Palaeoecological study of vegetation dynamics in the Neotropical Gran Sabana since the Late Glacial

Estudio paleoecológico de la dinámica de la vegetación en la Neotropical Gran Sabana desde el Tardiglaciar

Tania Marcela Ballesteros Larrotta

ADVERTIMENT. La consulta d'aquesta tesi queda condicionada a l'acceptació de les següents condicions d'ús: La difusió d'aquesta tesi per mitjà del servei TDX (**www.tdx.cat**) i a través del Dipòsit Digital de la UB (**diposit.ub.edu**) ha estat autoritzada pels titulars dels drets de propietat intel·lectual únicament per a usos privats emmarcats en activitats d'investigació i docència. No s'autoritza la seva reproducció amb finalitats de lucre ni la seva difusió i posada a disposició des d'un lloc aliè al servei TDX ni al Dipòsit Digital de la UB. No s'autoritza la presentació del seu contingut en una finestra o marc aliè a TDX o al Dipòsit Digital de la UB (framing). Aquesta reserva de drets afecta tant al resum de presentació de la tesi com als seus continguts. En la utilització o cita de parts de la tesi és obligat indicar el nom de la persona autora.

ADVERTENCIA. La consulta de esta tesis queda condicionada a la aceptación de las siguientes condiciones de uso: La difusión de esta tesis por medio del servicio TDR (**www.tdx.cat**) y a través del Repositorio Digital de la UB (**diposit.ub.edu**) ha sido autorizada por los titulares de los derechos de propiedad intelectual únicamente para usos privados enmarcados en actividades de investigación y docencia. No se autoriza su reproducción con finalidades de lucro ni su difusión y puesta a disposición desde un sitio ajeno al servicio TDR o al Repositorio Digital de la UB. No se autoriza la presentación de su contenido en una ventana o marco ajeno a TDR o al Repositorio Digital de la UB (framing). Esta reserva de derechos afecta tanto al resumen de presentación de la tesis como a sus contenidos. En la utilización o cita de partes de la tesis es obligado indicar el nombre de la persona autora.

WARNING. On having consulted this thesis you're accepting the following use conditions: Spreading this thesis by the TDX (**www.tdx.cat**) service and by the UB Digital Repository (**diposit.ub.edu**) has been authorized by the titular of the intellectual property rights only for private uses placed in investigation and teaching activities. Reproduction with lucrative aims is not authorized nor its spreading and availability from a site foreign to the TDX service or to the UB Digital Repository. Introducing its content in a window or frame foreign to the TDX service or to the UB Digital Repository is not authorized (framing). Those rights affect to the presentation summary of the thesis as well as to its contents. In the using or citation of parts of the thesis it's obliged to indicate the name of the author.

TESIS DOCTORAL
DEPARTAMENTO DE ECOLOGÍA, UNIVERSIDAD DE BARCELONA
PROGRAMA DE DOCTORADO: ECOLOGÍA FUNDAMENTAL Y APLICADA

Palaeoecological study of vegetation dynamics in the Neotropical Gran Sabana since the Late Glacial

Estudio paleoecológico de la dinámica de la vegetación en la Neotropical Gran Sabana desde el Tardiglaciar

Memoria presentada por Tania Marcela Ballesteros Larrotta para optar el grado de Doctora por la Universidad de Barcelona

Tania Marcela Ballesteros Larrotta
Barcelona, 2015

Visto bueno por parte de los directores de tesis

Dra. Teresa Vegas Vilarrúbia	Dra. Encarnación Montoya Romo
Profesora Agregada	Investigadora postdoctoral
Universidad de Barcelona	The Open University, Reino Unido.
	Instituto de Ciencias de la Tierra
	Jaume Almera (CSIC), España

I am grateful to Encarni Montoya for the photo of the cover of this thesis

A mis padres,

por darme la fuerza, la inspiración, y el amor que
me permitió hacer esta tesis….
A quién más sino a ellos

AGRADECIMIENTOS

Cuando empecé la tesis pensaba que al terminarla me acordaría de cada persona a la que de una u otra forma contribuyó para que la tesis se hiciera realidad. Hoy, cuatro años y medio después, no puedo recordar todas las personas (fueron muchas), que desde una sonrisa, una canción en un día difícil, hasta el consejo más científico, me acompañaron durante este tiempo, y por lo tanto quisiera agradecerles. Sin embargo, estoy tranquila porque en su momento les di las gracias, ya sea devolviéndoles la sonrisa o con las palabras más sinceras de agradecimiento. Así que aquí voy a agradecer a mis mejores parceros.

Mis papás, han sido mis principales parceros. Desde el día que decidí hacer el doctorado hasta el día que entregué la tesis, me han brindado cada día su apoyo incondicional en todas las formas que necesité, la mayoría de las veces, sin pedirlo. Así, que lo mínimo que puedo estar con ustedes es inmensamente agradecida y sentirme bendecida por haber contado con ustedes como mis cómplices. Este proyecto sin ustedes no hubiese sido posible, le hubiera faltado aire, inspiración y vida. Me enseñaron a ser más valiente.

Los chinos, Dora, Lucho y Daniel, mis hermanos (también **Esteban**). Aunque para ustedes mi tesis era algo abstracto que hacía con el polen, les agradezco sus esfuerzos por tratar de entender lo que hacía y todos sus buenos consejos, consejos de hermanos. Les agradezco por ser los amigos con quien contaba para compartir mis alegrías, mis dudas y mis preocupaciones. Con Dora y Lucho, tuve la bonita oportunidad de compartir mi tesis de primera mano estando los tres en Barcelona. Con Daniel, viví la última etapa de la tesis.

Jaimito, mi super parcero! Le agradezco mucho cariñito su amistad durante este tiempo. Sin buenos amigos con quien reírse y que le ayuden a uno mismo a tomarse el pelo, una tesis no sería algo sano. Gracias cariñito por darme la alegría y la locura cuando la necesitaba, y por ayudarme a ponerme sería cuando también era necesario (siga siendo así). Sé que usted también vivió esta tesis y siempre me mandó las mejores energías y deseos, muchas gracias.

Juan Pablo, siempre me acordaba de una frase que me solía decir: “china, ni por el xxx dé un paso atrás, como sea termina ese doctorado”. Esta misma frase dando vueltas en mi cabeza hacía algo inimaginable pensar siquiera en desviarme de mi objetivo, mil y mil gracias. Usted ha sido ese amigo incondicional, que uno sabe que pa' las que sea se puede contar, y efectivamente pude hacerlo durante el tiempo que duró el doctorado, qué chévere tener un amigo así!

Sandra, mi parcerita. Mi amiga sincera, leal, sensible, una gran persona….una de las cosas que más sabes de la vida es ser una buena amiga. Lo fuiste mientras estuve allí y seguiste siéndolo desde el otro lado del charco. Sin tu amistad el doctorado hubiera sido un poco absurdo. Me permitiste contarte mis ideas, mis alegrías, mis planes, mis dudas, mis angustias, desde los temas más filosóficos de la vida hasta el asunto más técnico del polen. Compartimos desde largas horas en el microscopio hasta la película oriental más loca, y me ofreciste no sólo tu amistad sino también la de tus padres y Owen. Me siento muy agradecida y afortunada de haber contado con tu amistad en un país en el que yo era una extranjera.

Aureita, muchas y muchas gracias por enseñarme que "todo es perfecto" y que se puede vivir en tranquilidad incluso en los momentos más difíciles porque "todo pasa". A el **doc Silva**, muchas gracias por ser como una papá, por recordarme el principio de incertidumbre en la vida. Comprenderlo me ayudó mucho durante mi tesis. A ustedes dos, mil y mil gracias por la bonita energía que siempre me brindaron, inclusive sin que yo estuviera físicamente con ustedes.

A mi último parcerito, **Jabs**, no por ser el menos importante sino por ser el último en aparecer. Como dice la canción que ambos nos sabemos "tu ayer cambiaste mi destino, me diste vida, mucha más vida que el vino, me diste fuerza en los días fríos". Gracias por darme esa fuerza llamada amor y tu inmensa ternura, por darme un abrazo cuando lo necesitaba y silencio cuando también lo necesitaba. Muchas gracias por tu apoyo incondicional, por ser la inspiración y la sonrisa en mi rostro cada día.

Gracias a mi misma, por permitirme soñar, ser flexible, crecer como profesional, pero más importante, como persona.

Y, gracias a la vida, por haber sido tan maravillosa en estos cuatro años y medio.

This thesis was supported by several institutions: the Spanish Ministry of Science and Innovation through the funded projects CGL2006-00974 (*BIOSABANA*) and CGL2009-07069/BOS (*ECOPAST*), Principal Investigator (PI): Valentí Rull; the BBVA Foundation with the project BIOCON-08-031 (*PANTEPUI II*), PI: Valentí Rull; the Spanish Superior Council for Scientific Research (CSIC) through the project 200830I258 (*Palynology & Paleoecology*), PI: Valentí Rull; finally acknowledgement goes to the Foundation for the Future of Colombia-COLFUTURO, which provided a scholarship-loan to Tania M. Ballesteros.

Abstract

The Gran Sabana (GS, Northern South America) is a humid savanna region (treeless savanna intermingled with forest patches) with a long history of vegetation changes under fire disturbances. A number of hypotheses seek to explain the importance of environmental factors (e.g., climate, fire) in the origin and maintenance of the GS savannas. In order to fully comprehend the ontogeny of the GS, this thesis was aimed at conducting a detailed palaeoecological evaluation of vegetation dynamics and ecological processes (e.g. feedbacks, resilience) from the Late Glacial to the present, analysing two sedimentary archives (Lacustrine: Lake Encantada, peat bog: Fidencio). Currently, the GS savannas are being highly threatened due to excessively frequent fires. In addition, forest patches are being replaced by grassland. Therefore, in order to achieve ecosystem sustainability, this investigation was also aimed at forecasting potential vegetation responses and suggesting some guidelines for the savannas management. To accomplish the objectives, the palaeoecological assessment was based on palynological analysis and multiproxy approach (e.g., geochemical proxies, ecological indices) where possible.

Lake Encantada's basin is currently dominated by grassland with *morichales* (*Mauritia flexuosa* palm stands). The results suggest that the multifactorial interplay between fire regime, diversity, grasses availability, moisture and rates of recovery (RR) could have caused the vegetation changes during the Holocene and also contributed to the degree of resilience of plant communities. Forest patches were resilient to fire during specific time intervals. The vegetation changes suggest the following general trend: expansion of forest patches between ~8700 and 6400 cal yr BP, probably driven by the interplay between fires, high RRs and diversity. Despite wetter climate from 5400 cal yr BP, the savanna expanded under higher fire occurrence, which was potentially related to human land-use practices. The modern grassland with *morichales* established around 1700 cal yr BP, coinciding with drier conditions. The interplay between fire and erosion could have promoted forests instability, and thereby playing a part in the savanna expansion since middle Holocene. Drier climate and high availability of grasses probably reinforced this interplay.

At the present, Fidencio's area is grassland. The palynological results indicate that dense forest patches within savanna existed at least between ~12,385 and 12,100 cal yr BP. The vegetation of forest-savanna mosaic was replaced suddenly by grassland around 12,100 cal yr BP. This vegetation shift seems to be the origin of grassland in

Fidencio and occurred during a period characterised by marked climate changes (Late Glacial). The origin of open vegetation may have been caused by the synergistic action between rapid warming at the end of the Younger Dryas (YD), drier climate, fire (natural and/or anthropogenic), decreased diversity and grasses availability. The aforementioned synergism could have played a role in reducing resilience of the Late Glacial forests. Considering the future scenario of abrupt warming and higher occurrence of fires for South America, the significant expansion of grasses at the YD-Holocene transition suggests that savanna vegetation in the GS might expand in the future, similarly to what was observed historically.

In both localities, the vegetation changes from forest areas to savanna appear to have been irreversible on the timescales studied. The positive feedback between fire and herbs has accentuated the savannisation processes, which were associated with loss of diversity. The valuable information obtained in this thesis could help to better understand the ecology of savanna, particularly that of moist savannas.

Resumen

La Gran Sabana (GS, Norte de Sur América) es una región de sabana húmeda (sabana inarbolada entremezclada con parches de bosque) con una larga historia de cambios de vegetación bajo perturbaciones de fuego. Varias hipótesis buscan explicar la importancia de factores ambientales (ej. clima, fuego) en el origen y mantenimiento de las sabanas de la GS. Con el fin de comprender completamente la ontogenia de la GS, esta tesis tuvo como objetivo principal realizar una evaluación detallada de la dinámica de la vegetación y de los procesos ecológicos (ej. retroalimentación, resiliencia) desde el Tardiglaciar hasta el presente, analizando para ello dos archivos sedimentarios (Lacustre: Laguna Encantada, turbera: Fidencio). Actualmente, las sabanas de la GS están siendo fuertemente amenazadas por la excesiva frecuencia de fuegos. Además, los parches de bosque están siendo reemplazados por pastizales. Por lo tanto, con el fin de lograr la sostenibilidad de la GS, esta investigación tuvo como segundo objetivo pronosticar futuras respuestas de la vegetación y sugerir algunas directrices para la gestión de las sabanas. Para llevar a cabo los objetivos propuestos, la evaluación paleoecológica se basó en análisis palinológico y un enfoque multi-indicadores (ej. indicadores geoquímicos, índices ecológicos) cuando fue possible.

La cuenca de la laguna Encantada es actualmente un pastizal con morichales (bosque de galería monoespecífico de la palma *Mauritia flexuosa*). Los resultados sugieren que la interacción multifactorial entre el régimen de fuegos, diversidad, disponibilidad de pastos, humedad y tasas de recuperación (RR) podría haber causado los cambios de vegetación durante el Holoceno y además contribuido al grado de resiliencia de las comunidades de plantas. Los parches de bosque fueron resilientes al fuego durante períodos específicos. Los cambios de vegetación sugieren la siguiente tendencia general: expansion de parches de bosque entre ~8700 and 6400 cal yr AP, probablemente determinada por la interacción entre el fuego, altas RRs y diversidad. Pese al clima más húmedo a partir de 5400 cal yr AP, la sabana se expandió a la vez que se produjo una mayor incidenica de fuegos, potencialmente relacionados con prácticas del uso del suelo. La vegetación actual de pastizales con morichales se estableció alrededor de los 1700 cal yr AP, coincidiendo con condiciones más secas. La interacción entre fuego y erosión podría haber favorecido la inestabilidad de los bosques y de esta manera, haber desempeñado un rol importante en la expansión de la sabana desde el Holocene medio. El clima más seco y alta disponibilidad de pastos probablemente reforzó esta interacción.

Actualmente, el area de Fidencio es un pastizal. Los resultados palinológicos indican que densos parches de bosque dentro de la sabana existieron al menos entre ~12,385 and 12,100 cal yr AP. La vegetación de mosaico bosque-sabana fue reemplazada abruptamente por pastizales alrededor de 12,100 cal yr AP. Este cambio de vegetación parece ser el origen de los pastizales en Fidencio, el cual ocurrió durante un período caracterizado por cambios climáticos marcados (el Tardiglaciar). Se sugiere que el origen de la vegetación abierta fue causado por la sinergia entre el calentamiento rápido al final del Dryas Reciente (*Younger Dryas,* YD), clima más seco, fuego (natural y/o hecho por eh hombre), disminución de la diversidad y disponibilidad de pastos. La sinergia mencionada podría haber influenciado la reducción de la resilencia de los bosques del Tardiglaciar. Considerando el futuro escenario de calentamiento abrupto y mayor ocurrencia de fuegos para Sur América, la expansión significativa de los pastos en la transición YD-Holoceno sugiere que la vegetación de sabana podría expandirse en el futuro en la GS, de forma similar a la que ocurrió históricamente.

En ambas localidades, los cambios de vegetación de áreas forestales a sabana parecen haber sido irreversibles en las escalas de tiempo estudiadas. La retroalimentación positiva entre el fuego y los pastos acentuó los procesos de sabanización, los cuales estuvieron asociados con pérdida de diversidad. La valiosa información obtenida en esta tesis podría ayudar a entender mejor la ecología de las sabanas, especialmente la de las sabanas húmedas.

Table of contents

List of figures

General introduction

Chapter 1

Chapter 2

Chapter 3

General discussion

List of tables

General Introduction

Chapter 1

Chapter 2

Chapter 3

List of abbreviations

GS: The Gran Sabana
BC: Before Christ
BP: Before present
cal yr BP: Calibrated years before present (being present calendar year 1950)
yr: Year(s)
kyr: Kiloyear
P/E: Precipitation/evaporation ratio, water balance or hydrological balance
SE: Southeast
SA: South America
ITCZ: Intertropical Convergence Zone
IPCC: Intergovernmental Panel on Climate Change
EHW: Early Holocene Warming
YD: The Younger Dryas
ACC: Abrupt Climate Change
SST: Sea surface temperatures
RR: Rate of Recovery


LOS ÁRBOLES
COMENZARON
SIENDO SEMILLAS.
Todo lleva
su tiempo.
labioguia.com
LA BIO GUIA

GENERAL INTRODUCTION

1. General Background

1.1. Palaeoecology: scope, approaches and proxies

Neoecology (traditionally known as ecology) is the branch of ecology that studies the timescale ranging from weeks to decades, rarely extending beyond a single human lifetime (Jackson 2001). It has been recognised that this period is often insufficient to fully evaluate ecological dynamics of ecosystems and the evolutionary processes associated. This is mainly due to many ecological processes operating over long periods of time (Birks and Birks, 1980). Therefore, long-term ecological studies (longer timescale than 100 yr) are needed to test ecological hypotheses involving time. Palaeoecology is the discipline that provides this longer temporal scope (Rull, 2010). Commonly defined as the “ecology of the past” (Birks and Birks, 1980), palaeoecology is the study of populations and communities of vascular plants, animals, algae and bacteria that lived in the past, and their interactions and responses with the environment in which they lived (Brenchley and Harper, 1998; Delcourt and Delcourt, 1991; Birks and Birks, 1980).

Most palaeoecological research has focused on the last 2.6 million yr (the Quaternary period), known as the Q-time domain. Studies comprising this period are considered key to understand the present-day ecological patterns and their underlying causal processes (Jackson, 2001). Phenomena typically occurring on this timescale include the assembly of communities, ecological succession, broad-scale migrations, global and regional extinctions, and generation of diversity patterns (Rull, 2012). Most palaeoecological studies concentrate on the last glacial stage of the Pleistocene epoch (from ~50,000 to 11,500 yr ago) and the Holocene epoch (last 11,500 yr). Palaeoecology is based on the principle of uniformitarianism (Simpson, 1970), which states that laws of nature are constant across time and space. It means that natural processes operating in the past are largely the same as those operating in the present, though rates might vary (Rull, 2010). Thus, the ecological knowledge of current species and communities can be applied to make ecological interpretations of past communities. Hence, palaeoecology must consider the past community as an alive, dynamic and continuous system, with a clear connection between the past, present and future (Rull, 2010). Long-term studies that evaluate ecological patterns and processes (having an ecological objective), rather than being merely palaeoenvironmental and/or palaoeclimatic reconstructions, constitute the cornerstone of the so-called ecological palaeoecology (Rull, 2010, 2012; Seddon, 2012).

Past ecosystems cannot be observed directly.Therefore, biotic and abiotic components of the ecosystem are studied through fossils and sediments (Birks and Birks, 1980). Fossils provide the biotic evidence (plant, animal, and other organisms). Different structures of biological origin are the type of fossil most commonly used in palaeoecology rather than entire organisms, which include: hard parts (e.g., plant cuticles, seeds, ostracoda shells, phytoliths, diatom valves), components prone to preservation under determined environments (e.g., pollen grains and fern-spores resistant to oxidative degradation), traces (e.g., coprolites) and chemicals (e.g., pigments and lipid biomarkers). Among them, pollen and spores are widely used in palaeoecological studies.These palynomorphs are indicators of vegetation, i.e., dominant taxa, types of plant communities and vegetation changes.Therefore, pollen/spores analysis (stratigraphic palynology) constitutes a branch of paleobotany and one of the palaeoecological disciplines most broadly studied. This is due to two main reasons (Birks and Birks, 1980): Firstly, pollen and spores are usually the most abundant fossil preserved in sediments, and because of their diminutive size, small amount of sediment is needed to perform palynological analysis. Secondly, vegetation (terrestrial, semi-aquatic and aquatic) is responsive to environmental factors. Thus, vegetation-environment interactions can be inferred from pollen analysis. In doing so, modern data of climate-plant relationships and pollen dispersion-deposition must be applied to pollen-based vegetation dynamics of the past environments (Roberts, 1998). Concerning aquatic component, algae are widely used in palaeolimnological studies. Algae remains (e.g., diatom valves, zygospores) are used frequently as palaeoindicators of lake-level fluctuations, which are mainly related with the hydrological balance (P/E, precipitation/evaporation), and as environmental indicators of pH, nutrient status, salinity and water pollution (Battarbee et al., 2001). Other aquatic elements are also utilised to infer environmental conditions (e.g., chironomids as indicators of temperature) (Walker, 2001).

On the other hand, physical (e.g., type and size of sediment particles) and chemical features (e.g., organic matter content, stable isotopes, trace element contents) of sedimentary archives (e.g. lakes and peat bogs) provide mainly the abiotic evidence. Sediments and accumulated organic matter are reflection of their depositional environment (Brenchley and Harper, 1998), and therefore provide valuable information about climate, catchment processes (e.g., erosion) and vegetation. Hence, the information provided by the physico-chemical indicators is key evidence to interpret environmental conditions.

