoecological sequence

#### 15.3–12.7 k cal a BP

This interval coincides with the end of the Oldest Dryas (OD; ~18.0–14.6 k cal a BP) and the B/A interstadial (14.6–12.85 k cal a BP) of the Northern Hemisphere (Rasmussen *et al.*, 2006). The absence of biological proxies was interpreted in terms of dry climates probably unable to support a dense and continuous plant cover or sufficient water to preserve its remains (Fig. 6). The lack of sediments of the same age in the Venezuelan–Guayana region prevents the extension of this vegetation cover to a regional level (Rull *et al.*, 2010a). The inferred aridity of this period may reflect high temperatures. This inference is supported by different palaeoecological and palaeoclimatical studies developed in other Neotropical regions. For instance, in the Cariaco Basin, a period that was warmer than the LGM and the YD has been proposed, with an average temperature similar or slightly higher than today, probably linked to a northward displacement of the ITCZ (Lea *et al.*, 2003; Mertens *et al.*, 2009). The Venezuelan Andes

**Table 2.** Main genera of GS shrublands and pollen assemblage found in CHO-II

| Acronym | Genus | Family |
|---------|-------|--------|
| Ac | *Acalypha* sp. | Euphorbiaceae |
| Al | *Alchornea* sp. | Euphorbiaceae |
| Be | *Befaria* sp. | Ericaceae |
| Bl | *Blepharandra* sp. | Malpighiaceae |
| Bn | *Bonnetia* sp. | Theaceae |
| Bo | *Bonyunia* sp. | Loganiaceae |
| By | *Byrsonima* sp. | Malpighiaceae |
| Ca | *Calea* sp. | Asteraceae |
| Ce | *Cedrela* sp. | Meliaceae |
| Ch | *Chalepophyllum* sp. | Rubiaceae |
| Ci | *Calliandra* sp. | Mimosaceae |
| Cl | *Clusia* sp. | Clusiaceae |
| Cp | *Cyrillopsis* sp. | Ixonanthaceae |
| Cr | *Carapa* sp. | Meliaceae |
| Cy | *Cyrilla* sp. | Cyrillaceae |
| Di | *Digomphia* sp. | Bignoniaceae |
| Ec | *Euceraea* sp. | Flacourtiaceae |
| Em | *Emmotum* sp. | Icacinaceae |
| Eu | *Euphronia* sp. | Euphroniaceae |
| Go | *Gongylolepis* sp. | Asteraceae |
| Hi | *Hirtella* sp. | Chrysobalanaceae |
| Hu | *Humiria* sp. | Humiriaceae |
| Il | *Ilex* sp. | Aquifoliaceae |
| LO | | Loranthaceae |
| Ma | *Mandevilla* sp. | Apocynaceae |
| Mc | *Macairea* sp. | Melastomataceae |
| Me | *Meriania* sp. | Melastomataceae |
| Mi | *Miconia* sp. | Melastomataceae |
| MR | | Marcgraviaceae |
| Ms | *Myrsine* sp. | Myrsinaceae |
| Mt | *Matayba* sp. | Sapindaceae |
| My | *Myrcia* sp. | Myrtaceae |
| No | *Notopora* sp. | Ericaceae |
| Oc | *Ochthocosmus* sp. | Ixonanthaceae |
| OD | *Odontadenia*-type | Apocynaceae |
| Ou | *Ouratea* sp. | Ochnaceae |
| Pa | *Passiflora* sp. | Passifloraceae |
| Pe | *Pera* sp. | Euphorbiaceae |
| Pg | *Pagamea* sp. | Rubiaceae |
| Ph | *Phyllantus* sp. | Euphorbiaceae |
| Pm | *Protium* sp. | Burseraceae |
| Pp | *Pagameopsis* sp. | Rubiaceae |
| Po | *Poecilandra* sp. | Ochnaceae |
| Pr | *Pradosia* sp. | Sapotaceae |
| Pt | *Phthirusa* sp. | Loranthaceae |
| Re | *Remijia* sp. | Rubiaceae |
| Ro | *Roupala* sp. | Proteaceae |
| Sa | *Sacoglottis* sp. | Humiriaceae |
| Si | *Simarouba* sp. | Simaroubaceae |
| Sp | *Spathelia* sp. | Rubiaceae |
| St | *Stomatochaeta* sp. | Asteraceae |
| Te | *Ternstroemia* sp. | Theaceae |
| Th | *Thibaudia* sp. | Ericaceae |
| Ti | *Tillandsia* sp. | Bromeliaceae |
| Va | *Vantanea* sp. | Humiriaceae |
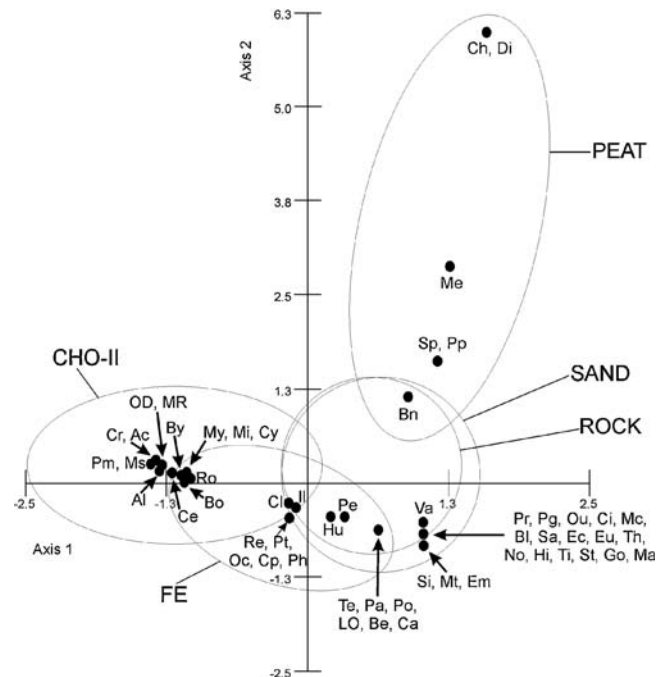