Another useful proxy is charcoal analysis. Although charcoal particles are of biotic origin (charred plant material), charcoal analysis is often used to reconstruct long-term variations in fire regime (Whitlock and Larsen, 2001). Fire occurrence can also provide indirect evidence of environmental conditions, such as available moisture or temperature. Commonly, combination of pollen and charcoal data are used to examine the relationships between vegetation and fire, both natural and human-driven (Whitlock and Larsen, 2001).

An integrated evaluation of fossils, geochemical proxies and sediments can help to confirm or refine interpretations made by using separately only one approach. Thus, in any palaeoecological assessment is essential to utilise all available evidence, both biotic and abiotic (Birks and Birks, 1980), and thereby having independent lines of evidence in order to prevent circular reasoning. In case of terrestrial ecosystems, palaeoecology and geology are powerful complementary approaches that allow the understanding of past vegetation dynamics and environmental processes that have shaped the current ecosystems. Therefore, the study of the past ecosystems can be considered a multidisciplinary task.

1.2. Global climate change, palaeoecology and conservation

Future global climate and environmental changes have been emerging as one of the major research priorities since the 90's (Delcourt and Delcourt, 1991). In the Fourth Report of the Intergovernmental Panel on Climate Change (IPCC), it was estimated based on climate models that temperatures will increase between 1.1°C and to 6.4°C by 2100 (Solomon et al., 2007). Later in 2013, the IPCC's Fifth report corrected downwards the temperature increases by almost a full degree Celsius, ranging from 0.2-0.3ºC to 5.5ºC (Stocker et al., 2013). This means a maximum global rate of 5.5ºC/century. Although the new scenario is less alarming, it is clear that the planet is warming. Hence, it is necessary to continue improving the accuracy of climate models and thus their projections. At present, one of the main concerns is to know how living organisms and their communities are responding and will respond to the climate change. To do so, one important question needs to be answered: is there any evidence of past biotic responses and ecosystem changes to similar IPCC climate projections? The last IPCC's report reiterated the need for palaeoecological studies to evaluate biotic responses to past climate shifts (e.g., lags, community turnover, large-scale range shifts and formation of novel communities). In this sense, the palaeoecological knowledge can be used to help forecast how communities might respond to the global warming.

To complement the study of biotic responses, some authors have proposed other research areas in which palaeoecology can help biodiversity conservation, such as (Willis et al., 2007a,b; 2010):

1) Identification of baselines and natural ecosystem variability.
2) Assessment of ecological resilience and thresholds.
3) Determination of rates of biotic response to climate changes.
4) Setting of realistic goals and targets for conservation.

Therefore, palaeoecology is one of the disciplines that provides scientific basis for biodiversity conservation of current and future communities (Stocker et al., 2013; Vegas-Vilarrúbia et al., 2011).

1.3. Tropical ecosystems. Case of study: Savannas

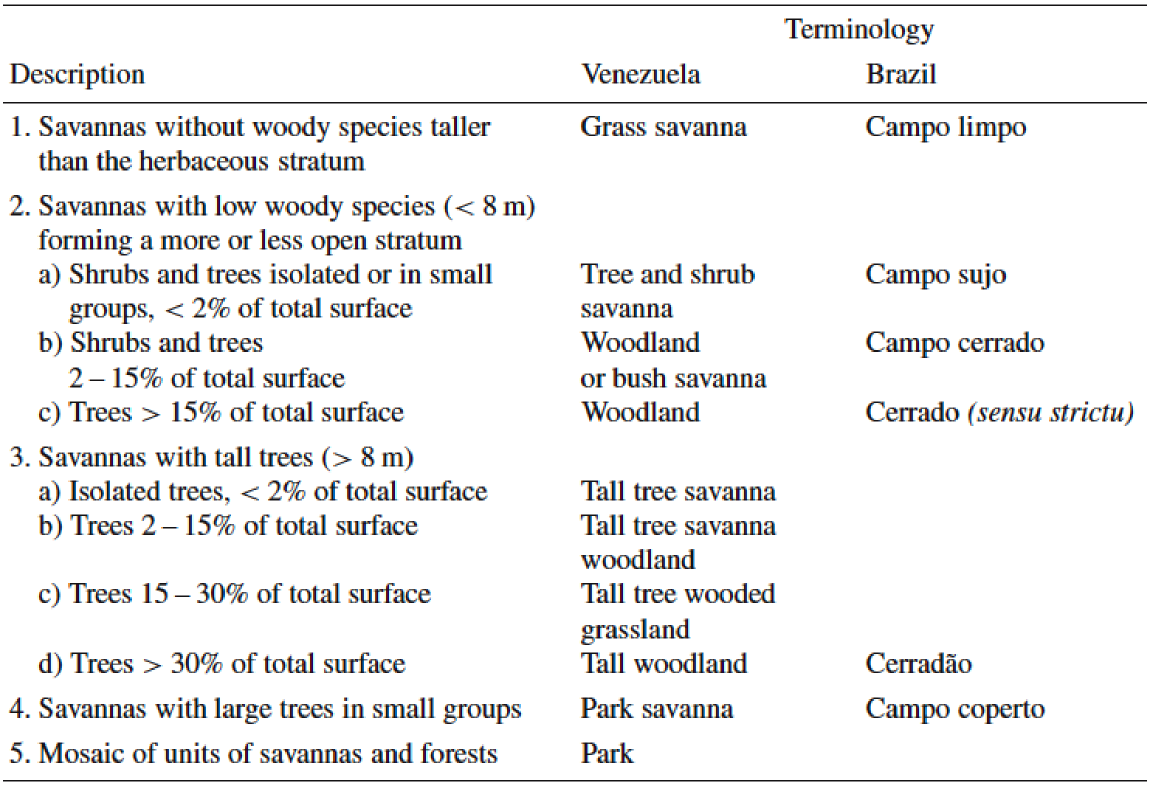
Savanna is the most extensive biome in the tropics (Marchant, 2010), covering approximately 40% of the area, i.e., 23 million km^2 (Gardner, 2006). Savannas are located at either side of the equator, on the edges of tropical rainforests. Savannas are open habitats typically dominated by non-perennial herbs and often strongly affected by seasonal changes of rainfall pattern (Lüttge, 2008). The herbaceous layer presents scattered woody plants (trees, shrubs and bushes), which are so widely spaced that canopy does not close completely. Therefore, open canopy allows sufficient light to reach the ground, favouring herbaceous taxa. The main features that define savanna ecosystems are:

i) Composition

The herbaceous layer is composed by grasses (graminoids), sedges and broad-leaved herbs. Thus, composition of herbaceous layer allows the distinction between “grass savannas *sensu stricto*” and “herb savannas” (Lüttge, 2008).

ii) Vegetation structure

Savannas consist of a discontinuous tree cover (between 20% and 80%) (Murphy and Bowman, 2012; Scholes and Archer, 1997), where trees can be dispersed or forming patches. An example of physiognomic description of savannas from two savanna areas in America is provided in table I.1. In Africa, there is the distinction between “wooded savanna”, where the trees stand more or less isolated, and “woodland savanna,” where the canopies of individual trees touch each other but without forming a closed canopy (Lüttge, 2008). In contrast to the African savannas, Asian savannas have been less studied, and consequently detailed knowledge of savanna structure in that continent is lacking (Sankara and Ratnam, 2013). Finally, most Australian savannas areas are dense grasses and scattered trees (Walker and Gillison, 1982).



	Terminology	
Description	Venezuela	Brazil
1. Savannas without woody species taller than the herbaceous stratum	Grass savanna	Campo limpo
2. Savannas with low woody species (< 8 m) forming a more or less open stratum		
a) Shrubs and trees isolated or in small groups, < 2% of total surface	Tree and shrub savanna	Campo sujo
b) Shrubs and trees 2 – 15% of total surface	Woodland or bush savanna	Campo cerrado
c) Trees > 15% of total surface	Woodland	Cerrado *(sensu strictu)*
3. Savannas with tall trees (> 8 m)		
a) Isolated trees, < 2% of total surface	Tall tree savanna	
b) Trees 2 – 15% of total surface	Tall tree savanna woodland	
c) Trees 15 – 30% of total surface	Tall tree wooded grassland	
d) Trees > 30% of total surface	Tall woodland	Cerradão
4. Savannas with large trees in small groups	Park savanna	Campo coperto
5. Mosaic of units of savannas and forests	Park	

Table I.1. Physiognomic description of various types of Venezuelan savannas and Brazilian *Cerrados*. Taken form Lüttge, 2008 (After Eiten 1972, Sarmiento 1984).

1.3.1. Main factors that contribute to the existence of savannas

i) Hydrological balance and seasonality

The wide distribution of savannas means that this biome occurs over a broad range of moisture conditions (Jeltsch et al., 2000). Even though climate is undoubtedly an important driver of tropical ecosystems distribution, relationships between vegetation-climate often break down on local and regional scales (Murphy and Bowman, 2012). According to average annual precipitation, savannas can be split into dries and humids

(Accatino and De Michele, 2013). The rainfall threshold between dry and humid savannas is generally located between 600 mm/year (Sankaran et al., 2005) and 820 mm/year (Higgins et al., 2010). In dry savannas, the tree-grass co-existence is often attributed to water scarcity, which limits the growth of forest trees. In humid savannas, rainfall abundance would allow the closure of canopy and therefore formation of forest. However, fire seems to prevent the occurrence of this phenomenon (Accatino and De Michele, 2013). Besides average annual precipitation, rainfall seasonality allows the distinction of several types of savannas. Considering dry and humid savannas, Sarmiento (1984) separated four main types of American savannas based on water status and seasonality:

(1) semi-seasonal savanna**,** with a long rainy period but without excess of water (i.e. flooding) and a short period with water shortage.
(2) seasonal savanna, characterised by periods with sufficient availability of water and periods of drought.
(3) hyperseasonal savanna, where periods of excess of water and drought provide strong seasonal contrast.
and **(4)** marsh savanna, with constant water supply (wetland).

ii) Soils

Savannas are often associated with deeply weathered and nutrient-poor soils. Herbs do not require high availability of soil water content (Murphy and Bowman, 2012). The dominance of shallow-rooted grasses results in more open nutrient cycles, and therefore less efficiency at accumulating nutrients and soil organic matter (Murphy and Bowman, 2012). Soil conditions have been traditionally considered a key environmental factor that prevents generally the formation of forest and maintain the savanna ecosystem (Murphy and Bowman, 2012). However, the hypothesis that forest fail to develop where the total nutrient pool is too small to construct foliage and wood has been evaluated using soil nutrient data from South American and African forests. The results suggest that forests can grow in poor soils except where the soil layer is highly leached and very shallow (Bond, 2010).

iii) Fires

Savannas represent ecosystems where fuels (e.g., grasses) and climate interact to create fire regimes, because fuels are naturally ample and widely distributed and rainfall pattern is often seasonal. These environmental conditions can be conducive to frequent fires (Hoffmann et al., 2012; Whitlock et al., 2010). Therefore, the savanna biome can be frequently burnt.

As it was mentioned previously, fire occurring mainly in humid savannas seems to prevent the closure of canopy and thus formation of forest, and as a result, the vegetation remains in savanna condition. Therefore, fire could be considered as one of the most prominent buffering mechanism in savannas, and at the same time, as one of their most important disturbance agents. This is due to fires often impedes the transition to woodland or forest by destroying juvenile trees and shrubs, and thereby preventing the development of larger trees to a mature and fire resistant stage (Beckage et al., 2011; Bond and Keeley, 2005; Jeltsch et al., 2000). Consequently, fire acts to regulate tree cover in savannas by imposing demographic bottlenecks (Sankaran and Ratnam, 2013; Murphy and Bowman, 2012). Furthermore, the effects of fire on savannas depend on some extent on tree traits. For instance, trees with thick bark (savanna trees, e.g., *Byrsonima crassifolia, Curatella americana* in South Ameria) are less affected by fires than those with thin and easily burnt barks (forest trees, e.g., *Brosimum alicastrum*, *Manikara sapota*). Therefore, frequent burning in savanna reduces the dominance of forest trees and maintains open and highly flammable vegetation (herbs) with savanna trees.

Humans have influenced fire regimes for thousands of years in a multitude of ways, including changing fuel types, modifying fuel structure and continuity, influencing ignition rates, or setting fires in different seasons (Bowman et al., 2011; Whitlock et al., 2010). In fuel-limited systems (e.g., arid grasslands), fires seem not to have played an important part in vegetation dynamics (Gillson and Ekblom, 2009).Thus, anthropogenic fires could have had similar influence than natural burning. Therefore, vegetation shifts from grassland to woody communities is likely to have been closely tied to climate changes in these ecosystems (Gillson and Ekblom, 2009; Withlock et al., 2010). On the contrary, in wetter more productive savanna systems, deliberate burning could have prevented natural succession to forests (Withlock et al., 2010). Fire activity has increased globally from the Last Glacial Maximum (~20,000 yr ago) to the present (Dube, 2009). In some savanna ecosystems, such increased fire regimes have been related with human activities. Nevertheless, it is difficult to separate the relative influence of human activities and climate in savannas where fires have been frequent for long and do not have any archaeological record. Hence, the separation of anthropogenic effect from natural background fire regimes is still open to debate (Bowman et al., 2011).

iv) Biotic interactions

Browsing (consumption of woody plants) can impede the transition from savanna vegetation to woodland or forest because browsers (e.g., elephants, prairie dogs, giraffes) reduce density, growth and regeneration of woody species (Jeltsch et al., 2000). Therefore, browsers prevent woody species from becoming established or dominant. Consequently, browsing maintains open grassy systems (Murphy and Bowman, 2012). Browsing occurs mainly in African savannas where big browsers mammals exist.

Herbivory (or grazing, consumption of grass) can favour woody vegetation by reducing grass biomass and tree-grass competition (Murphy and Bowman, 2012; Sankaran and Ratnam, 2013). Following heavy overgrazing, “bush encroachment” can occur. Additionally, herbivory might reduce fire frequency and intensity by limiting fuel availability and promoting the establishment of woody species.

In summary, understanding the factors that govern distribution of savannas wordlwide is particularly difficult because of multiple interacting factors (Lehmann et al., 2011). Climate (rainfall, seasonality), fire (natural of anthropogenic origin), soil characteristics and biotic interactions can all influence the distribution of this biome (Murphy and Bowman, 2012; Jeltsch et al., 2000). Furthermore, all the aforementioned factors interact to determine the levels of tree cover (Gillson and Ekblom, 2009).

1.3.2. Alternative ecosystem states and ecological resilience in savannas

An ecosystem state (e.g., forest, grassland) is a quasi-stable ecological condition in which ecosystem properties/conditions (e.g., woody vegetation abundance) fluctuate within certain boundaries (Gillson and Ekblom, 2009). The theory of “alternative ecosystem states” (AES) proposes that an ecosystem state results from a set of unique biotic and abiotic conditions, feedbacks, and ecological properties (Holling, 1973; Scheffer et al. 2001). The key premise of the AES theory is that strong stabilising feedbacks (positive or negative, depending on the interactions) promote the necessary environmental conditions to maintain an ecosystem state, and those environmental conditions are hostile to the alternative ecosystem states (Bond and Parr, 2010; Murphy and Bowman, 2012; Scheffer et al., 2001). In case of savannas, this ecosystem state is defined by the co-existence of trees and herbs (Accatino et al., 2013). Therefore, there may be several sub-states of savanna, which are characterised by variations in the proportions of trees within the grass layer. The theoretical basis of the AES might be extrapolated to evaluate the sub-states of savanna. Thus, it could be interpreted that the ecological processes and environmental drivers in a savanna sub-state (e.g. dense forest-savanna mosaic) could be different to those in another savanna condition (e.g. savanna-forest mosaic). In that case, the AES theory seems to be an appropriate framework for analysing vegetation changes in savanna ecosystems.

The "alternative ecosystem states" theory suggests that shifts between ecosystem states (or sub-states) are possible if stabilising feedbacks processes are interrupted (Murphy and Bowman, 2012). Ecological resilience is the capacity of a system to absorb disturbance and reorganise without changing self-organised processes and structures, i.e., retaining the same function, structure, identity, and feedbacks (Holling, 1973). Hence, ecological resilience is the property that mediates transition among (sub)states (Gunderson, 2000). For instance, if a savanna sub-state is resilient to disturbance, this sub-state will remain without changing to another one. However, if disturbance exceeds a threshold, the savanna sub-state will change to an alternative condition. Therefore, the study of ecological resilience would allow the identification of the ecological processes that determine permanency in a particular sub-state of savanna or the transition to another alternative sub-state.

Due to the lack of empirical information regarding the resilience of savannas, the multiple savanna sub-states and the processes that mediate change between them are still poorly understood (Gillson, 2004). Most resilience studies in savanna are restricted to short timescales or are conducted by mathematical models without empirical data (Accatino et al., 2010; Calabrese et al., 2011). There are a few long-term resilience studies in savannas, mainly in semi-arid/arid African savannas. The main findings from these palaeoecological studies suggest that: (*i*) once the savanna condition was established there was resilience to increase in fire frequency (Gillson and Ekblom, 2009), (*ii*) savanna could be resilient on a centennial timescale, stochastically controlled by disturbances caused by, for instance, rainfall pattern (including seasonality) or fire (Gil-Romera et al., 2010), and (*iii*) long-term vegetation responses to disturbance appear not to have been linear, which has implications for conservation and management of savanna areas (Gil-Romera et al., 2010).

Neoecological and palaeoecological studies have suggested a few feedback processes that mediate or impede transitions between alternative ecosystem states and savanna sub-states. The feedbacks proposed are explained below:

i) Positive feebacks

-Between fire and herbs. This feedback maintains savannas in open condition. This process occurs mainly in humid savannas (Accatino et al., 2013; Rull et al., 2013).

-Between increased water balance and vegetation. This interaction promotes higher biomass production and therefore mediates the transition from grassland to wooded savanna. This ecological process is especially important in semi-arid African savannas (Gillson and Ekblom, 2009).

-Between fire and browsing. Fire maintains bushes at a height within reach of browsers (Jeltsch et al., 2000). Thus, this interaction impedes transitions to savanna sub-states with higher levels of woody cover.

ii) Negative feedbacks

-Between fire and tree cover. Depending of the extent and distribution of tree cover, this feedback can mediate or impede transitions between alternative savana sub-states and between the ecosystem states of forest and savanna (Hoffmann et al., 2012; Murphy and Bowman, 2012). This feedback usually occurs in humid savannas.

1.3.3. Palaeoecology of Neotropical savannas

Neotropics is one of the terrestrial ecozones, which includes Central and South America (except the temperate forest ecoregions of southwestern South America), the Mexican lowlands, the Caribbean islands, and southern Florida. In the Neotropics, the savanna biome is widely represented. The most extensive savannas are the *Cerrado* in Brazil; *Llanos* of Orinoco, shared by Colombia and Venezuela; Beni savanna in Bolivia; Roraima savannas, shared by Venezuela (The Gran Sabana 16%), Brazil (63%) and Guyana (Rupununi savannas (21%) (Barbosa and Campos, 2011); and coastal savannas of Guayana (Fig. I.1). The savanna ecosystems are very diverse. There are dry and humid savannas, from slightly to highly seasonal. Floristic composition and physiognomy are also different among them. Hence, Neotropical savannas constitute very interesting ecosystems to study and test ecological hypotheses.

Palaeoecological studies have documented that savanna ecosystems have expanded and retracted several times in the last millennia, probably in response to variations in fires and hydrological balance (Salgado-Labouriau et al., 1997; Behling and Hooghiemstra, 1998; Montoya et al., 2011a). In forest-savanna ecotones, changes in available moisture and fires have influenced the dynamics on forest and savanna areas, modifying the boundaries of ecotones (Berrío et al., 2012; Behling and Hooghiemstra, 2000; Montoya et al., 2011a). Fires have strongly intensified during the late Holocene, likely promoting the recent savanna expansion in most savanna regions (Montoya et al., 2011b; Pivello, 2011). Concerning the role of soil, this factor has been scarcely evaluated in Neotropical savannas. Thus far, most edaphic studies have been conducted in the *Cerrado*. These studies suggest that soil has been one of the most important selective agents of vegetation in the Brazilian savannas (Pinheiro and Monteiro, 2010). Despite the advances in knowledge of Neotropical savannas, more neoecological and palaeoecological studies are required to better understand the separate and combined effects of multiple causal factors that have contributed to the development of current savanna regions.

In South America, human populations arrived in the continent approximately 15,000 yr ago (Meltzer, 1997). Based on this discovery, the increased fire regime in some Neotropical savannas since the Late Glacial (13,000-10,000 cal yr BP) has been suggested to be related to human activities (for instance, in The Gran Sabana; Rull, 2009a,b). More evidence of human-derived fire regimes is found for late Holocene. However, the scarcity (or absence) of archaeological studies and charcoal analysis in most Neotropical savanna areas prevent us from making conclusive assessments of the role played by humans in shaping these ecosystems.

Figure I.1. Map of South America. The numbers indicate the most extensive savanna regions: 1- the *Cerrado*; 2- *Llanos* of Orinoco; 3- Beni savannas; 4- Roraima savannas; 4.1- The Gran Sabana; 5- Coastal savannas. Google-Earth image modified of South America (accessed in June 2014).

In the last decades, Neotropical palaeoecology has been transformed from a discipline dominated by studies focused on the reconstruction of past vegetation and climate, into a more sophisticated multidisciplinary science involving a refined use of independent lines of evidence. This has been possible due to several reasons, such as better systems of carbon dating (for age control), new techniques to digest samples, more reference collections (e.g., pollen atlases), and better access to scientific literature. Currently, long-term records of vegetation dynamics are providing the basis for ecological hypotheses testing in Neotropical savannas (Rull et al., 2013). Nevertheless, this approach is still in early stages. The palaeoecological knowledge is progressively taken into account in the prediction of biotic responses to future regional climate changes and conservation practices in Neotropical forests (e.g. in Amazonia; Mayle and Power, 2008). In savannas, particularly African savannas, it is beginning to understand how the knowledge obtained from the ecological palaeoecological studies could be applied to management and conservation plans for savanna ecosystems (Gillson, 2004; Gil-Romea et al., 2010). However, the field research “applied ecological paleoecology” has been scarcely explored for Neotropical savannas.

The evidence is still scant to comprehend the environmental factors and ecological processes associated with vegetation dynamics in Neotropical savannas. Consequently, there are considerable research opportunities in studying these ecosystems, mainly since the palaeoecology. Hence, the palaeoecological investigation of this thesis was conducted in a savanna region of South America, which has particular ecological conditions and a long history of vegetation changes. The study site is explained below.

2. Study Area: environmental setting

2.1 Physiography, climate and soils

The Gran Sabana (GS) is a region located in the Venezuelan Guayana, in southeastern Venezuela (Bolívar state), northeast of the Precambrian Guiana Shield and between the Orinoco and Amazon basins (4º 36’-6º37’N and 61º4’ -74º2’W; Fig. I.2). The total extension of the GS is approximately 18,000 km^2, but because the GS extends further to the borders with Brazil and Guayana, the Venezuelan part comprises approximately 10,820 km^2. Huber (1995a) proposed a geo-ecological division of the Venezuelan Guayana into three altitudinal belts:

-Lowlands: from zero to 500 m altitude.
-Uplands (also called midlands): from 500 to 1500 m altitude.
-Highlands: > 1500 m altitude.

Figure I.2. Northern South America. Location of the Gran Sabana within northern South America is delimited by the white square. Google-Earth image modified (accessed in June 2015).

Two of these physiographic units are present in the GS: uplands, where the present study was carried out, which consist of a mid-elevation savanna plateau inclined from north at 1350 m to south at 700 m elevetaion (Huber and García, 2011); and highlands, which include the tabular mountains (*tepuis*). This high-elevation zone has been designated as the Pantepui province of the phytogeographic Guayana Region (Huber and García, 2011). Thus, the GS landscape is characterised by a strong contrast between flat and slightly undulating savanna landscape of uplands and the abrupt tabular tepuian mountains of the highlands (Fig. I.3).

Geomorphologically, the GS is a complex mosaic of quartzites, intrusive diabase outcrops and sandstones rocks, which are known as the Roraima group (Huber, 1995a). The Roraima geologic province consists of relatively undeformed continental clastic sedimentary sequence from early to middle Proterozoic eon (1.9-1.5 million yr; Precambrian supereon) (Huber and García, 2011). The sedimentary rocks are largely siliceous. Due to their very ancient origin, the rocks have been subjected to long weathering processes and produced iron- and aluminium-oxide-rich soils, such as oxisols, ultilsols, entisols and inceptisols (Hubber, 1995b). In addition, the soils have suffered intensive leaching (Guzmán, 1986).

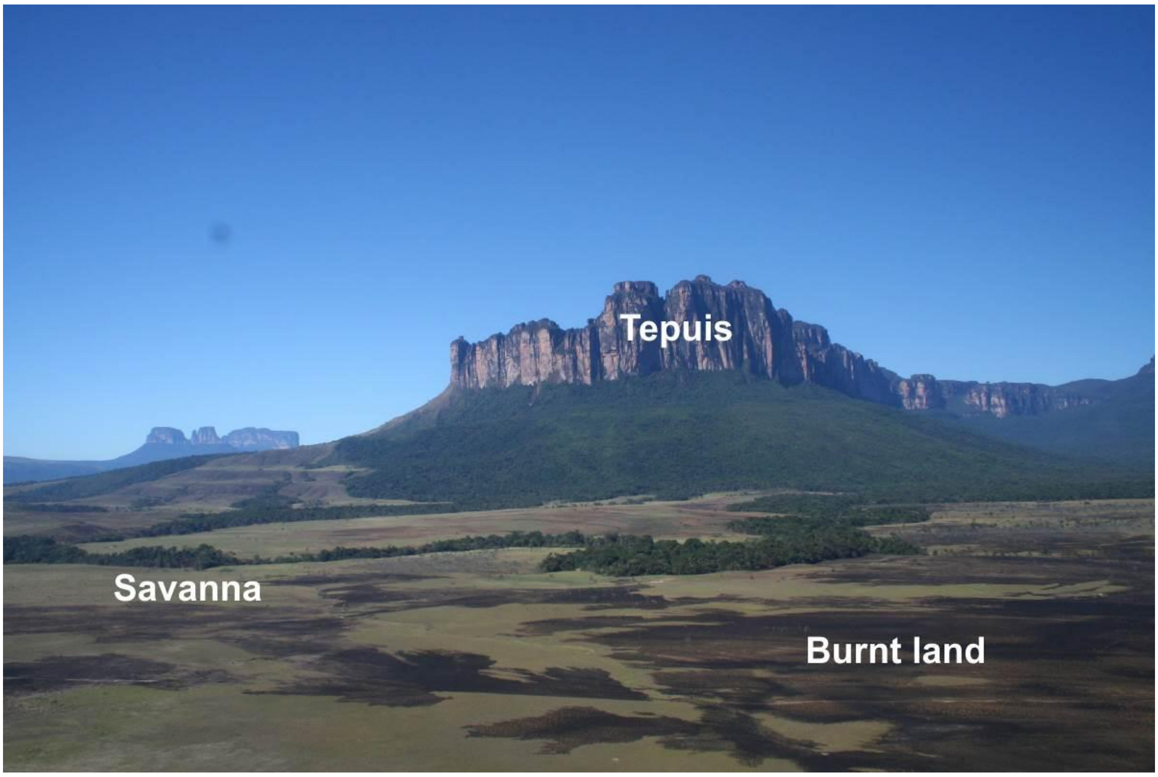


Figure I.3. Gran Sabana landscape. The upland savanna and highland tepuian mountains are indicated. Savanna is severely burnt in some areas (Photo: E. Montoya, 2007).

Because of the generally low alterability of the mineral content of the parent rocks, the soils have poor nutrient content with low levels of phosphorous, calcium and nitrogen (Huber, 1995b). Soils are impoverished in basic cations (Ca, Mg, K) and enriched in acid cations (Al, Fe, Mn). Therefore, the cation exchange complex is highly saturated, resulting low Ca/Al ratios (Fölster, 1986; Fölster et al., 2001). Consequently, soils in the region are extremely acidified (pH: 3.6-4.5; Fölster et al., 2001). Ca-deficiency in acid soils with high Al saturation is a well-documented constellation of chemical stress that affects various physiological processes of trees (Fölster, 1986; Fölster et al., 2001). Concerning the soil layer, the organic surface layer is very thin (20-30 cm depth) preventing the growth of plant roots below 30 cm. Therefore, the root system is very shallow and is associated with high root mortality (Fölster et al., 2001). Ca-deficiency is considered the main element of the chemical stress responsible for the extremely shallow root system in the GS, which causes the sensitivity of forest patches to drought stress and fire (Fölster et al., 2001). In addition, soils in the GS have low capacity of water retention, which is caused by the low efficiency of the rooting system (Fölster, 1986). In summary, because of the low soil status the plants in the GS live under a continuous chemical and water stress, which render the soils difficulty to support certain types of vegetation, especially forests in some sites (Fölster et al., 2001).

Concerning climate, the annual rainfall distribution is affected by the seasonal variations of the Intertropical Convergence Zone (ITCZ). According to the position of the GS, migrations of the ITCZ cause a long rainy season from April to November, and a dry season between December and March (Huber and Febres, 2000). Due to the average annual rainfall, most Guayana uplands are considered as humid. Submesothermic ombrophilous climate occurs in northern GS and is characterised by average temperatures between 18 and 24ºC and precipitation of 2000-3000mm/yr (Huber, 1995b). In the south, the climate becomes submesothermic tropophilous, which is less humid (1600-2000 mm/year) and slightly seasonal, likely due to local rain shadows (Huber, 1995a). Both climatic parameters (temperature and humidity) have a clear gradient from north to south, increasing trend for temperature and decreasing for precipitation (Huber and Febres, 2000). Hydrologically, the GS is enclosed in the basin of the Caroní River. This basin covers approximately 95,000 km^2 and is by far the largest river basin fully contained within the Venezuela Guayana (Hubber, 1995a). The Caroní River is one of the main tributaries of the Orinoco in the lowermost part of its course (Huber, 1995a).

2.2. Vegetation

In the Guayana region, the principal vegetation types are evergreen montane and gallery forest, but the majority of the GS is covered by savanna. Forests together with shrublands, secondary woody communities and *helechales* (dense fern communities) are patchily distributed forming vegetation mosaics dominated by savanna.

Forests composition and structure vary with the altitude (Huber, 1995a). Atop the large plateaus, forests are medium-sized and evergreen; while at lower slopes, they are also evergreen but multilayer, with tall trees and dense understories (Huber and García, 2011). Dominant taxa are Myristicaceae (*Virola*), Burseraceae (*Protium*), Annonaceae (*Anaxagorea*), Bignoniaceae (*Tabebuia*), Vochysiaceae (*Ruizterania*), Chrysobalanaceae (*Licania*), Fabaceae (*Alexa*), Fabaceae (*Dimorphandra*), Malpighiaceae (*Byrsonima*), Elaeocarpaceae (*Sloanea*), Caryocariaceae (*Caryocar*) (Huber, 1995a; Huber, 1986). After episodes of intense fire, characteristic of this region (fire regime is explained in detail below), secondary successional forest establishes on the burnt land, which are composed basically by Cecropiaceae (*Cecropia*), Melastomataceae (*Miconia*), Clusiaceae (*Vismia*), Saliacaceae (*Casearia*), Lamiaceae (*Hyptis*), Clethraceae (*Clethra*), and some pioneer ferns (Huber, 1986).

Shrublands are considered as azonal vegetation, that is to say, they are not related to the general macroclimatic conditions, but rather with edaphic or local hydric factors (Huber, 1986). In the GS, shrublands are found in four types of soils: rocky, sandy, ferruginous and peaty (Hubber, 1995a). Shrub formations are more frequent in the north than in the south of GS, growing especially on sandstone layers. Shrublands vary in height, density and floristic composition. Common taxa are Euphroniaceae (*Euphronia*), Loganiaceae (*Bonyunia*), Theaceae (*Bonnetia* and *Ternstroemia*), Clusiaceae (*Clusia*), Asteraceae (*Gongylolepis*), Melastomataceae (*Macaireae*), and Humiriaceae (*Humiria*) (Huber, 1995b; Huber, 1986).

The most extensive vegetation type, as indicated by the place name, is savanna. Three primary types of savanna occur in this area. Based on the non-herbaceous taxa that appear as minor elements, Huber (1995b) typified the savannas of the GS as follows:

(1) Treeless savannas (or grassland*): The dominant grasses are *Axonopus*, *Trachypogon*, *Echinolaena* and *Leptocoryphium*, and the most important sedges are *Bulbostylis* and *Rhynchospora*. Other occasional herbs are *Buchnera* (Scrophulareaceae) and *Polygala* (Polygalaceae). This savanna type is widespread throughout the GS, where it usually grows on poor oxisols, highly weathered.
*some authors consider grassland vegetation as a special savanna type because of the predominance of grass layer.

(2) Shrubs savannas: This type of savanna occurs primarily on rocky hills and slopes in southern GS. The herbaceous layer is very sparse and irregular, and is dominated by sedges.

(3) Open savannas with *morichales* (Figure I.4), which are mostly monospecific dense stands of the Arecaceae *Mauritia flexuosa* (locally known as *moriche*). Tall grasses dominate the herbaceous stratum (e.g., *Hypogynium*, *Andropogon*, *Panicum*). The stands of *morichales* grow on the flat valley along river courses and around lakes on

poorly drained soils with high clay content. Due to the altitudinal limit of this palm (Huber, 1995b), this type of monospecific gallery forest is an important vegetation component occurring in southern and central parts of the plateau at elevations lower than 1000 m a.s.l.

Figure I.4. Open savanna with *morichales*. (Photo: S. Nogué, 2007).

2.3. Fires and human occupancy

Fire currently plays a significant role in the landscape dynamics of the GS (Fig. I.3), with a fire frequency between 5000 and 10,000 fires per year (Gómez et al., 2000). It is estimated that most the GS is burned every 1-3 years (Hernández and Fölster, 1994). Nearly 70% of detected fires start in savanna areas, but some cross the savanna-forest boundary causing forest degradation. The vast majority of fires are of anthropogenic origin. Ground fire is the most common type of fire in the GS, which has a devastating effect on vegetation and soils due to the organic surface layer often being burnt and therefore its thickness decreases. As consequence, there is considerable loss of fine root mass and the rooting system remains shallow (Fölster, 1986; Fölster et al., 2001). Neoecological studies have documented that the recent change from forest areas to savanna has been caused by fire (Fölster et al., 2001). This vegetation change has implied a drastic reduction of biomass in terms of basal area and a remarkable change in the floristic composition, which has resulted in loss of organic surface layer and decrease in soil fertility (Dezzeo et al., 2004). Based on neoecological studies, it has been hypothesized that the present-day savanna is the result of a long-term process of savannisation, originally produced by fires, but conditioned by the intrinsic low resilience of the forest, soil chemical stress and episodic droughts (Dezzeo et al., 2004; Fölster et al., 2001).

Pemón indigenous people inhabit the GS. This group belongs to the Carib linguistic family (Huber, 1995a). Fire plays an essential role in the *Pemón* way of life since many of their subsistence and cultural activities are associated with the use of fire (Bilbao et al., 2010). There are documented approximately fifty activities linked to fires. The most common include cooking, fire prevention, hunting, communication and magic (Rodríguez, 2007). *Pemón* people use fire in the landscape in three ways, and each one has a different impact on it (Bilbao et al., 2010): (1) Fires within forests. These fires take place in small plots cleared inside the forest (locally known as *conucos*), which are destined to be agricultural crops. This slash-and-burn practice represents a shifting cultivation system; however, extensive agricultural practices are not characteristic of the *Pemón* culture; (2) Fires along forest-savanna borders. These fires occur during hunting activities or sometimes accidentally. These fires burn huge forest areas and are little controlled, promoting the savanna expansion (Fólster, 1986); and (3) Fires in open savannas occur at any time of the year and are the dominant type in the GS landscape (Fig. I.3).

The arrival timing of the *Pemón* in GS is still uncertain. Based mainly on historical documents, it has been postulated that this culture became established approximately 300 years ago coming from Guayana to east (Thomas, 1982; Colson, 1985), or approximately 500-600 years ago, migrating from Brazil to the south of GS (Huber, 1995b). Nevertheless, recent palaeoecological studies based on charcoal analysis suggest that human groups with landscape management practices, probably similar to the *Pemón* culture, could have been present in the GS at least since 2000 cal yr BP (Montoya and Rull, 2011; Montoya et al., 2011b). In the past, *Pemón* indigenous were semi-nomadic. Nevertheless, over the last decades, cultural changes associated with the arrival of European religious missionary groups have altered the semi nomadic pattern, leading *Pemones* to settle near missions, and thereby having a sedentary lifestyle (Bilbao et al., 2010). Today they live in small villages, usually in open savanna. These changes have promoted a considerable increase in the *Pemón's* population (Dezzeo et al., 2004; Fölster et al., 2001). Montoya et al., (2011a) proposed the presence of a different, forest-like, indigenous culture in the southern boundary of the GS during the middle Holocene.

From a protection/conservation point of view, the GS is within the Canaima National Park (CNP), which also includes the Caroní River. This river supplies a series of large hydroelectric plants, which produce the majority of Venezuela's hydroelectric power. Fire management in the GS has been under the purview of the parastatal electricity company-EDELCA since the early 80's. Since then, there has been a huge conflict over the fire use in the CNP (Sletto, 2008). On the one hand, *Pemón* depend on fire for their subsistence and cultural identity. As it was mentioned previously, this indigenous group has a long tradition of burning the savanna, in part as a means to reduce dry fuel loads in grassland-forest boundaries (Sletto and Rodríguez, 2013). This practice aims at preventing the penetration of uncontrollable fires in the forest patches (Rodríguez, 2007; Sletto, 2008; Sletto and Rodríguez, 2013). On the other hand, EDELCA considers fires detrimental to forests. The hydroelectric company has long pursued a strategy of fire suppression in an attempt to prevent the loss of riverine forests (Sletto and Rodríguez, 2013). EDELCA managers see *Pemón* burning practices as uncontrolled and destructive (Sletto and Rodríguez, 2013). Fire exclusion experiments performed by some scholars (Bilbao et al., 2010) have shown to be detrimental in the sense of favouring the growth of fuel loads, and thereby leading more severe fires, as well as contributing to decrease in vegetation diversity. Bilbao et al. (2010) proposed a change from "fire suppression" to "fire management". Understanding of the GS landscape is a socio-ecological construction, other authors have proposed a strategy of "intercultural fire management", with participation of scholars (Sletto and Rodríguez, 2013). Therefore, in order to build appropriate fire management plans, more long-term studies of fire regime and its impact on the ecosystems may provide new findings, which will enable to better understand fire-vegetation dynamics.

3. Palaeoecology of the upland savannas of the Gran Sabana: framework of this thesis

It is worth noting that most published studies have been performed in the south of the GS. Even though there are a few studies in the north, most of them have not been published yet, and those published did not include the original pollen diagrams. Therefore, this section is focused only on the south of the GS.

3.1. Late Glacial (13,000-10,000 cal yr BP)

Past ecological records document that no tropical region in the world remained in the same ecological state during the Late Pleistocene, especially during the Pleistocene-Holocene transition (Late Glacial) (Bush et al., 2011). Therefore, it would be expected that vegetation during this period of unstable climate in the GS exhibited a noticeable shift (Rull et al., 2015).

Between the 60's and the 80's, the first geochronologic analyses in the GS, using peat deposits recovered from the summits of the Tepuis, indicated that formation of sedimentary archives began in early Holocene around 8000 ^{14}C yr BP (Rull et al., 1988; Schubert, 1985; Schubert et al., 1986). Based on this result, it was hypothesized that climate was arid and extensive grasslands dominated the GS during late Pleistocene (Eden, 1974; Schubert, 1985; Schubert et al., 1986). According to the aforementioned hypothesis, the current forest patches in the uplands savannas would represent a progressive forest recovery since the Late Glacial Maximum. However, subsequent authors proposed that savannas have always been present in the region, and human action has greatly contributed to their current expansion by the use of fire (Huber, 1995b). Therefore, in order to understand the origin and development of savanna vegetation in the GS, the first sequences from the savanna uplands were recovered from lacustrine sediments and peat bogs in the 90's (locations: Mapaurí, Divina Pastora, Santa Teresa, Urué; Fig. I.5; Rinaldi et al., 1990; Rull, 1991, 1992, 1999). The oldest available sequence was of early Holocene age (similarly to the highlands), obtained from the locality Mapaurí (Rinaldi et al., 1990). The authors made a very preliminary Holocene pollen study for this sequence, which suggested continous existence of open savanna. However, later Rull (2007) re-analysed the Mapaurí sequence using new pollen atlases, including the analysis of charcoal particles and calibrating the dating results. In this way, it was recognised a previously unnoticed and remarkable vegetation change occurring during the early Holocene, which was the replacement of forest by open savanna. This important finding suggested that savanna landscape originated during the Late Glacial and also provided evidence to refute the hypothesis about the dominance of extensive grassland since the Late Pleistocene (Eden, 1974). The findings about the origin of savanna in Mapaurí (as the first evidence of this topic) are provided below.

In early Holocene, a *Catostemma* (Bombacaceae)-dominated cloud forest occupied the Mapaurí area. The forest was abruptly replaced by open savanna around 10,200 cal yr

BP (Rull, 2007; Rull, 2009a,b). A similar forest (modern analogue) is currently situated on tepuian slopes at higher altitudes. Based on this knowledge, it was proposed that an upward displacement of this forest probably occurred in response to increase in average temperature of approximately 2-3ºC during the Pleistocene/Holocene transition (Rull, 2007). Therefore, vegetation turnover was therefore interpreted in climatic terms, which may indicate that the global Early Holocene Warming (EHW) occurred in the GS region (Rull, 2009a,b; Rull, 2007; Rull et al., 2013). The presence of the first fires of high intensity/frequency in Mapurí's area began just after the vegetation shift, supporting the climatic hypothesis (Rull, 2007). These fires were considered potential indicators of human presence in the region during the early Holocene (Rull, 2009b). In addition to the climatic hypothesis, Rull (2007, 2009a) postulated three potential scenarios during the origin of open savanna: (*i*) savannas simply expanded from existing small savanna patches; (*ii*) open savanna emerged as a new vegetation type in the region, and (*iii*) savanna vegetation possibly migrated upwards from adjancent lowlands due to the warming.

One lacustrine sequence obtained recently from Lake Chonita has maximum ages around 15,000 cal yr BP, covering the Late Glacial (Fig. I.5; Montoya et al., 2011c). The pollen analysis indicated that a shrubland community occurred in the Lake Chonita's basin between ~12,700 and 11,700 cal yr BP (Montoya et al., 2011c). This woody community, characterised by *Bonyunia* (Loganiaceae), shares some similarities with the present-day shrublands located on ferruginous-rocky soils in northern sites of the GS. However, the present-shrubland does not represent a modern analogue of the Late Glacial shrubland (Montoya et al., 2011c). The *Bonyunia*-dominated community declined suddenly around 11,700 cal yr BP (Pleistocene-Holocene boundary), concurring with the first high-occurrence of fires for Chonita's basin. Based on this result, it was hypothesized that fire could have influenced the replacement of shrubland by open savanna, therefore, a driver of the origin of savanna (Montoya et al., 2011c). The sudden and significant increase in fires in ~11,700 cal yr BP was suggested to be related to climate change (warming and/or drier conditions) or early human occupation in the region, or both (Montoya and Rull, 2011; Montoya et al., 2011c; Rull et al., 2015). The high influence of human fires on most areas of current savannas is recognised and has been used to suggest potential anthropogenic origin of many of these grassy ecosystems (Rull et al., 2015). However, the evidence from the two sequences (Mapaurí and Chonita) is insufficient to support the hypothesis of human influence on the fire regimes and origin of savanna in the GS during the Late Glacial.