**Figure 5.** Biplot using the first two axes of correspondence analysis, with the genera of the four types of GS shrublands and the pollen assemblage found in Zone CHO-II. PEAT, shrublands on peaty soils; SAND, shrublands on sandy soils; ROCK, shrublands on rocky soils; FE, shrublands on ferruginous soils. See Table 2 for genera acronyms.

a BP, when dry forests expanded (Berrío *et al.*, 2002). In the Amazon Basin (Fig. 1), Bush *et al.* (2004) documented the occurrence of mesic forests during the last glaciation, and an increase in lianas and dry forest elements during the Late Glacial (22–12 k cal a BP). In northern Brazil (Fig. 1), a *Podocarpus* peak was recorded between 15.0 and 14.5 k cal a BP, suggesting cool and moist climatic conditions (Ledru *et al.*, 2001). A probably wet and warm climate has been inferred in a few records containing this interval from Central America (Islebe *et al.*, 1995; Hodell *et al.*, 2008). Therefore, it seems that during the B/A interstadial, climates in the northern South American tropics were probably warmer than during the LGM, but cooler than today and possibly dry.

*12.7–11.7 k cal a BP*

This phase corresponds to the YD chron of the Northern Hemisphere, dated at 12.85–11.65 k cal a BP (Rasmussen *et al.*, 2006). During this time, the region around Lake Chonita was covered by the CHO-II shrubland mentioned above, and the climate was interpreted as slightly wetter than during the previous interval, but still dry, as the present lake was seasonally desiccated (Fig. 6). The basin was occupied by a shrubland with no modern analogues. The most similar extant community known is a shrubland, located at 1000–1150 m elevation, close to the Quebrada Pacheco (1078 m elevation, Fig. 1). As the lake is at 884 m elevation, it could be hypothesized that a northward altitudinal displacement of 115–265 m with respect to the present occurred during this phase. Using a present-day altitudinal lapse rate of −0.6 °C/100 m (Huber, 1995a), average temperatures were estimated to be 0.7–1.5 °C lower than present during this period. Such an inferred decrease in average temperatures during this interval is supported by similar studies in regions closer to the lake. The Cariaco Basin record also showed a decrease in precipitation and sea surface temperatures, which were around 3–4 °C lower than today, between ~12.6 and 11.5 k cal a BP (Haug *et al.*, 2001; Hughen *et al.*, 1996; Lea *et al.*, 2003), with