Thus far, only two sequences of Late Glacial age have assessed whether savanna vegetation originated during this period and the drivers involved in its origin. The available results suggest that the origin of the savanna vegetation in the GS occurred in the Late Glacial. However, in each location the main driver and ecological process appear to have been different. With the available evidence is not possible to discern if the origin of savanna was a regional event driven by similar environmental drivers (including potential human role) or local vegetation changes occurred randomly. Therefore, the origin of open savanna, the role-played by environmental drivers and the potential human influence are research areas that deserve further study.

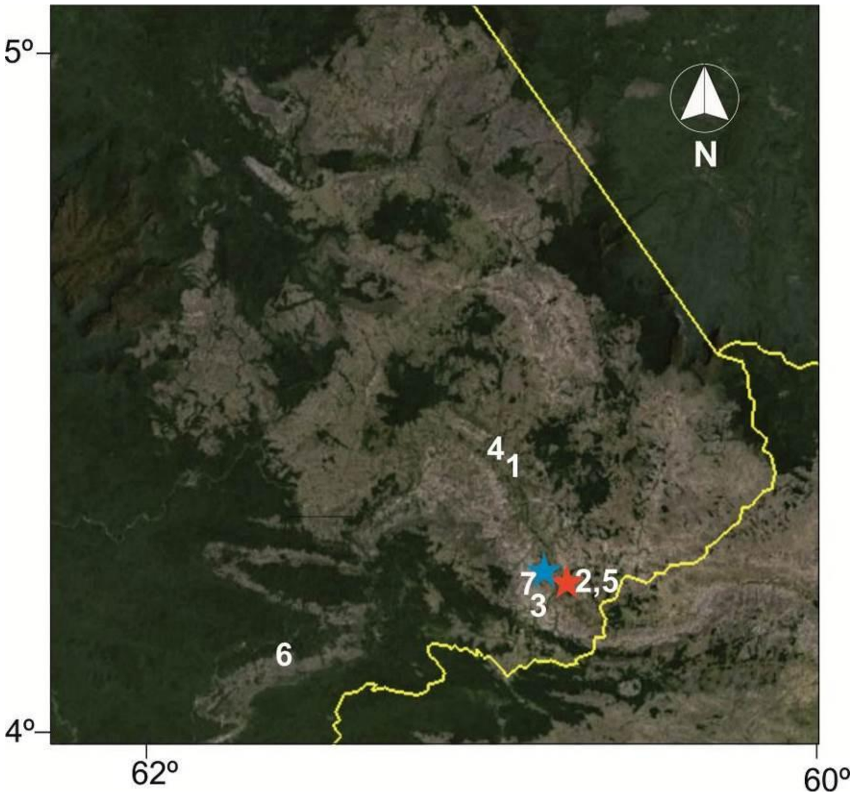


Figure I.5. The Gran Sabana. Numbers indicate the sites with palaeoecological information mentioned in the text: 1—Mapaurí; 2 —Divina Pastora; 3—Santa Teresa; 4 —Urué; 5—Lake Chonita; 6—El Paují; 7—Encantada peat bog. The locations studied in the present thesis are indicated with a star: Lake Encantada with a light-blue star and Fidencio peat bog with a red star. Images modified from Google-Earth (accessed in May 2015).

3.2. Middle and late Holocene (last ~8000 years)

In the 90's, other sequences of Holocene age were studied (locations: Divina Pastora-DP, Santa Teresa-ST, Urué; Fig. I.5; Rull, 1991, 1992, 1999), which spanned the last ~5000 yr. Rull (1991) made a reconstruction of vegetation and climate (inferred from algal record) of the localities aforementioned. A bit later, the trajectories of vegetation succession of those localities were evaluated (Rull, 1992). A preliminary analysis of charcoal particles was conducted only for the Urué sequence. This palaeoecological study was the first one to introduce the idea that past forests were not resilient to fire in the GS. Subsequently, Rull (1999) re-analysed the Urué sequence, improving the charcoal analysis and providing a more detailed reconstruction of the secondary succession after fire. The pollen analysis of all these studies documented a general successional trend from secondary forests within savana to open savanna since middle Holocene, triggered by dry episodes (DP, ST) or fire events (Urué) (Rull, 1991, 1992, 1999). The succession ended with the establishment of *morichales*. In DP and ST, evaluation of the potential role played by fires was not possible due to the absence of charcoal analysis for these sequences. The succession process described was characterised by continuous impoverishment of taxa, but steady increase in *Mauritia*-palm abundance (Rull, 1992, 1999). The coincidence of *morichales* with fire occurrence supported the view that this palm is a coloniser plant, which occupies rapidly new habits after disturbance (Rull, 1999).

Between 2007 and 2011, two new sequences of Holocene age (Encantada peat bog and El Paují; Fig. I.5) and the youngest part (last three millennia) of Lake Chonita's were studied (Montoya and Rull, 2011; Montoya et al., 2009, 2011a,b). The main objectives of these studies were to: (1) reconstruct vegetation dynamics; (2) discern the role played by climate and fire, and the interplay between them, on plant communities; (3) identify potential relationships between the fire regimes and past indigenous practices, and their effects on vegetation, and (4) evaluate the recent occurrence and establishment of *morichales*, and what factors and processes have driven their maintenance until the present-day. The main findings in relation to the aforementioned objectives are explained below:

-In the southernmost part of the GS region, close to the Brazilian border and Amazonian forest, the savanna in El Paují (Fig. I.5) expanded between 8250 and 7720 cal yr BP, probably favoured by the interplay between dry climate and fire events (Montoya et al., 2011a). Between 7720 and 5040 cal yr BP, savanna vegetation in El

Paují and Encantada (shore of the Lake Encantada) exhibited a remarkable shift to a more forested condition (forest-savanna mosaic), coinciding with an increase in the hydrologic balance and persistent presence of fire (Montoya et al., 2011a, 2009). The results suggested that vegetation changes were mainly climate-driven during early-middle Holocene. Nonetheless, fire appears to have been an important disturbance agent.

-Forests retracted and savanna expanded in El Paují between 5000 and 2700 cal yr BP, coinciding with increased fire incidence (Montoya et al. 2011a). A climatic explanation is unlikely due to this vegetation change occurred under higher available moisture. Instead, forest burning was the preferable interpretation (Montoya et al., 2011a). The coexistence of wet climate, rainforests and fires in this locality was explained in terms of land use practices linked to slash-and-burn of local forests (*conucos*). Therefore, it was hypothesized potential human presence in El Paují during the aforementioned period (Montoya et al., 2011a). Fires declined and the area was occupied by *Centrolobium* (Fabaceae)-dominated dry forest around 2700 cal yr BP, concurring with drier climate. The expansion of a forest dominated by coloniser taxa was interpreted as a consequence of land abandonment by humans (Montoya et al. 2011a).

-Open savanna with *morichales* established in the basin of Lake Chonita and the shore of Lake Encantada under intensive fire events and drier climate around 2000 cal yr BP (Montoya et al., 2009, 2011b). In El Paují, the dry forest retracted and open savanna established under wetter conditions around 1440 cal yr BP (Montoya et al., 2011a). The authors suggested that the retraction of forests and the subsequent expansion of pre-existing savannas in the three localities could have been caused by fire (Montoya and Rull, 2011; Montoya et al., 2009, 2011a,b). The simultaneous increase in fire and *Mauritia* supported the hypothesis of a potential pyrophilous nature of this palm in the region (Montoya et al. 2011b). Based on biogeographic analysis, it was suggested that humans could be the dispersal agents of *Mauritia* (Montoya et al, 2011b). If so, humans could have also influenced the fire regimes in southern GS for the last two millennia (Montoya et al., 2011b). In El Paují, this vegetation change was interpreted as humans returned in the area, but their patterns of land use were completely different from those used during the previous period. This was probably due to the arrival of a culture that used fire intensively in open areas (Montoya et al., 2011a). Thus, the evidence from the new sequences suggested that the present-day southern GS landscape is the result of land highly managed and altered by humans, instead of being the consequence of only climate variations (Montoya and Rull, 2011; Rull et al., 2013). Recently, it was hypothesized that selective burning (fire practices in open areas and savanna-forest ecotones, and rarely in *Maurita*-swamps) could explain the expansion of *morichales* (Rull and Montoya, 2014), rather than the pyrophilous character of *Mauritia.*

Recently, Rull et al. (2013) re-evaluated the available evidence in the GS, and made some inferences and hypotheses: (1) upland savannas have not been linked to the dominant climate, but largely conditioned to burning practices; (2) the shifts from forests to savanna have been abrupt and irreversible due to the existence of tipping points, no matter the cause (e.g., natural of antropogenic fires); however, the palaeoecological evidence is still insufficient to identify such potential thresholds, (3) the most likely cause of origin of treeless savanna during the Late Glacial was the synergy between warming, fire, and availability of fuel loads, (4) the projected global warming will likely exarcebate the expansion of upland savannas by favouring positive fire-climate feedbacks.

Despite the accumulated evidence and the advances in knowledge of vegetation dynamics in the GS during middle and late Holocene, the available evidence is still limited to comprehend some ecological processes that probably influenced the vegetation development, such as potential land use practices and their change through time; feedback processes between environmental drivers and vegetation; diversity patterns; and catchment processes (e.g., erosion). In addition, the topics resilience and regime shifts (ecological processes that mediate change between savanna sub-states) have been virtually unexplored for the GS (Rull et al., 2013).

4. The thesis

Thus far, a number of hypotheses have been put forward about the interplay between environmental factors (including humans) and vegetation in the GS from the Late Glacial to the present. However, these hypotheses need further evaluation to fully comprehend the role played by the factors (abiotic and biotic) and the ecological processes associated with the origin and development of savanna vegetation. Similar knowledge gaps exist in savannas in general, and more specifically in other humid savanna regions, in which the ecological processes that have governed alternative savanna sub-states have not been recognised or understood completely.

This thesis provides new evidence (for instance, a new Late Glacial sequence) to test the hypotheses of the GS and evaluate in detail the ecological processes of humid savannas. In addition, this thesis goes further and forecasts potential future vegetation responses, as well as suggests some guidelines for savannas management of the GS.. The analyses were based on palynological analysis and multiproxy approach where possible, in which independent lines of evidence were used to determine environmental (e.g., climate, fires, watershed processes) and vegetation changes. This thesis covers since the Late Glacial (~12,750 cal yr BP) to the present. The general and specific objectives are explained in pages 64 and 65.

This thesis was supported - i.e. scientific basis, funding, field trip to Venezuela, stay at the University of Pittsburgh (USA) and methodological and material support - by four research projects (described previously), led by Dr. Valentí Rull (Spanish Superior Council for Scientific Research, CSIC for its acronym in Spanish). Among them, the following two projects were focused on the Gran Sabana and underpined my thesis:

1. "Responses of neotropical vegetation to past climate changes and applications to biodiversity conservation (ECOPAST)". Ref.: CGL2009-07069/BO.

2. "Potential effects of global warming on neotropical vascular plant biodiversity: the case of the Gran Sabana in the Venezuelan Guayana (BIOSABANA)". Ref.: CGL2006-00974.

The Spanish Ministry of Science and Innovation and the Spanish Ministry of Education and Science respectively funded both projects.

In 2007 an international and multidisciplinary expedition formed by palaeoecologists, geologists and botanics from the research group "Tropical Paleoecology and of High Mountain" (PATAM, for its acronym in Spanish) and from the University of Pittsburgh (Department of Geology and Planetary Science, USA) * travelled to the south of the GS, and obtained several sequences from sedimentary archives (lake and peat bog records). During that trip, several localitites were visited and a number of cores were collected in the upland savannas, using modified Livingstone piston corer and Russian corer (Figure I.6). Of these cores, two sequences obtained from two savanna areas were analysed in this thesis. The description of the two sequences and their coring sites is provided below.

---

* Participants of the expedition from: (Spain): Valentí Rull, Sandra Nogué and Encarni Montoya, affiliated to the Autonomous University of Barcelona in the year of the field campaign, and Teresa Vegas-Vilarrúbia of Barcelona University. The United States of America: Nathan Stansell and Broxton Bird, affiliated to the University of Pittsburgh at that time. Italy: Otto Huber of Botanical Garden of Merano; and Venezuela: Wilmer Díaz, affiliated to Botanical Garden of Orinoco in the year of the expedition.

Figure I.6. Core sampling during PATAM 2007 field trip**. A-C:** Lake sampling with modified Livingston squared-rod piston. **D-F:** Peat bog sampling with Livingston squared-rod piston. (Photos: E. Montoya, 2007).

1) Lake Encantada (Figures I.5 and I.7; core PATAM4 C07; 4º 42’ 37.44” N - 61º 05’ 03.29” W). Lacustrine core extracted from the centre of the lake, 2.13 m in length (Figure I.8).

Figure I.7. Lake Encantada. *Morichales* bordering the lake shore. The basin is currently dominated by grassland vegetation. (Photo: E. Montoya, 2007).

Figure I.8. Lake Encantada sequence analysed in the present thesis. Drives obtained from the core PATAM4 C07. (Photos: taken in the Department of Geology and Planetary Science, University of Pittsburgh, Pittsburgh, USA).

2) Fidencio peat bog (Location Fidencio peat bog, Figures I.5 and I.9; core PATAM3 A07; 4º40‘N and 61º00’W). Peat bog sequence of 3.21 m in length (Figure I.10).

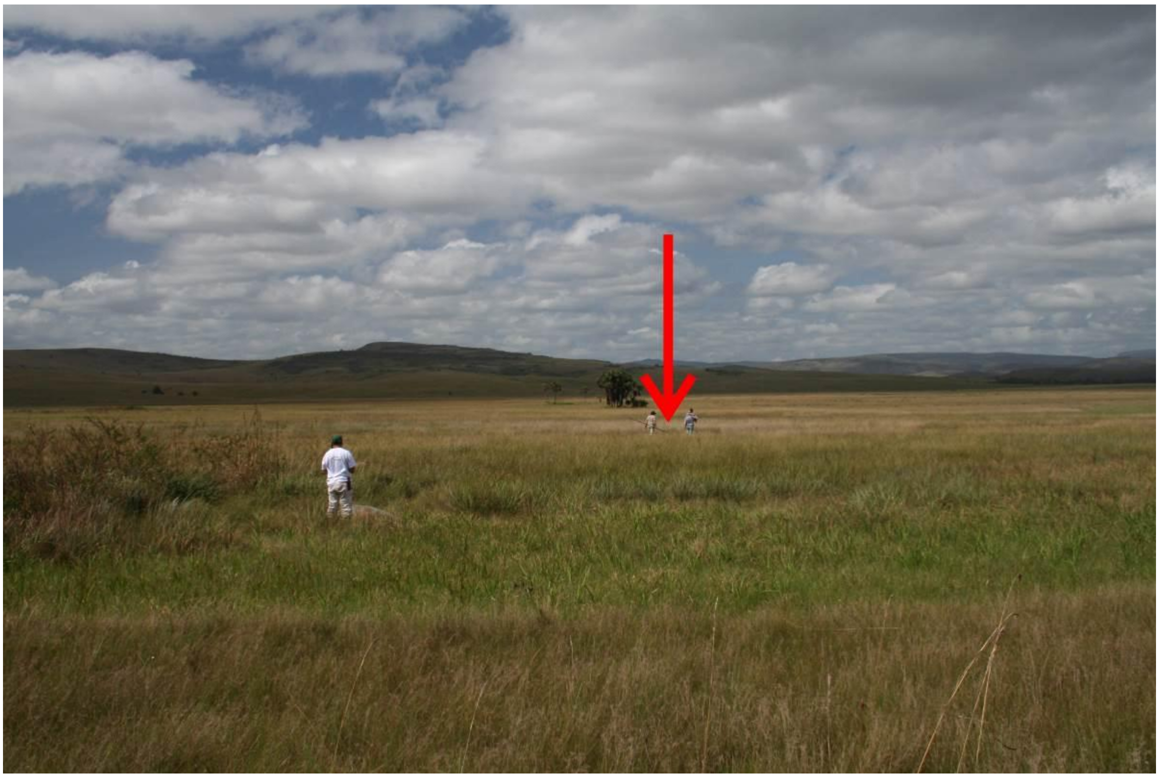


Figure I.9. Image of grassland vegetation in Fidencio’s area. There are few *Mauritia flexuosa* palms scattered in the landscape. The coring site is indicated by a red arrow. (Photo: E. Montoya, 2007).

Figure I.10. Fidencio peat bog sequence analysed in the present thesis. Drives obtained from core PATAM3 A07. (Photos: taken in the Department of Geology and Planetary Science, University of Pittsburgh, Pittsburgh, USA).

OBJECTIVES

Main objectives

The main objectives of this thesis were to:

(1) Generate a robust and detailed reconstruction of vegetation changes from the Late Glacial to the present, based on the sedimentary archives Lake Encantada (PATAM4C 07) and Fidencio peat bog (PATAM3A 07).

(2) Evaluate the interplay between vegetation and environmental drivers, and the associated ecological processes (e.g. feedbacks, resilience) during the periods studied.

(3) Assess the hypotheses of the origin and maintenance of savanna vegetation in the Gran Sabana.

To accomplish these objectives, palaeoecological analyses of the two sequences were based on pollen grains (the main proxy), pteridophyte spores, algal remains, microcharcoal particles, geochemical proxies, analysis of sediments and ecological indices.

The specific objectives of the present research are presented below, sorted out by the following chapters of the thesis:

Chapter 1 (Lake Encantada, core PATAM4C 07), the main aims were to:

- Evaluate the interplay and synergies between vegetation, climate (hydrological balance), fire and soil erosion, and the associated feedback processes, since early Holocene.

-Test the hypotheses about the maintenance of the savanna vegetation.

Chapter 2 (Fidencio peat bog, core PATAM3A 07), the main objectives were to:

- Analyse the vegetation responses to the abrupt climates changes during the Late Glacial.

- Evaluate the alternative hypotheses about the origin of the southern GS savannas.

- Assess whether vegetation shift at the Younger Dryas-Holocene transition could be considered a past analogue of the global warming.

Chapter 3 (Lake Encantada, core PATAM4C 07; Fidencio peat bog, core PATAM3A 07), this chapter aimed to:

- Assess ecological resilience and regime shifts for the last ~13,000 cal yr BP, based on the palaeoecological information provided by the two sequences studied in the previous chapters.
- Suggest some guidelines for savannas management of the GS.

4. References

Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D., Scholes, R.J., 2010. Tree-grass coexistence in savannas: Interactions of rain and fire. *Journal of Theoretical Biology*. 264, 235-242.

Accatino, F., De Michele, C., 2013. Humid savanna–forest dynamics: A matrix model with vegetation–fire interactions and seasonality. *Ecol. Model*. 265, 170–179.

Barbosa, R.I., Campos, C., 2011. Detection and geographical distribution of clearing areas in the savannas ('lavrado') of Roraima using Google Earth web tool. *Journal of Geography and Regional Planning.* 4, 122-136.

Battarbee, R.W., Jones, V.J., Flower, R.J., et al., 2001. Diatoms. In: Smol, J.P., Birks, H.H., Last, W.M (eds.) Tracking Environmental Changes Using Lake Sediemnts. Volume 3. Terrestrial, Algal and Siliceous Indicators. Kluwer Academic Publisher, Dürdrecht. pp. 155-202.

Beckage, B., Gross, L.J., Platt, W.J., 2011. Grass feedbacks on fire stabilize savannas. *Ecol. Model*. 222, 2227-2233.

Behling, H., Hooghiemstra, H., 1998. Late Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. *Palaeogeogr. Palaeoclimatol. Palaeoecol*. 139, 251–267.

Behling, H., Hooghiemstra, H., 2000. Holocene Amazon rainforest-savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia. *J. Quat. Sci*. 15, 687–695.

Berrío, J.C., H. Wouters, H., Hooghiemstra, H., Carr, A.S., Boom, A., 2012. Using paleoecological data to define main vegetation dynamics along the savanna-forest ecotone in Colombia: implications for accurate assessment of human imoacts. In: R. Myster (ed.), Ecotones between forest and grasslands. pp 209-228. Springer, New York.

Bilbao, B.A., Leal, A.V., Méndez, C.L., 2010. Indigenous Use of Fire and Forest Loss in Canaima National Park, Venezuela. Assessment of and Tools for Alternative Strategies of Fire Management in Pemón Indigenous Lands. *Hum. Ecol*. 38, 663–673.

Birks, H,J., Birks, H.H., 1980. Quaternary Palaeoecology. The Blackburn Press, New Jersey.

Bond, W.J., 2010. Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. *Plant Soil*. 334, 47-60.

Bond, W.J., Keeley, J., 2005. Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol*. 20, 387–394.

Bond, W.J., Parr, C.L., 2010. Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biological Conservation*. 143, 2395-2404.

Bowman, D. et al., 2011. The human dimension of fire regimens on Earth. *Journal of Biogeography.* 38, 2223-2236.

Brenchley, P.J., Harper, D.A.T., 1998. Palaeoecology: ecosystems, environments and evolution. Chapman and Hall, London.

Bush, M.B., Flenley, J.R., Gosling, W.D., 2011. Tropical Rainforest Responses to Climatic Cahnge. Springer Berlin.

Calabrese, J.3M., Deffuant, G., Grimm, V., 2011. Bridging the Gap Between computational models and viability based resilience in Savanna ecosystems. In: Deffuant, G., Gilbert, N. (Eds.) Variability and resilience of complex Systems: concepts, methods and case estudies from ecology and society. Chapter 5. Springer, pp. 107-130.

Colson, A.B., 1985. Routes of knowledge, and aspects of regional integration in the circum-Roraima area of the Guayana highlands. *Antropológica.* 63/64, 103-149.

Delcourt, H.D., Delcourt, P.A., 1991. Quaternary ecology: a palaeoecological perspective. Chapman and Hall, London.

Dezzeo, N., Chacón, N., Sanoja, E., Picón, G., 2004. Changes in soil properties and vegetation characteristics along a forest-savanna gradient in southern Venezuela. *For. Ecol. Manag.* 200, 183–193.

Dube, O.P., 2009. Linking fire and climate: interactions with land use, vegetation, and soil. *Curr. Opin. Environ. Sustain*. 1, 161–169.

Eden, M.J., 1974. Paleoclimatic influences and the development of savanna in southern Venezuela. *J. Biogeograr.* 1, 95-109.

Eiten, G., 1972. The Cerrado vegetation of Brazil. *Bot. Rev*. 38, 201-341.

Fölster, H., 1986. Forest-savanna dynamics and desertification processes in the Gran Sabana, *Interciencia*. 11(6), 311-316.

Fölster, H., Dezzeo, N., Priess, J., 2001. Soil-vegetation relationship in base-deficient premontane moist forest-savanna mosaics of the Venezuelan Guayana. *Geoderma*. 104, 95-113.

Gardner, T.A., 2006. Tree-grass coexistence in the Brazilian Cerrado: demographic consequences of environmental instability. *J. Biogeogr.* 33, 448–463.

Gillson, L., 2004. Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity*. 1, 281– 298.

Gillson, L., Ekblom, A., 2009. Resilience and Thresholds in savannas: Nitrogen and Fire as drivers and responders of vegetation transition. *Ecosystems.* 12, 1189-1203.

Gil-Romera, G., López-Merino, L., Carrión, J.S., González-Sampériz, P., Martín-Puertas, C., López Sáez, J.A., Fernández, S., García Antón, M., Stefanova, V., 2010. Interpreting Resilience through Long-Term Ecology: Potential Insights in Western Mediterranean Landscapes. *The Open Ecology Journal.* 3*,* 43-53.

Gómez, E., Picón, G., Bilbao, B., 2000. Los incendios forestales en Iberoamérica. Caso Venezuela. In: Vélez-Muñoz, R. (Eds.), La defensa contra incendios forestaes. Fundamentos y experiencias. McGraw-Hill, Madrid.

Gunderson L.H., 2000. Ecological resilience-in theory and application. *Annu. Rev. Ecol. Syst.* 31,425–39.

Guzmán, F., 1986. Aspectos fisiográficos y edáficos de la Cuencia del Caroní. *Interciencia*. 11(6), 290-294.

Hernández, L., Fölster, H., 1994. Vegetación en transición. *Sci. Guayanae*. 4, 118-144.

Higgins, S.I., Scheiter, S., Sankaran, M., 2010. The stability of African savannas: insights from the indirect estimation of the parameters of a dynamic model. *Ecology.* 91, 1682–1692.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett*. 15, 759–768.

Holling C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst*. 4, 1-23.

Huber, O., 1986. La vegetación de la Cuenca del río Caroní. *Interciencia.* 11(6), 301-307.

Huber, O., 1995a. Geographical and physical features. In: Steyemark, J.A., Berry, P.E., Holst, B.K. (Eds.) Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Bot. Gard. Press. St, Louis. pp 1-62.

Huber, O., 1995b. Vegetation. In: Steyemark. J.A., Berry, P.E., Holst, B.K. (Eds). Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Bot. Gard. Press, St. Louis. pp 97-160.

Huber, O., Febres, G., 2000. Guía ecológica de la Gran Sabana. Nature Conservancy, Caracas

Huber, O., García, P., 2011. The Venezuelan Guayana Region and the Study Areas: Geo-ecological characteristics. In: Peatlands of the Western Guayana Highlands, Venezuela, Ecological Studies. Springer Berling Heiderbelg, Berlin, Heiderberg. pp 29-89.

Jackson, S.T., 2001. Integrating ecological dynamics across timescales, realtime, Q-time and deep time. *Palaios.* 16, 1-2.

Jeltsch, F., Weber, G.E., Grimm, V., 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant. Ecology.* 161, 161-171.

Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A., Bond, W.J., 2011. Deciphering the distribution of the savannah biome. *New Phytol*. 191,197-209.

Lüttge,U., 2008. Savannas. I Physiognomy, Terminology and Ecotones: Why do savannas exist? In: Physiological Ecology of Tropical Plants. Springer Berling Heidelberg. Chapter 9. pp 293-312.

Marchant, R., 2010. Understanding complexity in savannas: climate, biodiversity and people. *Curr. Opin. Environ. Sustain.* 2, 101–108.

Mayle, F.E., Power, M.J., 2008. Impact of a drier Early-Mid-Holocene climate upon Amazonian forests. Philos. *Trans. R. Soc. B Biol. Sci*. 363, 1829–1838.

Meltzer, D.J., 1997. Anthropology: Monte Verde and the Pleistocene Peopling of the Americas. *Science*. 276, 754-755.

Montoya, E., Rull, V., 2011. Gran Sabana fires (SE Venezuela): a paleoecological perspective. *Quat. Sci. Rev*. 30, 3430–3444.

Montoya, E., Rull, V., Nogué, S., Díaz, W.A., 2009. Paleoecología del Holoceno en la Gran Sabana, SE Venezuela: Análisis preliminar de polen y microcarbones en la Laguna Encantada. *Collect. Bot.* 28, 65-79.

Montoya, E., Rull, V., Nogué, S., 2011a. Early human occupation and land use Changes near the boundary of the Orinoco and the Amazon basins (SE

Venezuela): Palynological evidence from El Paují record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 413–426.

Montoya, E., Rull, V., Stansell, N.D., Abbott, M.B., Nogué, S., Bird, B.W., Díaz, W.A., 2011b. Forest–savanna–*morichal* dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quat. Res*. 76, 335–344.

Montoya, E., Rull, V., Stansell, N.D., Bird, B.W., Nogué, S., Vegas-vilarrúbia, T., Abbott, M.B., Díaz, W.A., 2011c. Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron. *J. Quat. Sci.* 26, 207–218.

Murphy, B.P., Bowman, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna? *Ecol. Lett.* 15, 748–758.

Pinheiro, MH.O., Monteiro, R., 2010. Contribution of the discussions on the origin of the *Cerrado* biome: Brazilian savanna. Brazilian *Journal of Biology*. 70(1), 95-102.

Pivelo, V.R., 2011. The use of fire in the Cerradi and Amazonian Rainforests of Brazil: Past and Present. *Fire Ecology*. 7(1), 24-39.

Rinaldi, M., Rull, V., Schubert, C., 1990. Análisis paleoecológico de una turbera en la Gran Sabana (Santa Cruz de Mapaurí), Venezuela: Resultados preliminaries. *Acta Científica Venezolana*. 41, 66-68.

Roberts, N., 1998. The Holocene: An environmental History. Wiley-Blackwell.

Rodríguez, I., 2007. Pemón perspectives of fire management in Canaima National Park, southeastern Venezuela. *Human Ecology.* 35, 331-343.

Rull, V., 1991. Contribución a la paleoecología de Pantepui y la Gran Sabana (Guayana Venezolana): clima, biogeografía y ecología. *Scientia Guayanae*, Volumen 2.

Rull, V., 1992. Successional patterns of the Gran Sabana (southeastern Venezuela) vegetation during the last 5000 years and tis responses to climatic fluctuations and fire. *J. Biogeograf.* 19, 329-338.

Rull, V., 1999. A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela. *J. Quat. Sci.* 14, 137–152.

Rull, V., 2007. Holocene global warming and the origin of the Neotropical Gran Sabana in the Venezuelan Guayana. *J. Biogeogr.* 34, 279–288.

Rull, V., 2009a. On the Use of Paleoecological Evidence to Assess the Role of Humans in the Origin of the Gran Sabana (Venezuela). *Hum. Ecol.* 37, 783–785.

Rull, V., 2009b., New palaeoecological evidence for the potential role of fire in the Gran

Sabana, Venezuelan Guayana, and implications for early human occupation. *Veget Hist Archaeobot*. 18,219–224.

Rull, V., 2010. Ecology and Palaeoecology: Two Approaches, One Objective. *Open Ecol. J*. 3, 1–5.

Rull, V., 2012. Community ecology: diversity and dynamics over time. *Community Ecol.* 13, 102–116.

Rull, V., Montoya, E., 2014. *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a Neotropical context. *Quaternary Science Reviews*. 99, 17-33.

Rull, V., Schubert, C., Huber, O., Aravena, R., 1988. Estudios paleoecológicos sobre aluviones y turberas de sabana y tepuyes de la Gran Sabana (Estado: Bolívar). *Pantepui*. 4, 25-29.

Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T., Safont, E., 2013. Ecological palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. *Perspect. Plant Ecol. Evol. Syst*. 15, 338–359.

Rull, V., Montoya, E., Vegas- Vilarrúbia, T., Ballesteros, T., 2015. New insights on palaeofires and savannisation in northern South America. *Quaternary Science Reviews.* 122,158-165.

Salgado-Labouriau, ML., Casseti, V., Ferraz-Vicentini, K.R., Martin, L., Soubiès, F., Suguio, K., Turcq, B., 1997. Late Quaterarny vegetational and climatic changes in Cerrado and palm swamp form Central Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 128, 215-226.

Sankaran, M. & Ratnam, J. 2013. 355: African and Asian Savannas. In ‘Encyclopedia of Biodiversity’ 2nd Edition. Simon Levin (Editor-in-Chief). Elsevier Press.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. *Nature.* 438, 846–849.

Sarmiento, G., 1984. The ecology of neotropical savannas. Harvard University Press, Cambridge.

Scheffer, H., Carpenter, S., Foley, J.A., Folke, C., Wlaker, B., 2001. Catastrophic shifts in ecosystems. *Nature*. 413, 591-596.

Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544.

Schubert, C., Fritz, P., 1985. Radiocarbon ages of peat, Guayana highlands (Venezuela). *Naturwissenschaften.* 72, 427-429.

Schubert, C., Briceño, H.O., Fritz, P., 1986. Paleoenvironmental aspects of the Caroní-Paragua river basin (southeastern Venezuela). *Interciencia.* 11, 278-289.

Seddon, A.W.R., 2012. Paleoecology. In: Gibson, D. (Eds), Oxford Bibliographies Online: Ecology, Oxford. Univ. Press, New York.

Simpson, G. G., 1970. Uniformitarianism. An inquiry into principle, theory and methd in geohistory and biohistory. In: Hect, M.K. and Steere, W.C. (Eds.), Essays in Evolution and Genetics in honour of Theodosius Dobzhansky. North Holland.

Sletto, B., 2008. The Knowledge that counts: Institutional identities, policy science, and the conflict voer fire management in the Gran Sabana, Venezuela. *World Development*. 36(1), 1938-1955.

Sletto, B., Rodríguez, I., 2013. Burning, fire prevention and landscape productions among the Pemon, Gran Sabana, Venezuela: towards and intercultural approach to widland fire management in Neotropical savannas. *Journal of Environmental Management.* 115, 155-166.

Solomon, S., Quin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M.M.B., Miller, H.L., 2007. Climate change 2007: the scientific basis. Cambridge University Press, Cambridge.

Stocker, T.F., Quin, D., Plattner, G.K., Tignor, M.M.B., Allen, S.K., Boschung, J., Naules, A., Xia, Y., Bex, V., Midgley, P.M., 2013. Climate Change 2013. The Physical Science Basis, working group I Contribution to the Fifth Assesment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Thomas, D.J., 1982. Order without government: The society of the Pemons Indians of Venezuela. University of Illinois Press, Illinois.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E., 2011. Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. *Quat. Sci. Rev.* 30, 2361–2388. doi:10.1016/j.quascirev.2011.05.006.

Walker, J., Gillison, A.N., 1982. Australian Savannas. In: Huntley, B.J., Walker, B.H (eds.) Ecology of Tropical Savannas. Springer Berlin Heidelberg. pp.5-24.

Walker, I.R., 2001. Midges: Chironomidae and Related Diptera. In: Smol, J.P., Birks, H.H., Last, W.M eds.) Tracking Environmental Changes Using Lake Sediements. Volume 4. Zoological Indicators. Kluwer Academic Publisher, Dürdrecht. pp. 43-66.

Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.). Tracking environmental change using lake sediments. Vol 3: Terrestrial, algal and siliceous indicators. Kluwer, Dordrecht. pp 75-98.

Whitlock, C., Higuera, P.E., McWethy, D.B., Briles, C.E., 2010. Paleoecological Perspectives on Fire Ecology: Revisiting the Fire-Regime Concept. *The Open Ecology Journal*. 3, 6-23.

Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, .B., Froyd, C.A., Myers, N. 2007a. How can knowledge of the past help to conserve the future? Biodiversity conservarion and the relevance of longterm ecological studies. *Philosophical Transactions of the Royal Society B.* 362, 175-186.

Willis, K.J., Gillson, L., Knapp, S., 2007b. Biodiversity hotspots through time: an introduction. *hilosophical Transactions of the Royal Society B. 362,* 169-174.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birks, H.J.B., 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology and Evolution*. 25, 583-591.

CHAPTER I:

An 8700-year record of the interplay of environmental and human drivers in the development of the southern Gran Sabana landscape, SE Venezuela

The contents of this chapter have been published as:
Tania Ballesteros, Encarni Montoya, Teresa Vegas-Vilarrúbia, Santiago Giralt, Mark Abbott and Valentí Rull (2014) *The Holocene*. 24, 1757-1770.

1.0. Abstract

The vegetation of the southern Gran Sabana (SE Venezuela) consists primarily of a treeless savanna with *morichales* (*Mauritia flexuosa* palm stands), despite the prevailing climate being more favourable for the development of extensive rainforests. Here we discus the results of our 8700-year palaeoecological reconstruction from Lake Encantada based on analysis of pollen, algal remains, charcoal and geochemical proxies. We use the findings to assess a number of hypotheses that seek to explain the dominance of savanna vegetation and consider the relative importance of factors such as climate, fire and erosion on the landscape. The reconstruction of vegetation changes suggests the following trends: open savanna with scattered forest patches (8700-6700 yr BP), forest-savanna mosaic (6700-5400 yr BP), open savanna with forest patches (5400-1700 yr BP) and treeless savanna with *morichales* (1700 yr BP-the present). We conclude that the interplay between climate and fire and the positive feedback between the presence of grasses and increased fire frequency played a major role in the vegetation dynamics from the early to middle Holocene (8700-6700 yr BP). The synergistic action between reduced fires and wetter conditions appears to be a determinant in the development of rainforest around 6700 yr BP. Despite higher available moisture at ~5400 yr BP, the savanna expanded with the increased frequency of fire, potentially driven by human land-use practices. We also propose that the interplay between fire and erosion created forest instability during the middle and late Holocene. The current southern Gran Sabana landscape is the result of the complex interplay between climate, fire, erosion and vegetation.

1.1. Introduction

Savanna is one of the most extensive tropical ecosystems, covering approximately 20% of the Earth's land surface, and occurring over a broad range of climatic, edaphic and topographic conditions. Fire frequency is high in savanna ecosystems from both natural and anthropogenic causes. This biome occurs in areas showing annual precipitation values between 300 to 1800 mm; values above 600 to 820 mm/yr correspond to humid ecosystems (Accatino and De Michele, 2013). The presence of savanna in this high-rainfall areas suggests that climate alone is not responsible for the distribution of this biome (Murphy and Bowman, 2012). Instead, the interplay of environmental drivers such as climate, soil development, geomorphology, land use and fire frequency are important factors that influence the presence of savanna in areas that could be covered by tropical rainforest. Despite an increased understanding of how these drivers influence the evolution of savanna (Jeltsch et al., 2000; Murphy and Bowman, 2012), the underlying ecological processes and interactions that maintain this ecosystem are not well understood. Probably multiple factors operate at different spatial and temporal scales (Jeltsch et al., 2000), and their feedbacks with vegetation and soils contribute to the establishment and maintenance of the savanna physiognomy (Beckage et al., 2009; Hoffmann et al., 2012a,b). Savanna areas have experienced remarkable expansions in the last millennia (Behling and Hooghiemstra, 1999; Breman et al., 2011; Montoya and Rull, 2011) largely caused by the increased occurrence of human caused fires. In order to prevent further expansion, an improved understanding of the interplay between human and environmental drivers is needed.

The Venezuelan Gran Sabana (GS) region is an upland savanna located in southeastern Venezuela (Fig. 1.1a) and is situated within the extensive Guayanan and Amazon rainforests (Barbosa and Campos, 2011). Even though the regional climate is suitable for the development of rainforest vegetation, the vegetation of the GS is savanna and has persisted since the beginning of the Holocene (Montoya et al., 2011a; Rull, 2007). Three hypotheses have been proposed to explain the long-term presence of savanna vegetation in the GS. First, the climatic hypothesis suggests that the GS savannas are the relicts of larger savanna extensions that originated in drier and/or colder epochs (e.g, Last Glacial Maximum) (Eden, 1974). Second, the fire hypothesis presumes that frequent burning, potentially from anthropogenic sources, formed and maintained the savanna ecosystem. The more recent savanna expansion (~ 2000 yr BP to the present) appears to have been caused by human-induced forest clearing through burning (Montoya et al., 2011b, c). The absence of archaeological studies to date in the GS currently limits our knowledge of the timing of human occupancy, as well as the associated land-use practices. Third, the edaphic hypothesis suggests that unfavourable soil conditions in the GS, such as low nutrient concentrations, low water retention and a shallow soil profiles suppress forest growth resulting in savanna development (Dezzeo et al., 2004; Fölster et al., 2001). Modern short-term studies limited to the last several decades highlight the negative impacts of soil stress on vegetation and the landscape (Dezzeo et al., 2004; Fölster et al., 2001), although there are no studies to date that have focused on the influence of soil development on vegetation over longer timescales (centuries to millennia). A study of the long-term vegetation dynamics is required in order to assess these hypotheses and determine the interplay between climate, vegetation, fire ecology, soil related factors and the associated feedback processes.

In this work, we present a multiproxy investigation of a lacustrine sediment record recovered from a region in the southern GS covering the last 8700 yr. We integrated pollen, spores, algal remains, charcoal and geochemical analyses to generate a detailed reconstruction of the environmental changes in the region, with a specific focus on the interplay and synergies between the environmental drivers (climate and fire), soil erosion and vegetation.

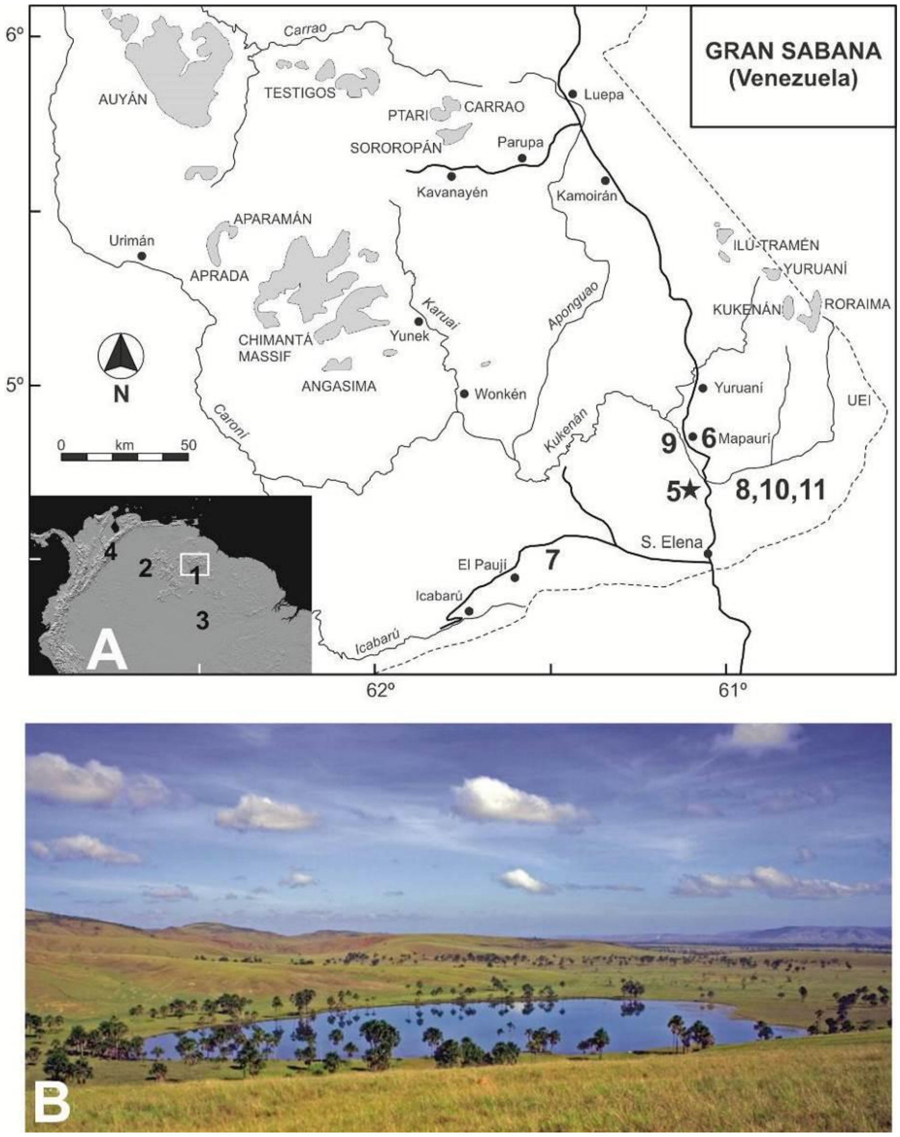


Figure 1.1. A) Location of the study area and its position within northern South America. The Gran Sabana is delimited by the white square. The coring site is indicated by a star. Numbers indicate the sites with paleoecological information mentioned in the text: 1—Roraima savannas; 2—*Llanos* (*Llanos Orientales* of Colombia and Venezuelan Orinoco *llanos*); 3—Northern Amazonia; 4—Northern Andes; 5—Encantada peat-bog; 6—Mapaurí; 7—El Paují; 8—Lake Chonita; 9—Urué; 10—Divina Pastora); 11—Santa Teresa. **B)** Lake Encantada. *Morichales* bordering the lake shore. Regional open savanna landscape. (Photo: V. Rull, 2007).