(Fig. 1) were characterized by warmer climates with sparse vegetation between 13.9 and 12.7 k cal a BP (Rull *et al.*, 2005; Stansell *et al.*, 2005), coinciding with the Mucubají Warm phase, as documented by Salgado-Laboriau (1989). In the Colombian Andes (Fig. 1), van der Hammen and Hooghiemstra (1995) documented the Guantiva interstadial (between 15.1 and 12.8 k cal a BP), with higher average temperatures than the LGM, as equivalent to the European Allerød. In the Colombian midlands (Fig. 1), no palaeoecological information could be obtained possibly because of poor preservation until 13.3 k cal

| Age (cal k a BP) | Dominant taxa | Vegetation | Climate |
|---|---|---|---|
| Early Holocene — 10.6 | Poaceae / Byrsonima / Algae / Cyperaceae (CHO-III) | Savanna | Wetter / Warmer |
| Younger Dryas — 11.7 | Bonyunia, Weinmannia / Marcgraviaceae, Myrsine / Miconia, Pteridophyte spores (CHO-II) | Ligneous community | Dry / Likely cooler |
| Bølling/Allerød — 12.7 / Oldest Dryas — 15.3 | (CHO-I) / Barren | Unknown | Very dry |

**Figure 6.** Summary of the palaeoecological interpretation.

lower temperatures during the early YD (until 12.3 k cal a BP). From this, the authors inferred a southward displacement of the ITCZ during the YD chron. In the Venezuelan Andes, a significant altitudinal decline in vegetation was recorded between 12.9 and 11.75 k cal a BP, suggesting a decrease in average temperatures of around 2–3 °C that probably started to increase again after 12.3 k cal a BP, and a more arid climate (Rull et al., 2010b; Stansell et al., 2010). In the Colombian Andes, a sudden drop in average temperatures to about 1–3 °C lower than today, known as El Abra Stadial, was documented between 11 and 10 k [14]C a BP (~12.8–11.5 k cal a BP) (van't Veer et al., 2000).

At lower elevations, as in the Lake Valencia catchment (Fig. 1), the inferred occurrence of intermittent and shallow ponds suggested drier climates between 12.6 and 10 k [14]C a BP (~14.8–11.5 k cal a BP) (Bradbury et al., 1981; Leyden, 1985; Curtis et al., 1999). In the Colombian midlands, the replacement of dry forests by open grass-dominated vegetation occurred around 10.5 k [14]C a BP (~12.6 k cal a BP) onwards (Berrío et al., 2002). In Amazonia, a wet phase is recorded at southern latitudes (~10 °S) around 12.1–11.7 k cal a BP, not wet enough to promote speleothem growth, but sufficient to produce travertine deposits, which the authors also linked to a possible southward displacement of the ITCZ (Wang et al., 2004). In Central America, a likely cold interval with average temperatures 2–3 °C lower than today was suggested between around 11.1 and 10.4 k [14]C a BP (13.0–12.3 k cal a BP) in Costa Rica (Islebe et al., 1995). In Guatemala, a dry phase was suggested to have been occurred between 12.8 and 10.4 k cal a BP (Hodell et al., 2008).

In summary, the Neotropical continental evidence for palaeoclimatic and palaeoecological shifts around the YD chron is still scarce and poorly bracketed, especially at the end of the event. The Lake Chonita record, however, clearly shows a significant vegetation shift, tentatively linked to climate, which coincides with the YD chron.

### 11.7–10.6 k cal a BP

The end of the YD chron and the beginning of the Holocene has frequently been characterized in many northern Neotropical and Atlantic Ocean-influenced records by an increase in temperature and wetter conditions (e.g. Stansell et al., 2005). This phase is known as the EHW in the Northern Hemisphere (Kaufman et al., 2004; Kaplan and Wolfe, 2006). In Lake Chonita, the appearance of diatoms and algae assemblages clearly indicates a shift to a more humid environment. An evident replacement of the shrubland by a treeless savanna took place at 11.7 k cal a BP in the lake basin, coinciding with an increase of regional fire incidence and the appearance of the first local fires. Therefore, the likely northward migration of the shrublands on ferruginous soils and the rise in water levels was interpreted in terms of a warmer and wetter climate (Fig. 6). This inferred warmer climate agrees with different palaeoecological and palaeoclimatic studies from regions to the lake. In the nearby Mapaurí region (Fig. 1), a similar increase of regional fires was recorded at the beginning of the Holocene, with an increase in average temperature of about 2–3 °C, as suggested by a forest migration to higher altitudes and its replacement by expanding savannas (Rull, 2007, 2009a). In the Cariaco Basin, an increase of precipitation was observed at ca. 11.5–10.5 k cal a BP (Haug et al., 2001; Lea et al., 2003). In the Venezuelan Andes, an increase in temperature and humidity was recorded during this phase (Rull et al., 2005; Stansell et al., 2010), whereas in the Colombian Andes, average temperatures also increased after the El Abra stadial (van der Hammen and Hooghiemstra, 1995). In the Colombian Llanos (Fig. 1), Behling and Hooghiemstra (1998) documented a maximum in the savanna expansion during the early Holocene, whereas also in Colombia, Berrío et al. (2002) proposed an increase in aridity starting around 9.9 k cal a BP. Lake levels increased in Lake Valencia between 10 and 8.2 k [14]C a BP (~11.5–9.2 k cal a BP) (Curtis et al., 1999). In the Amazon Basin, the continuity of tropical rain forests was reported for the Pleistocene/Holocene boundary and onwards, but with changes in composition with respect to the Pleistocene forests (Bush et al., 2004). In Central America, Hodell et al. (2008) proposed the occurrence of moist conditions around 10.3 k cal a BP, probably caused by a northward displacement of the ITCZ. Hence, the widespread occurrence of the EHW in the northern Neotropical region seems well supported by the existing evidence.

### On the origin of the Gran Sabana

As previously mentioned, the savannas of the GS are considered anomalous, given the warm and wet climate, apparently more suitable for rain forests. This has led to the development of different hypotheses regarding the age and origin of these herbaceous ecosystems (Eden, 1974; Fölster,

1986; Rull, 1999; Fölster et al., 2001; Dezzeo et al., 2004; Huber, 2006). Among these proposals, those based on climatic (dryness, seasonality) and anthropogenic (frequent and extensive fires) factors are the more accepted. Until recently, the data supporting these hypotheses were from present-day biogeographical and ecological studies, with palaeoecological data beginning to contribute to the discussion about two decades ago (Rull, 1992). So far, the oldest record available for the origin of the GS was from the Mapaurí peat bog, some 35 km north of Lake Chonita. In Mapaurí, the replacement of a *Catostemma*-dominated cloud forest by treeless savanna was recorded around 10.2 k cal a BP, slightly preceding the onset of local and regional fires and supporting a climatic origin for the savannas (Rull, 2007). The causes of fires remain unknown, but the possibility of early human occupation of the GS has been suggested (Rull, 2009a).

The Chonita record is around 5000 years older, but the treeless savanna was not documented until 11.7 k cal a BP, around 1500 years earlier than in Mapaurí. In this case, regional fires were already occurring, even at low intensity/frequency, whereas local fires began more or less at the same time as the shrubland/savanna replacement occurred. Therefore, fire seems to have been influential in the observed vegetation change, which is supported by the abrupt shrubland decline just after regional fire initiation, and the subsequent peak of fern spores commonly associated with secondary colonization of burnt areas in the GS (Rull, 1999). Moisture indicators (diatoms and other algae) did not show any significant change linked to the vegetation shift, suggesting that water balance was less influential. If the previously suggested EHW was real, it could have had some influence but, at this stage, empirical support is not sufficient for a definitive assessment. Despite a significant increase in water balance, the same savanna vegetation remained until 10.6 k cal a BP, probably caused by local and regional fires. This is supported by the continued medium to high abundance of charcoal and the increase in *Byrsonima*, a common fire-resistant small tree in Neotropical savannas (Marchant et al., 2002). Therefore, in contrast to the Mapaurí record, fire appears to have been a determinant in the origin and expansion of savanna vegetation in the Lake Chonita area. The more likely scenario for the Pleistocene/Holocene boundary and the early Holocene in the present GS region could be a complex vegetation composed of forests, shrublands and patches of savannas progressively changing to a treeless savanna under the influence of climate (warming) and fire (Rull, 2009b). Moisture seems to have played a minor role, if any.