1. 2. Present-day environmental setting

1.2.1. Regional features

The GS is an extended region (~10,800 km^2) located in the Venezuelan Guyana, in southeastern Venezuela (Bolívar state). This region lies in northeast of the Precambrian Guiana Shield, and between the Orinoco and Amazon basins (4º36’ to 6º37’N and 61º4’ to 74º2’W) (Fig. 1.1a). The climate of the GS has been described as submesothermic tropophilous, with average annual temperatures of approximately 18–22 ºC and precipitation of 1600–2000 mm/yr. The GS is a high, undulating erosion surface that forms an *Altiplano* inclined from north (1350 m asl) to south (700 m asl). The GS is situated on quartzite and sandstone bedrock, known as the Roraima group. These rocks have been subject to long weathering processes and produce iron- and aluminium-oxide-rich soils (Huber, 1995a), which have poor nutrient content, with low concentrations of phosphorous, calcium and nitrogen (Huber, 1995a). The soil-chemical stress caused by the calcium deficiency and aluminium toxicity combined with the thin profile render the soils incapable of supporting certain types of vegetation, especially forests (Fölster et al., 2001). This reduces the capacity of the soil to withstand external and internal impacts such as burning and drought (Fölster et al., 2001;Schubert and Huber, 1989).

In the Venezuelan Guayana region, the principal vegetation types are evergreen montane and gallery forest, but the majority of the GS is covered by savanna. Three primary types of savanna occur in this area (Huber, 1995b): (1) open treeless savannas, (2) shrubs savannas and (3) open savannas with *morichales*, which are mostly monospecific dense stands of the Arecaceae *Mauritia flexuosa* (locally known as *moriche*). The stands of *morichales* grow along river courses and around lakes on poorly drained soils with high clay content (Rull, 1999). This type of gallery forest is an important vegetation component occurring in the central and southern regions of the GS at elevations lower than 1000 m asl (Huber, 1995b). Other vegetation types in the GS landscape that form patchy mosaics in the savanna (Huber, 1986) are montane rain forests (800-1500 m asl; Huber, 1995b; Hernández, 1999), shrublands, secondary woody communities and *helechales* (dense fern communities). Generally, *helechales* establish after repeated burning, as part of successional trend (Huber, 1986). A more detailed description of the vegetation composition is provided in previous studies (Huber 1995b). For the main taxa, refer to the Appendix A1.

Fire currently plays a significant role in the landscape dynamics of the GS, with a fire frequency between 5000 and 10,000 fires per year (Gómez et al., 2000). Nearly 70% of detected fires start in savanna areas, but some fires cross the savanna-forest boundary (Bilbao et al., 2010), causing forest degradation (Dezzeo et al., 2004; Fölster, 1986; Fölster et al., 2001). The vast majority of these fires are of anthropogenic origin (Bilbao et al., 2010). Fire is a key element of the *Pemón* culture. This indigenous group currently inhabits the GS, and belongs to the Carib-speaking ethnic group. They use fire daily to burn wide extensions of treeless open savanna (Kingsbury, 2001). Fires in savanna-forest borders are scarcely controlled and cause concern about further savanna expansion. The anthropogenic fires have caused an impoverishment of tree species, a drastic reduction of biomass in terms of basal area, a strong change in the floristic composition and the loss of the organic-rich soil surface layer, which negatively impacts on soil fertility (Dezzeo et al., 2004). Therefore, the forest recovery may be strongly impaired by fire. To prevent further land degradation, studies and strategies for fire management in the GS are currently under investigation (Bilbao et al., 2009, 2010).

1.2.2. Study site

Lake Encantada (4º42'37. 44" N to 61º05'03. 29" W; 857 m asl; Fig. 1.1a) is located near the town of Santa Elena de Uairén on a private farm named "Hato Santa Teresa". Lake Encantada is shallow with a maximum water depth of 2.6 m (measured in January 2007). The lake surface is <1km^2 and its watershed is also small, both of which suggest that the sediment record contains a local vegetation history (Mayle and Iriarte, 2012). Treeless savanna and scattered *morichales* patches currently surround the Lake Encantada (Fig. 1.1b). Therefore, pollen signal of *M. flexuosa* may indicate the local occurrence of *morichales* around the shores of the lake. However, wind-transported pollen taxa (e.g., Urticales pollen grains) might have been sourced extra-locally from neighbouring forests (Jones et al., 2011).

1.3. Methodology

1.3.1. Core recovery and radiocarbon dating

The core discussed here, (Fig. I.8, PATAM4 C-07; 2.13 m-long), was obtained in January 2007 and was taken from the deepest part of the lake using a modified Livingstone squared-rod piston (Wright et al., 1984). Four samples were taken along the core for AMS radiocarbon dating, which was carried out at the Radiocarbon Laboratory of the University of California, Irvine (UCI) and Beta Analytic (Beta). Three samples were produced from a pollen residue (Table 1.1), due to the absence/insufficiency of suitable macrofossil material. These samples were processed using a simplification of standard palynological techniques (KOH, HCl and HF digestions). The radiocarbon dates were calibrated with the CALIB 6.0.1 and the IntCal09.14c database (http://calib.qub.ac.uk./calib/, last accessed on October 2012). The age-depth model was produced with the Clam R statistical package (Blaauw, 2010).

Lab. number	**Sample**	**Depth (cm)**	**Material**	**Age (yr ^{14}C BP)**	**Age (cal yr BP) 2σ**	**Age (cal yr BP) WA***
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

Table 1.1. AMS radiocarbon dates used of the age-depth model. *Weighted average of the probability distribution function. This method is recommended as the best central-point estimate.

1.3.2 Magnetic, physical and chemical analyses

Magnetic susceptibility (MS) was measured on half-core sections at 5 mm intervals with a Bartington Susceptibility Meter. Bulk density (BD) was measured on 1 cm^3 samples that were taken every 5 cm down the core and dried at 60 ºC for 24 h. The organic matter and inorganic carbon content of the sediments were determined for each sample by loss on ignition (LOI) at 550ºC and 1000ºC, respectively (Bengtsson and Enell, 1986; Heiri et al., 2001). Elemental determinations were performed with an ITRAX X-Ray Fluorescence (XRF) core scanner at the Large Lakes Observatory of the University of Minnesota, Duluth. Measurements were made at 1 cm intervals during 60 seconds of exposure time. The elements are expressed as counts per second (cps), and those over 1500 cps were selected (Si, K, Ti, Mn, Fe, Co, Ni, Zn, As, Se, Br, Rb, Sr and Zr), because they are usually considered to be statistically significant. Excluding Fe, Co and Br, the remaining elements are considered a terrigenous-sourced group. Total Organic Carbon (TOC) and Nitrogen (TN) and $\delta^{13}C$ and $\delta^{15}N$ were measured after acid pre-treatment using an elemental analyser coupled with a Finnigan Delta-plus mass spectrometer. The isotope sample reproducibility was ± 0.2‰. Carbon and nitrogen isotope ratios are reported in δ-notation, with $\delta = ([R_{sample}/R_{standard}] - 1) \times 1000$ and $R = {}^{13}C / {}^{12}C$ or ${}^{15}N/{}^{14}N$. The isotopes are expressed per mil (‰) relative to the following international standards: Vienna Peedee Belmnite (VPDB) for carbon and air (VAIR) for nitrogen.

1.3.3. Pollen analysis

Forty-three volumetric samples (2 cm^3) were taken at 5 cm intervals. The samples were processed using standard palynological techniques (KOH, HCl, acetolysis, HF digestion and dehydration). *Lycopodium* tablets were added as exotic markers (batch 177745, average of 18584 ± 1853 spores/tablet). The slides were mounted in silicone oil without sealing and stored in the same mounting medium. Counts were conducted until a minimum of 300 terrestrial pollen grains was attained. Pollen count was performed until diversity saturation was reached (Rull, 1987). Identified pollen and pteridophyte spores were classified according to the vegetation types previously described for the region (Huber, 1995b). The pollen sum included pollen from trees, shrubs and herbs and excluded pollen from aquatic (e.g., *Utricularia*, *Ludwigia*) and semi-aquatic plants (e.g., Cyperaceae, *Sagittaria*). The identification of pollen and spores was based on Burn and Mayle (2008), Colinvaux et al (1999), Herrera & Urrego

(1996), Leal et al (2011), Roubik & Moreno (1991) and Rull (2003). Pollen diagrams were plotted with *PSIMPOLL 4.26*. The zonation for the pollen diagrams was performed using the optimal splitting by information content (OSIC) method, and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Only pollen types exceeding 1% abundance were used for zonation. Sample PATAM4C 07_D3/50 at 213 cm was excluded because of methodological problems, so pollen diagrams up to 208 cm were created. Algal remains (e.g., *Botryococcus*, *Spirogyra*, *Mougeotia*) were counted on pollen slides and, together with aquatic plants, were plotted in terms of percentages based on pollen sum. The identification of the assemblages was based on comparison with modern pollen samples from previous studies (Leal et al., 2013; Rull, 1999) and the known autoecology of the taxa (Burn and Mayle, 2008; Burn et al., 2010; Marchant et al., 2002). Charcoal counts were carried out using the same pollen slides and were classified according to the two size classes defined by Rull (1999) for this study area: Type I (smaller microcharcoal particles of 5–100 μm) consists of windborne charcoal dispersed over long distances and represents regional fire events (Clark, 1998; Blackford, 2000), and Type II (larger microcharcoal particles >100 μm) is indicative of local fire events because it is not transported far from the fire source (Clark et al., 1998).

Influx values (unit-cm^{-2}/yr) were obtained using concentration values (unit-cm^{-3}) and accumulation rates (cm/yr) for charcoal particles and main taxa. Additionally, we measured the woody: non-woody ratio after classifying the taxa into woody (trees and shrubs) and non-woody (herbs and sedges) types. This ratio is indicative of the vegetation cover (Bhagwat et al., 2012) and can be used to differentiate between forested and savanna vegetation.

1.3.4. Silicobiolith analysis

Diatoms and sponge spicules were considered as silicobioliths, which are sediment from the remains of living organisms formed by amorphous silica. Forty-three samples taken at 5 cm intervals (1 cm^3) were digested according to their organic matter content with either a mixture of sulphuric acid and potassium dichromate or hydrogen peroxide. Most samples were barren of silicobioliths. In the remaining samples, because of the extremely low number of valves and spicules in different stages of preservation (e.g., 0.2 valves/field on average), counting was stopped after approximately 500 fields and the results were expressed as “traces”. Diatoms were identified using specialized literature (Krammer & Lange-Bertalot, 1986). The identified spicules correspond to adult oxas type, so their taxonomic identification was not possible (Frost et al., 2001).

1.3.5. Statistical analysis

Canonical Correspondence Analysis (CCA) was performed with the Multivariate Statistical Package (MVSP) v.3.13 software using all physico-chemical data and the influx of charcoal and algae as environmental variables. All data were root-square transformed and rare pollen taxa were down weighted. Six samples (3, 123, 128, 138, 143 and 173 cm) were excluded because of a lack of physico-chemical data. The interval 213-173 cm was also excluded because it is barren of biological proxies. Additionally, correlation analysis was carried out between the environmental variables and the main pollen taxa by using influx values calculated according to the Pearson product-moment correlation coefficient (*r*) and its corresponding significance (*p*-value).

1.4. Results

1.4.1. Stratigraphy and chronology

The Encantada lacustrine sequence was characterised by three lithological units from bottom to top (Fig. 1.2). The first unit is from 213 to 173 cm and is characterised by homogeneous, well-sorted and fine white sands. The second unit is from 173 to 113 cm and is made up of homogeneous, yellowish-white clays, but between 150 and 131 cm, a yellowish-brown clay layer is present. The third lithological unit is present from 113 cm to the top and consists of massive, brown clay sediments.

The results of AMS radiocarbon dating (Table 1.1) were used to build the age-depth model for the sequence. The best fit was obtained with a smooth-spline model (Blaauw, 2010) (Fig. 1.2). Sedimentation rates fluctuated between 0.04 and 0.02 cm/yr and progressively decreased from the bottom to the top. The sequence encompassed most of the Holocene (~9700 cal yr BP to the present), and the time interval between consecutive samples ranged from approximately 100 to 300 yr (centennial to multi-centennial resolution). We focused on the last 8700 yr for the palaeoecological analysis because of the absence of biological proxies prior this time (see section 1.4.3-ENC-BZ).

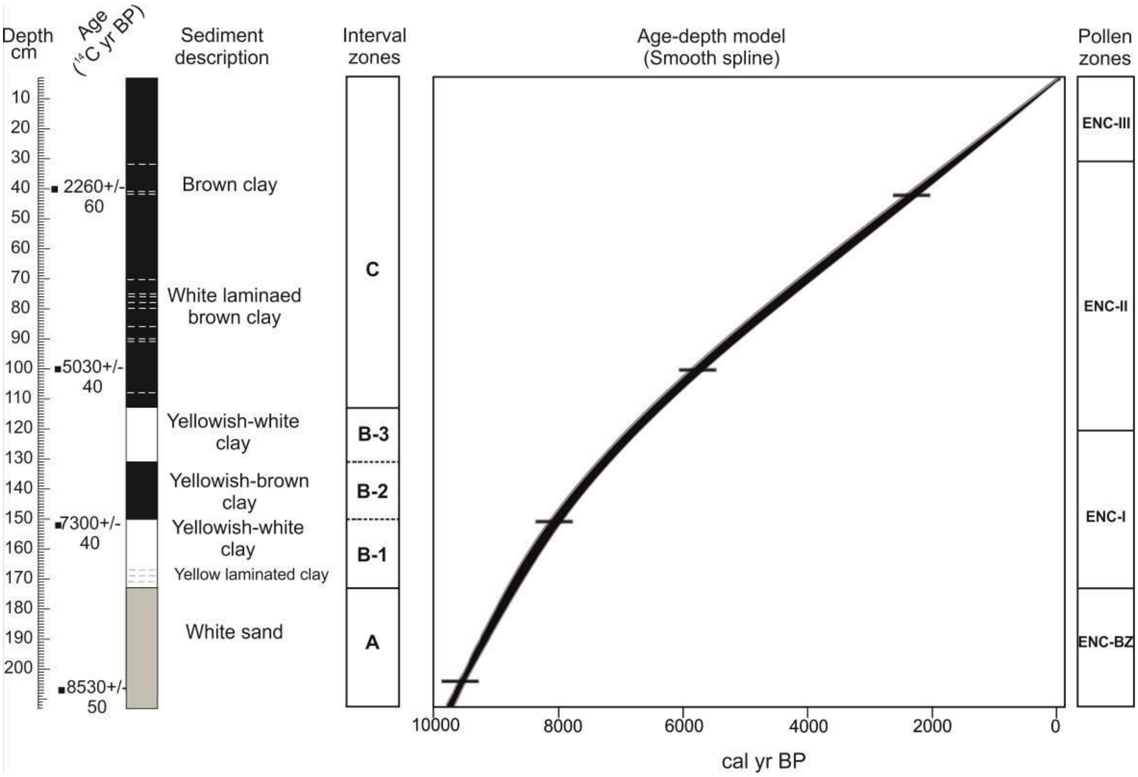


Figure 1.2. Core stratigraphy with radiocarbon ages, sediment description, age-depth model of the sequence, pollen and lithological zones.

1.4.2. Geochemical proxies

Figure 1.3 shows the results of the geochemical analyses. According to variations along the entire sequence, three intervals (listed below) were identified that coincide with those based on the sediment description.

Interval A (213 to 173 cm)

This interval corresponds to the oldest described lithological unit. All geochemical elements had values that were low to very low and roughly constant, except Si (up to 8,330 cps) and BD (ranging between 1.3 to 1.5 g/cm^3), which exhibited the highest values of the entire record.

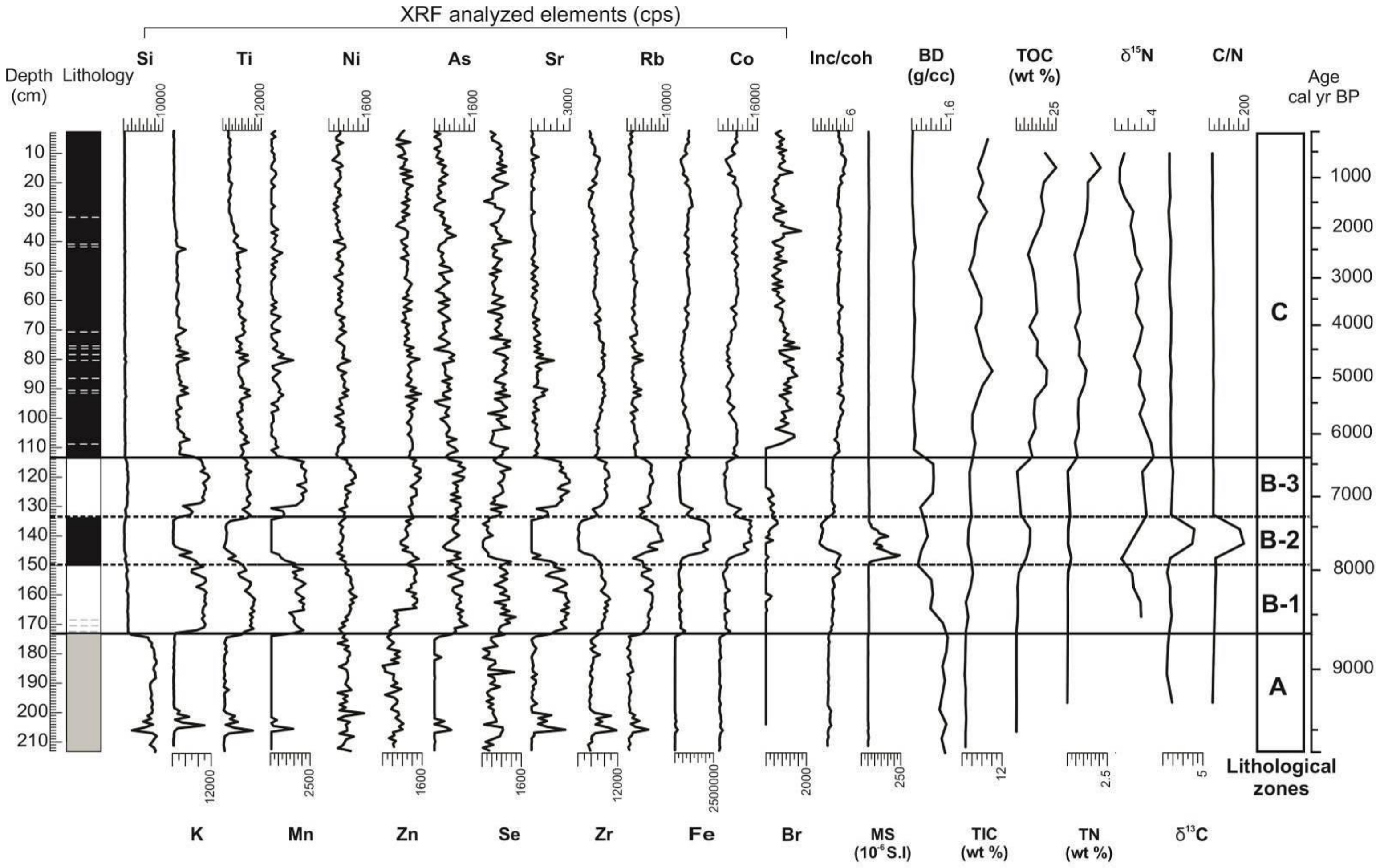


Figure 1.3. Elemental counts (Si, K, Ti, Mn, Fe, Co,Ni, Zn, As, Se, Br, Rb, Sr, Zr), Inc/coh fraction, magnetic susceptibility (MS),bulk density (BD),Total inorganic carbon (TIC), total organic carbon (TOC), total nitrogen (TN), nitrogen isotope (δ15N), carbon isotope (δ13C) and C/N ratio in terms of depth.Calibrated ages shown on the right side are based on the age depth model outputs.

Interval B (173 to 113 cm)

Most physico-chemical proxies displayed high variability related to the lithological changes present in this interval, which allowed three sub-intervals to be defined: B-1, B-2 and B-3. B-1 and B-3 coincided with the yellowish-white clay layers, whereas B-2 corresponded to the intermediate yellowish-brown clays of lithological unit 2 (Fig. 1.3). B-1 and B-3 were characterized by a high cps of K, Ti, Mn, Se, Sr and Zr; these chemical elements abruptly dropped in B-2, whereas Fe ($22.9*10^5$ cps) and Co ($13.6*10^3$ cps) were found at their maximum values. MS (up to $240*10^{-6}$ S.I), $\delta^{13}C$ (1.3 ‰), C/N (191) and TOC (ca. 10 %) peaked in B-2. $\delta^{15}N$ reached minimum values in B-2 (up to 1‰).

Interval C (113 to 0 cm)

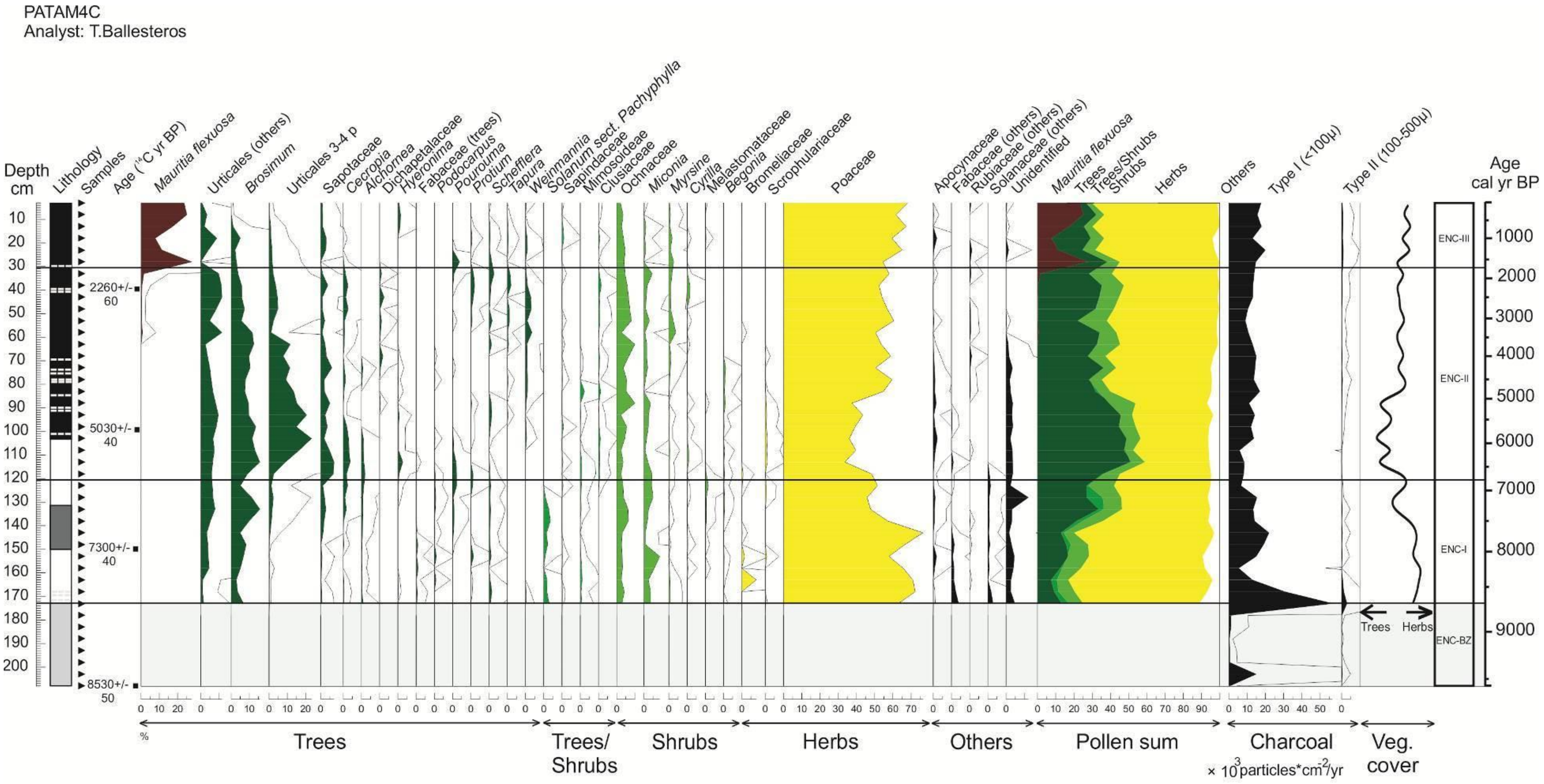
Most of the elements showed medium to low values in interval C in comparison with values from two previous intervals, but Br displayed the highest ones (up to 1,737 cps) of the entire record. TOC (from 8 to 31%), TN (ranging between 0.5 and 2.1 %) progressively increased upwards, and $\delta^{15}N$ decreased (varying from 0.8 to -1.3 ‰).

1. 4.3. Biological proxies

The stratigraphic variations of pollen assemblages allowed us to subdivide the pollen diagram into four zones. Because silicobioliths were only found in trace amounts, they could not be plotted in a taxa percentage diagram; however, these results were included in the diagram of aquatics and expressed qualitatively.

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

Palynomorphs were absent (Figs. 1.4 and 1.5) and therefore this zone was considered barren (BZ). Charcoal particles remained at low abundances but exhibited a pronounced increase at the boundary with the upper zone (ENC-I).



Representation of the lithology:

▢ White sands; ☐ Yellowish-white clays; ▨ Yellowish-brown clays; ■ Brown clays

Figure 1.4. Diagram showing percentage of pollen taxa and influx of charcoal. Solid lines represent x10 exaggeration

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

ENC-I coincides both with the physico-chemical interval B and with the second lithological unit (Fig. 1.2). The pollen assemblage was dominated by herbaceous elements, with Poaceae as the most important taxa. The percentage of herb pollen (~50-80%) decreased towards the top of the zone and was synchronous with an increase in tree pollen, which can also be observed in the vegetation cover ratio (Fig. 1.4). Woody elements were represented primarily by *Brosimum* (the most abundant), Ochnaceae, *Miconia*, *Solanum*. section *Pachyphylla*, *Cecropia* and Urticales (others). Pteridophyte spores were primarily dominated by psilate monoletes and psilate triletes (Fig. 1.5), which showed two peaks at approximately 158-153 cm and 128-123 cm, that co-occurred with the peaks of *Miconia* (Fig. 1.4) and maximum abundances of Cyperaceae (at 158-153 cm; Fig. 1.5). *Mougeotia* appeared in the lower half of the zone, whereas *Sagittaria*, *Botryococcus* and *Spirogyra* appeared for the first time at the top of the zone (Fig. 1.5). Charcoal particles showed the highest values of the entire record at the base of the zone (Fig. 1.4). Regarding the influx values, Poaceae displayed an abrupt maximum at 143 cm, which coincided with a charcoal peak (Fig. 1.6). These values occurred in the lithological/stratigraphical sub-interval B-2.

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

The ENC-II zone is represented by marked increase in forest elements, primarily Urticales 3-4p, in its lower half. Vegetation cover ratios (in average 1.33) showed the same trend. *Cecropia* was more abundant (2-3%) towards the bottom and the top of the zone. In the lower half of the zone Urticales reached its highest proportion (>40%) and influx (> $5*10^2$ grains*cm^{-2}/yr) (Figs. 1.4 and 1.6). Among the aquatic elements, *Sagittaria* was nearly constant along the zone and increased slightly near the top (∽1.5%). *Spirogyra* was abundant in the lower half (3-4%), while *Botryococcus* was the dominant aquatic element in the upper region of the zone (5-6.5%, Fig. 1.5). Total algal remains had the highest values in the upper half (up to 110 elements*cm^{-2}/yr; Fig. 1.6). From 103 cm upwards, the presence of sponge spicules was almost constant (Fig. 1.5). Charcoal particles presented the lowest values of all the sequences at the base of the zone but exhibited a subsequent increase. Excluding the upper region, this zone broadly coincided with interval *C*.

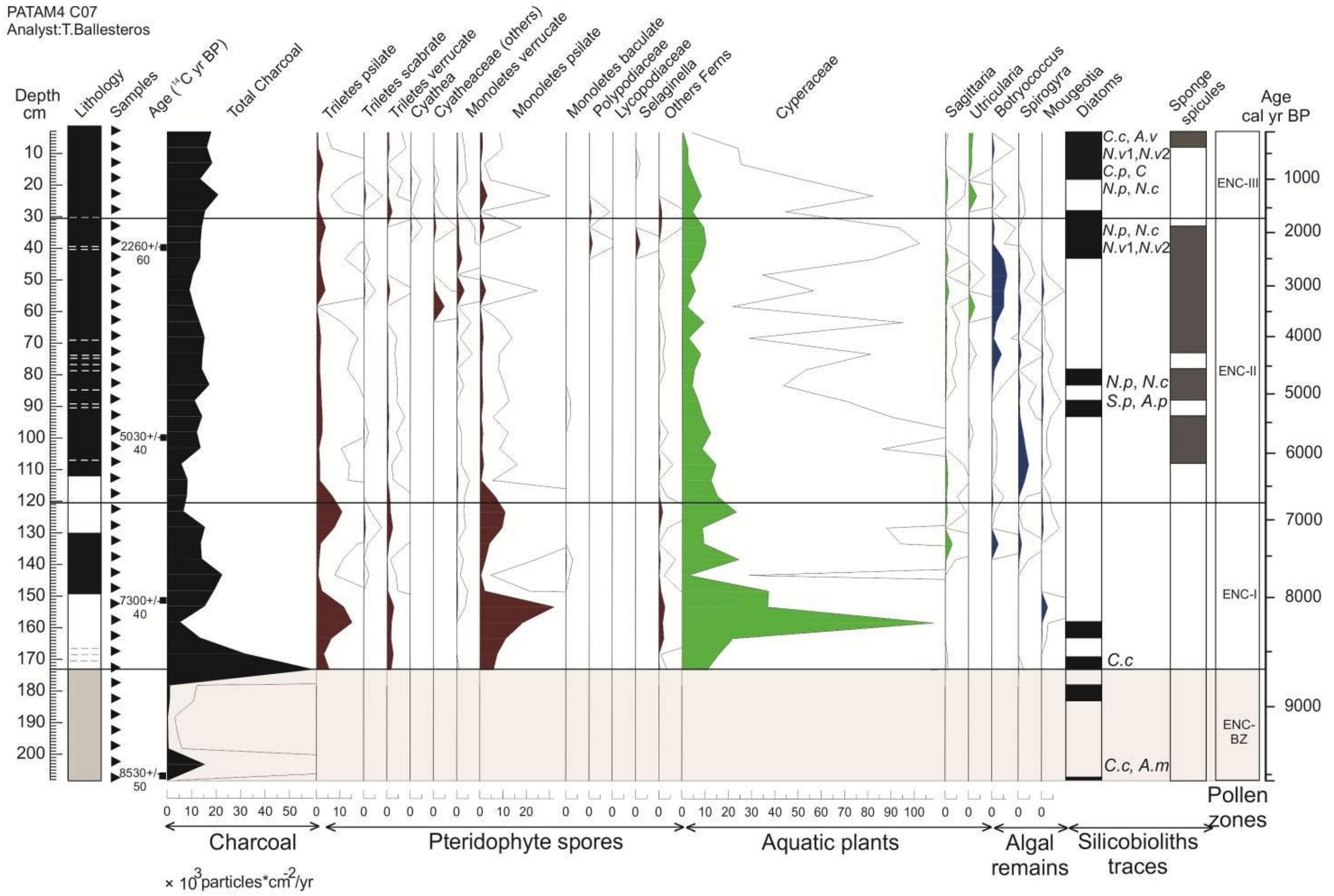


Figure 1.5. Diagram showing the elements outside the pollen sum, such as the aquatic and semi-aquatic plants, pteridophyte spores, algal remains, and silicobiolith traces. The abundances are expressed in percentages with respect to the pollen sum. Silicobiolith traces are expressed as barren (empty space) and present (filled space). Diatoms taxa: C.c = Cyclotella cyclopuncta, A.m= Achhanthidium minutissimum, N.p=Nitzschia capitellata, S.p= Sellaphora pupula, A.p= Amphora pediculus, N.vl= Navicula veneta, N.V2= Navicula viridula var. rostellata, A.V= Amphora veneta, C.p= Coconeis placentula var. euglypta, and C= Craticula sp.

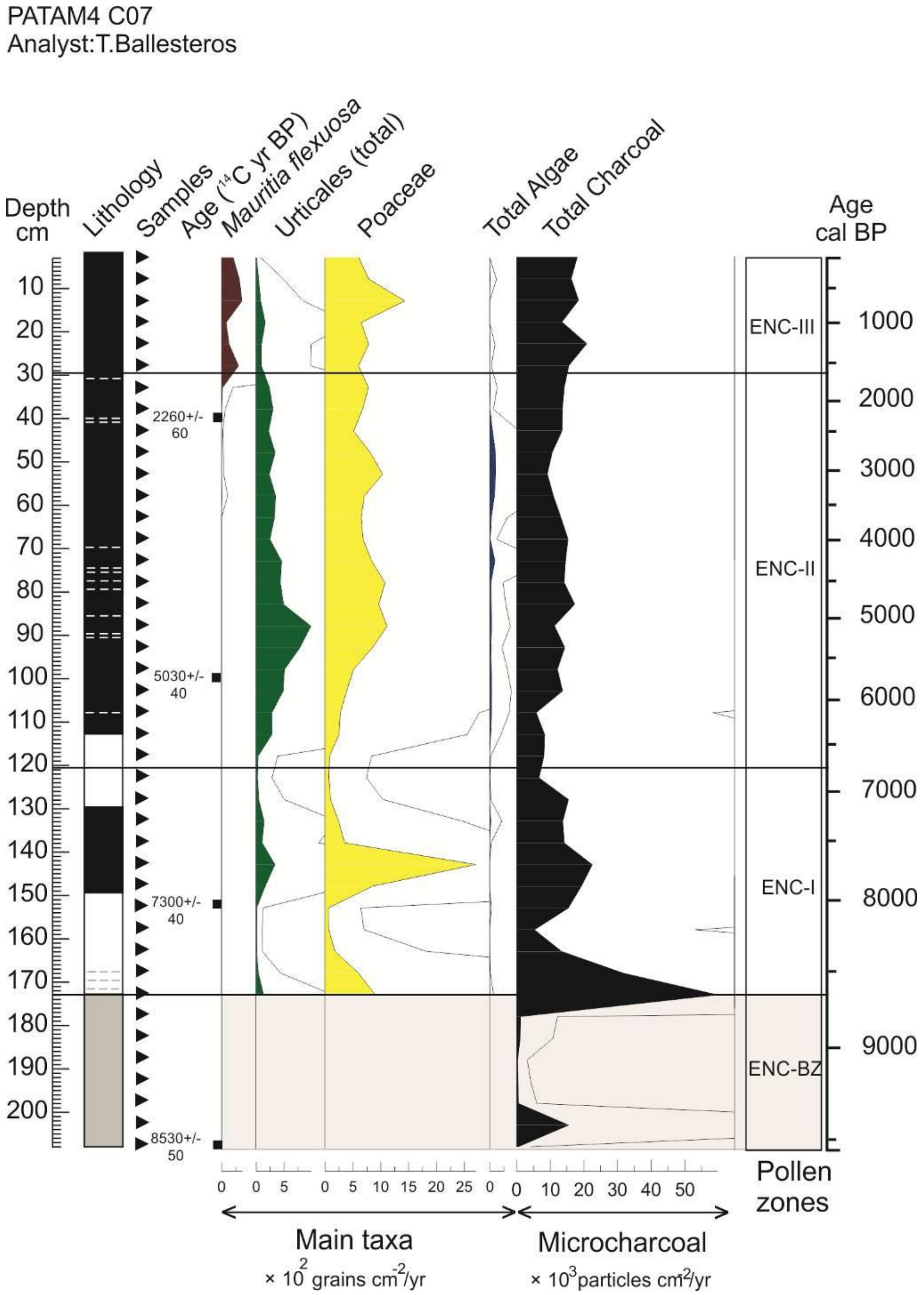


Figure 1.6. Diagram showing the influx values of the main taxa, total algae and microcharcoal particles. Calibrated ages shown on the right side are based on the age depth model outputs

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

The pollen assemblage of the ENC-III zone showed an abrupt change in composition. *M. flexuosa* increased dramatically from 1.5% to 27.7%, while pollen of woody taxa underwent a drastic reduction from >40% to 3% (Fig. 1.4). From 23 to 18 cm, *M. flexuosa* declined whereas a tree pollen recovery (32%) was observed, synchronous with a subtle decrease in charcoal particles (Types I and II). A return to former *Mauritia* values was recorded shortly thereafter and was coeval with a severe reduction of pollen of woody taxa to ~3%. Urticales and *M. flexuosa* influx values followed similar trends with their respective relative abundances, confirming the trends inferred from the percentage values (Fig. 1.6). In the upper region, Poaceae dominated the pollen assemblage, reaching almost 70% of the pollen sum. Pteridophyte spores were common but occurred in low percentages (Fig. 1.5). Aquatic elements remained at low abundances (< 2%, Fig. 1.5). Charcoal particles showed values that were roughly similar to those of the previous zone (~$16*10^3$ particles*cm^{-2}/yr).

1. 4.4. Statistical analysis

Figure 1.7 shows the results of the CCA along the biplot of the first two axes, which explain 47.88% of the total variance (Axis 1=28.42%, Axis 2= 19.46%). Positive values on axis 1 are represented by TN and, to a lesser extent, by TOC, the inc/coh ratio (indicator of the organic matter content of the sample; see Croudace et al., 2006, Sáez et al., 2009, Ziegler et al., 2008), Co and Fe, whereas negative values are represented by Ti, Zn and Zr and, to a lesser extent, by As, Ni, Rb, K, Mn, Si, Sr and BD. Charcoal and MS represent the positive values on axis 2, whereas algae and Br have more influence on the negative values.

Within the space defined by these two axes, samples are clustered according to the previously defined pollen zones. Pollen zone ENC-I falls on the negative side of axis 1 and the positive side of axis 2, which is linked to a suite of elements (As, Ni, Rb, K, Mn, Si, Sr and BD). Pollen zone ENC-II is situated in the middle of axis 1 and the negative side of axis 2, showing a widespread arrangement of samples that are linked to a variety of elements (such as TOC, TN, $\delta^{13}C$, $\delta^{15}N$ and algae). Zone ENC-III is located on the positive sides of both axes, showing no relationship with physico-chemical proxies.

Charcoal and *M. flexuosa* showed no significant relationship when considering the whole diagram; however, when only zone ENC-III is taken into account (*Mauritia* is absent from the other pollen zones), the linear correlation between charcoal and *M. flexuosa* is positive and significant ($r = 0.68$; $p = 0.015$). Charcoal also shows a strong positive relationship with psilate spores ($r = 0.66$; p-value < 0.001) and these are highly associated with *Miconia* ($r = 0.70$; p-value < 0.001).

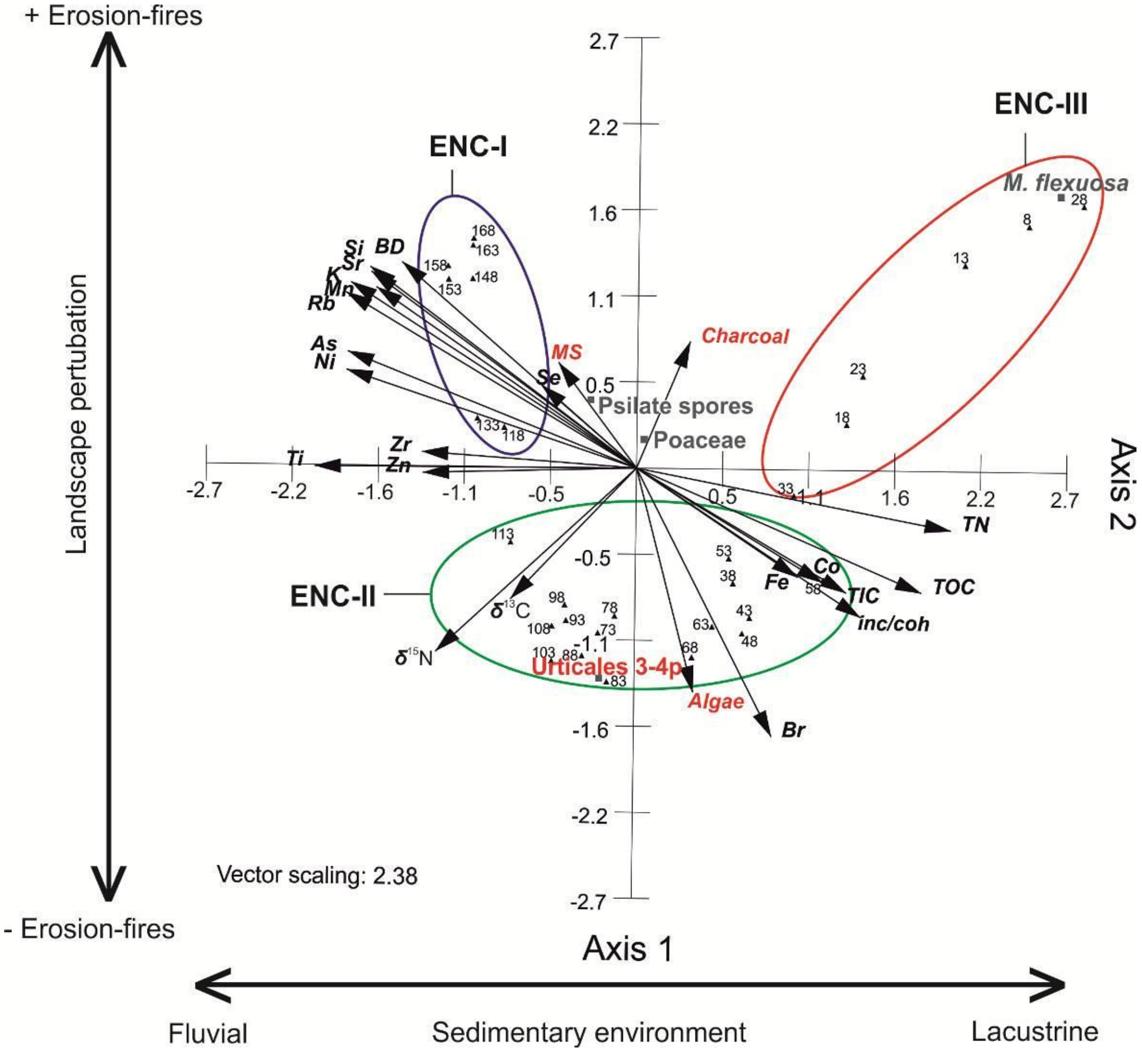


Figure 1.7. Biplot of the canonical correspondence analysis (CCA). Numbers correspond to the sample's core depth (cm). ENC-I, ENC-II and ENC-III correspond to pollen zones. Barren zone ENC-BZ is not included.