An increase in fire incidence immediately after the YD, after around 11.7 k cal a BP, has been reported in several Neotropical regions and elsewhere (e.g. Haberle and Ledru, 2001; Ledru et al., 2002; Daniau et al., 2007). Marlon et al. (2009) documented a general increase in fire incidence in North America at the boundaries of the YD, being greater around the end of the YD (11.7 k cal a BP), both in the amount of burnt localities and in fire magnitude. Owing to the synchrony of fire occurrence along widespread regions, this has been related to abrupt climate change (Alley, 2000; van der Hammen & van Geel, 2008; Marlon et al., 2009). The Lake Chonita record has documented a similar, well-dated increase in fire frequency at the end of the YD. The sudden fire increase around Lake Chonita might be caused by climate, but human presence cannot be dismissed, even in the absence of land-use changes (Bush et al., 2007), as was tentatively proposed in the nearby Mapaurí area (Rull, 2009a). The onset of regional fire incidence around Lake Chonita has been dated to ~12.4 k cal a BP, the oldest fire evidence in the GS so far (Fig. 3). The two discussed GS sequences (Chonita and Mapaurí) have clearly shown the presence of fire in the region

since at least the late Pleistocene, in agreement with the situation in Central and northern South America, where both rapid climatic changes or early human activity have been suggested for the increase in fire incidence along the YD interval and onwards (Bush et al., 1992; Haberle and Ledru, 2001). This potential early human occupation of the GS is supported by archaeological studies in areas closer to the lake (Fig. 1), where preceramic human evidence, such as spearheads and bifacial worked knives, has been found around the Late Pleistocene/Early Holocene boundary (Gassón, 2002).

## Conclusion

The Neotropical, mid-altitude Lake Chonita sequence analysed here has been subdivided into three palaeoecological/palaeoclimatic intervals (CHO-I, CHO-II and CHO-III), which are coeval with the Northern Hemisphere OD-B/A, YD and EHW, respectively. During the OD-B/A, very dry conditions have been inferred, in good agreement with other widespread northern Neotropical records. A dry and probably cold phase was documented between 12.7 and 11.7 k cal a BP, coinciding with the Northern Hemisphere YD cold reversal. During this period, a shrubland with no modern analogues was the dominant vegetation in the catchment area. This shrubland is absent today and it has been proposed, as a working hypothesis, that it could have migrated northwards at slightly higher altitudes where a similar, but different, shrubland occurs today. Such displacement would imply an increase in averaged temperatures of 0.7–1.5 °C. At the end of the YD, the shrubland was replaced by a treeless savanna similar to that at present. This coincides with the onset of local fires, suggesting that they could have influenced the vegetation change. Therefore, both climate and fire seem to have induced the shrubland/savanna turnover. The following phase (after 11.7 k cal a BP) coincides with the quasi-global EHW and is characterized, in Lake Chonita, by the establishment of treeless savannas and a significant increase in water levels, suggesting wetter and warmer conditions than during the YD. The continuity of savannas despite the increase in humidity suggests that fire prevented shrubland recovery, thus favouring savanna expansion. The manifest fire increase after 11.7 k cal a BP could have been related to climatic change or early Holocene human occupation of the region, or both. This supports the hypothesis of a mixed origin of the GS savannas, due to both climate and fire, and the important role of fire in their further persistence. This record is unique for northern South America midlands and lowlands. The analysis of other sequences of similar age is in progress to verify the local or regional extent of the documented trends.

## Supporting information

Additional supporting information can be found in the online version of this article:

Table S1. Dominant taxa in rocky soil shrublands.
Table S2. Dominant taxa in sandy soil shrublands.
Table S3. Dominant taxa in ferruginous soil shrublands.
Table S4. Dominant taxa in peaty soils shrubland.

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*Abbreviations.* AMS, accelerator mass spectrometry; B/A, Bølling/ Allerød (interstadial); BD, bulk density; CA, Correspondence analysis; EHW, early Holocene warming; GS, Gran Sabana; ITCZ, Intertropical Convergence Zone; LGM, Last Glacial Maximum; LOI, loss-on-ignition; MS, magnetic susceptibility; OD, Oldest Dryas; YD, Younger Dryas.

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