1. 5. Reconstruction of environmental changes

The environmental variations in the sediments of Lake Encantada allowed us to differentiate four periods.

Period 1: 9700 to 8700 cal yr BP (from 213 to 173 cm)

The presence of well-rounded and sorted siliclastic sediments together with the highest sedimentation rates (0.04 cm/yr) suggests that these sediments were likely deposited in a fluvial environment. We believe that flowing waters would have prevented the deposition and/or preservation of most biological proxies.

Period 2: 8700 to 6700 cal yr BP (from 173 to 120 cm)

Pollen analysis suggests that during this period the landscape was covered by open savanna with scattered small forest patches. Regional fires peaked and decreased several times, and when fires decreased the forest patches expanded. This expansion is indicated by the wind-pollinated taxa of the Moraceae family (Fig. 1.4; Burn et al., 2010) (from ~8500 to 8000 cal yr BP, and from ~7500 to 7000 cal yr BP). After more intense burning events, *Miconia* increased in parallel to a significant increase in psilate-fern spores. Both *Miconia* and pteridophytes with psilate spores are colonizers of burnt areas during early stages of succession (Berry et al., 1995; Hernández and Fölster, 1994; Marchant et al., 2002). In the GS, a similar assemblage formed by *helechales* (fern communities), intermingled with patches of shrubs (*matorrales*), is considered to be a degrading successional stage after secondary forest burning (Fölster et al., 2001; Rull, 1999). Conversely, when regional fires increased, the forest and *helechales-matorrales* retreated and the savanna expanded (from ~8000 to 7500 cal yr BP). Around 7700 cal yr BP, higher $\delta^{13}C$ values (indicative of C_4-land plants; Meyers and Lallier-Vergés, 1999), higher C/N ratios (Fig.1.3) and greater Poaceae-influx values coincided with the enhancement of fires (Fig. 1.6). According to modern plant surveys (see Appendix A1), most herbs in GS have C_4-photosynthetic pathway. This evidence confirms the dominance of expanding open vegetation when fires were more intense. Other paleorecords from the area indicate that this period was dry across the greater region (*Llanos Orientales*: Behling and Hooghiemstra, 1998; Amazonia: Mayle and Power, 2008) which is also consistent with a previous work in the GS (Montoya et al., 2011b) and the evidence presented here.

At the beginning of the period, the abrupt change from clastic sediments to yellowish-white clays (interval B-1) might indicate the change from fluvial to lacustrine conditions. Most geochemical (TOC and TN) and biological (algal influx) proxies suggest that the aquatic productivity was negligible or not preserved in the sediments (Figs. 1.3 and 1.6). During the periods from 8700 to 8000 cal yr BP and from 7200 to 6700 cal yr BP yellowish-white clays (intervals B-1 and B-3) were deposited (Fig. 1.3). The change in sediments combined with higher terrigenous inputs (Fig. 1.3) indicates the disconnection with the fluvial system (Fig. 1.3). Based on the analysis of biological proxies, we believe these intervals represented wetter conditions. Conversely, during the period from 8000 to 7200 cal yr BP the lithological change to brown clays (interval B-2) suggests the deepening of the water body. However, based on palynological results we suggest that during this interval the conditions were drier. According to the MS results (Fig. 1.3) and axis 2 of the CCA (Fig. 1.7), the intense erosional events may be interpreted as soil instability caused by fires (see a detailed explanation below, in the subsection “Interpretation of the environmental gradients: CCA”) instead of being driven by enhanced rainfall, which commonly occurs in tropical regions (Warrier and Shankar, 2009). Evidence may be indicating a temporal connection with the fluvial system. Thus, the interplay of fires, open landscape and long-distance transport of terrigenous elements (Fig. 1.7) might have promoted high erosion events. Poaceae pollen grains are airborne and waterborne transported (Brown et al., 2007), and hence can be transported a long distance. So the high amount of Poaceae pollen grains during interval B-2 (Fig. 1.6) would have been locally and extra-locally sourced. On other hand, the decrease in the $\delta^{15}N$ values (<0‰) suggests the lake primary productivity might be ruled by nitrogen-fixing bacteria (Fig.1.3). In summary, this period might be considered as highly variable, with an alternation of drier and wetter intervals. We tentatively suggest that disconnection-connection dynamics with the fluvial system could have been driven by variations in the river’s drainage pattern.

Period 3: 6700 to 1700 cal yr BP (from 120 to 30 cm)

The pollen assemblage showed a remarkable compositional and structural change in plant communities during this period. The vegetation shifted to patches of dense rainforest within savanna from 6700 to 5400 cal yr BP. As noted by modern ecological studies (Leal et al., 2013; Rull, 1999), the percentages of herbs and tree pollen would indicate the occurrence of a forest-savanna mosaic during this period. Forest was highly dominated by Urticales with 3-4p pollen grains, *Brosimum*, Sapotaceae, *Cecropia*, *Pourouma* and *Hyeronima*. Urticales values suggest that an evergreen tropical forest with a closed-canopy was established nearby or patchily distributed in the location (Gosling et al., 2009). An additional local environmental reconstruction for the area was provided by a peat core extracted from the shore of Lake Encantada (Montoya et al., 2009). This sequence also showed a notable development of forest roughly at the same time interval. Hence, it seems to indicate that dense forest patches expanded locally. However, the palynological signal of some regional forest expansion expressed by the arrival of some wind-borne pollen grains to the sampling location cannot be disregarded. The rainforest development occurred when fires (regional and local) declined dramatically, which enabled *Cecropia,* as a pioneer tree, to colonize the land cleared by the fire disturbances (Burn et al., 2010; Marchant et al., 2002) and subsequently rainforest expanded. Because of the humidity requirements of rainforests and the higher abundances of *Spirogyra*, we consider this to be a period of higher available moisture during forest development.

In the upper half of this period, a clear shift to more open vegetation occurred. The region near Lake Encantada was dominated by either open savanna with forest patches or reduced forest-savanna mosaic, under higher fire intensity and moisture availability and than before 5400 cal BP. This is supported by maximum values of aquatic elements (e.g., *Botryococcus*, deeper water inhabitant; Fig. 1.5). Similar forest development and wetter climates during the middle to late Holocene are supported by similar studies from other locations in the GS (Montoya et al., 2011b; Rull, 1992), and in the neighbouring savannas of Colombia *Llanos Orientales* and northern Amazonia (Behling and Hooghiemstra, 2000; Pessenda et al., 2010; Fig. 1.1a). This increase in humid conditions was the opposite of the trend toward drier conditions that occurred in the northernmost South American Andes (Vélez et al., 2003). Thus, the wet climate inferred in our study fits with regional climatic trends recorded in localities north of the Amazon basin, which would have been strongly influenced by moisture coming from the basin.

The sedimentological change to brown clays and the pronounced increase in Br, TOC and TN (Fig. 1.3) occurred at the base of the interval C. The lake probably became more productive.

Period 4: 1700 cal yr BP to the present (30 to 3 cm)

In the period from 1700 cal yr BP to the present, the vegetation experienced an abrupt change towards the establishment of treeless savanna with *morichales* stands (*Mauritia* palm), that is, the modern-day landscape. The continuous presence of small *helechales* indicates a network dynamic of fern patches. Rull (1999) interpreted these communities as a transitional stage from open secondary forest cleared by fires to open savanna with *morichales* (Rull, 1999). The high percentage of *M. flexuosa* pollen in sediments indicates the local occurrence of *morichales* (Rull, 1999). According to its ecology, this palm seems to be opportunistic and able to colonize new habitats created by fire and poorly drained soils resulting from wet conditions (Rull, 1999). Although fire evidence is not conclusive with regard to the initial establishment of the *morichales* (Figs. 1.4 and 1.7), the correlation analysis (r =0.68; p =0.015) indicates some level of fire influence on this plant community, which is also suggested by several former studies (Montoya et al., 2009, 2011c; Rull, 1999). On the other hand, the marked rise in TOC and slight rise in TN indicate an increase in primary lake productivity, which occurred in synchrony with decreased $\delta^{15}N$ values and algae scarcity. These results suggest that aquatic productivity was almost entirely dominated by nitrogen-fixing bacteria. The scarcity of algal remains and predominance of bacteria might indicate drier conditions and/or nutrient-limited conditions.

Interpretation of the environmental gradients: Canonical Correspondence* Analysis *(*CCA*)

Chemical elements such as Ti, Zr and Zn are usually associated with terrigenous inputs of sediments to the lake, whereas total nitrogen (TN) and total organic carbon (TOC) commonly reflects variations in the organic productivity of the lake (Cohen, 2003). A careful analysis of the sample distribution in the plane defined by the two first CCA axes reveals that they are stratigraphically ordered, with the deepest elements located on the left side of the graph (sandy lithological unit 1) and the uppermost elements located on the right side (clayish lithological unit 3). Therefore, the first axis could be related to the suggested progressive change from a fluvial sedimentary environment to a lacustrine one.

Despite absence of archaeological evidence, previous palaeoecological studies in the southern GS suggest that the consistent presence and abundance of charcoal (fire proxy) could be related to land highly managed and altered by humans for at least the last two millennia (Montoya & Rull, 2011; Montoya et al., 2011c). Thus, axis 2 might reflect changes in the anthropogenic management of the catchment. The presence of charcoal particles associated with MS at the positive end of axis 2 suggests that the burning of vegetal cover could initiate or enhance the erosion of the soils. When fires were reduced and *Cecropia* established (Fig. 1.4), the development of middle to late successional rainforest might have been favored, as indicated by the presence of Urticales (Burn and Mayle, 2008; Gosling et al., 2009) on the negative side of axis 2. The algae were located parallel to Urticales 3-4p, suggesting a positive relationship with forest expansion and a negative relationship with fire frequency.

1. 6. Discussion and conclusion

1.6.1.The role of environmental drivers in the SE Gran Sabana

Interplay between climate and fire

Climate alone was not the determining factor affecting the vegetation dynamics during both dry (~8700 to 6700 cal yr BP) and wet (~6700 cal ky BP to the present) periods. The moisture content of a fuel source, which is determined by the preceding rainfall, affects how readily it will burn, thus acting as a regulator of fire in tropical systems (Cochrane and Ryan, 2009). Thus, higher available moisture restricted the incidence of fire (Fig. 1.7). Hence, the predominance of savanna during early to middle Holocene would be the result of the positive feedback between dry conditions, fires and grassy vegetation. A similar reinforcing feedback of open savanna occurred near Mapaurí record during early Holocene (Rull, 2007; Fig.1.1a). When climate conditions turned wetter ~6700 cal yr BP, fire ignition was reduced. After longer fire-free intervals, trees would have reached a fire-suppression threshold through the development of a sufficient canopy cover, which prevented the growth of grasses (Hoffmann et al., 2012a). The synergistic action between reduced fires and a wetter climate appears to be a determinant in the development of rainforest. Thus, we suggest that during early to middle Holocene the fire regime may have been unaffected by humans.

Despite the wetter conditions that occurred since ~5400 cal yr BP, the savanna expansion would have been the result of forest burning, which could be caused by fires set by humans (Montoya et al., 2011b). The coexistence of wetter conditions, forest vegetation and fires might be explained by land-use practices similar to those currently found in many neotropical forested landscapes (e.g., slash-and-burn), in which small forest spots are cleared and burned for shifting agriculture (known locally as *conucos*). Shifting cultivation practices apparently occurred in the El Paují region, south of Lake Encantada, from 7700-to 2700 cal yr BP (Montoya et al., 2011b; Fig. 1.1a). Considering a lag of about 2300 years between the start of *conucos* in El Paují and Lake Encantada, palaeoecological results might suggest that semi-nomadic and forest-like indigenous culture migrated northward from the southernmost part of the GS. Fires increased after 6200 cal yr BP and since 5400 cal yr BP forest retreated gradually. The forest communities in the GS have been considered low resilient to burning (Fölster et al., 2001). However, this evidence might indicate that forest communities may have been resilient and recurrent burns could have reduced their resilience. This ecological feature of GS forest communities needs further assessment. An apparent shift in land-use practices towards more extensive use of fire in open landscapes was recorded ~2000 yr ago and continued to the present in several of the GS localities (El Paují, Lake Chonita, Urué, Divina Pastora, Santa Teresa; Montoya et al., 2009, 2011b,c; Rull 1992,1999; Fig. 1.1a). In El Paují, humans appear to have abandoned the study area around 2700 cal yr BP, although the area could have been populated again from 1400 cal yr BP onwards by a different culture (Montoya et al., 2011b). A change to a new-savanna like culture could have also occurred near Lake Encantada around 1700 cal yr BP. Drier conditions may have been influential in the maintenance of savanna vegetation and continuity of fires. Recurrent burns were required to maintain the openness of the landscape and allowed the development of highly flammable vegetation, which drove the ecosystem to a treeless savanna state during the last two millennia (Montoya & Rull, 2011).

Interplay between erosion and fire

In the GS, soil erosion is greatly enhanced when the organic-rich surface layer is lost along with the forest vegetation (Fölster, 1986). Thus, the prolonged loss of forests could be associated with the progressive loss of soil water and nutrients, which could have subsequently hindered re-establishment of tree species. Moreover, because of the shallow root system (Dezzeo et al., 2004), calcium deficiency and limited water retention capacity of the soils, tree mortality (Fölster et al., 2001) and drying of the soils might have been significantly affected by fire. Therefore, the synergism between fire and erosion could have resulted in forest instability, promoting an increase in soil erosion and nutrient loss. This synergism would have favored the establishment of the grass stratum. This process was likely triggered by fires, but maintained by enduring soil-stress conditions. Rull (1992) suggested that the burning of the GS forests has initiated a degenerative and irreversible process that when coupled with soil degradation (Rull et al., 2013), results in the savanna expansion (Rull, 1992,1999). The interplay between fire, erosion and the grass vegetation was probably intensified around 5400 cal yr BP, enabling the landscape change to open savanna with forest patches. That state remained until ~2000 yr ago, when the shift of land use practices allowed surpassing the tipping point towards an irreversible expansion of savanna, reinforced by drier climates. Thus, due to the opening of the landscape, the synergistic action between fire and erosion appears to have increased during the last 2000 years.

The Lake Encantada record, combined with former paleoecological studies (e.g., El Paují, Chonita, Urué), allows the reconstruction of the regional picture of environmental change and land-use patterns in the southern GS, and for the assessment of competing hypotheses (climate, fire, soils) for explaining the maintenance of the savanna.

1.6.2. Relationship between GS savannas and other moist savanna areas

Although the GS has different vegetation types, human history and lower climatic variability than the Brazilian savannas (*Cerrado* biome), it shares a long-history of fire regime, poor soil conditions (e.g., low pH, high aluminum concentrations, poor nutrient availability) and climatic fluctuations during the Holocene. Humid climate conditions would also favor the establishment of forest instead of savanna (Oliveira-Filho and Ratter, 2002). It is widely accepted that climate, soils and fire have been highly interactive in their effect on *Cerrado* vegetation (Oliveira-Filho and Ratter, 2002). The complex interaction of these factors in the GS was first assessed and recognized in this study. Climate alone does not explain the current predominance of savannas in these two humid regions. We consider that, as in *Cerrado* biome (Pinheiro and Monteiro, 2010), climate has been the trigger of this assumed interaction in vegetation history of the GS during the early Holocene. Seasonal and/or dry climate may have produced conditions prone to fires (Oliveira-Filho and Ratter, 2002) in *Cerrados*, and our evidence shows that this also occurred in the GS. Recurrent fires apparently tended to prevent forest recovery and caused soil impoverishment in these two regions (Cerrados: Oliveira-Filho and Ratter, 2002). In some areas of the *Cerrado*, the transition from forest to savanna seems to have been related to edaphic factors rather than to fire action (Pinheiro and Monteiro, 2010). However, limited data in the GS (this study) suggests that fires would have primarily driven this vegetation shift. Fires and soils have shown to be selective agents of savanna vegetation (e.g., fire-adapted and fire-dependent species) in the Brazilian savanas (Pinheiro and Monteiro, 2010), in which environmental factors are better understood (Oliveira-Filho and Ratter, 2002). Therefore, further assessment of the role played by fires and soils and the interplay between these two drivers is required in the GS. Since the middle Holocene, the failure of the *Cerrado* (Ledru et al., 1998) and GS forests (Montoya et al., 2011b) to expand into savanna may be largely caused by human-induced fires through shifting cultivation (Pivello 2011), overriding the effect of wetter conditions (Ledru, 1993; Montoya et al., 2011b). We believe that the interplay between fires and soil conditions has played a role in the vegetation history in humid Neotropical savanna areas and that humans may have largely influenced it.

1.7. Acknowledgements

The authors wish to thank to Aquiles and José Luis Fernández (owners of the Hato Santa Teresa) for their interest and goodwill during our work and Sandra Nogué, Nathan Stansell and Broxton Bird for their collaboration in the fieldwork.

1.8. Funding

This work was supported by the Spanish Ministry of Science and Innovation (projects CGL2006-00974 and CGL2009-07069/BOS to V. Rull), the BBVA Foundation (project BIOCON-08-031 to V. Rull), the Spanish Council for Scientific Research (CSIC, project 200830I258 to V. Rull), and the Foundation for the future of Colombia-COLFUTURO, which provided a scholarship-loan to Tania Ballesteros. Permits to develop this research in Venezuela were provided by the Ministry of Science and Technology (DM/0000013, 5 Jan 2007), and sampling permits were provided by the Ministry of Environment (no IE-085, 9 Feb 2007).

1.9. References

Accatino, F., De Michele, C., 2013. Humid savanna-forest dynamics: Amatrix model with vegetation-fire interactions and seasonality. *Ecological Modelling*. 265,170-179.

Barbosa, RI., Campos, C., 2011. Detection and geographical distribution of clearing areas in the savannas ('lavrado') of Roraima using Google Earth web tool. *Journal of Geography and Regional Planning.* 4, 122-136.

Beckage, B., Platt, W.J., Gross, L.J., 2009. Vegetation, Fire, and Feedbacks: A

Disturbance-Mediated Model of Savannas. *The American Naturalist.*174, 805–818.

Behling, H., Hooghiemstra. H., 1998. Late Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. *Palaeogeography, Palaeoclimatology,Palaeoecology.* 139, 251–267.

Behling. H., Hooghiemstra, H .,1999. Environmental history of the Colombian savannas of the Llanos Orientales since the LGM from El Piñal and Carimagua. *Journal of Paleolimnology.* 21, 461-476.

Behling, H ., Hooghiemstra, H., 2000. Holocene Amazon rainforest-savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science.* 15, 687–695.

Bengtsson, L., Enell, M., 1986. Chemical analysis. In: Berglund BE (eds). Handbook of Holocene Palaeoecology and Palaeohydrology*.* John Wiley & Sons Ltd. Chichester: pp. 423–451.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist.* 132, 155–170.

Berry, P.E., Yatskievych, K., Holst, B.K., 1995. Miconia. In: Steyemark, J.A., Berry, P.E., Holst, B.K., (eds) Flora of the Venzuelan Guayana. Volume 6. Missouri Bot. Gard. Press.St. Louis: pp. 387-468.

Bhagwat, S.A., Nogué, S., Willis, K.J., 2012. Resilience of an ancient tropical forest landscape to 7500 years of environmental change. *Biological Conservation.* 153, 108–117.

Bilbao, B., Leal, A., Méndez, C et al., 2009. The role of fire in the vegetation dynamics of upland savannas of the Venezuelan Guayana. In: Cochrane, M.A., Ryan, K.C., (eds) Tropial fire ecology: Climate Change, Land Use and Ecosystem Dynamics. Springer, pp 451-476.

Bilbao, B.A., Leal, A.V., Méndez, C.L., 2010. Indigenous Use of Fire and Forest Loss in Canaima National Park, Venezuela. Assessment of and Tools for Alternative Strategies of Fire Management in Pemón Indigenous Lands. *Human Ecology.* 38, 663–673.

Blaauw, M., 2010. Methods and code for “classical” age-modelling of radiocarbon sequences. *Quaternary Geochronology.* 5, 512–518.

Blackford, J., 2000. Palaeoclimatic records from peat bogs. *Trends in Ecology*

& Evolution. 15, 193-198.

Breman, E., Gillson. L., Willis, K., 2011. How fire and climate shaped grass-dominated vegetation and forest mosaics in northern South Africa during past millennia. *The Holocene*. 22, 1427–1439.

Brown, A.G., Carpenter, R.G., Walling, D.E., 2007. Monitoring fluvial pollen transport, its relationship to catchment vegetation and implications for palaeoevironmental studies. *Review of Palaeobotany and Palynology.* 147, 60–76.

Burn, M.J., Mayle, F.E., 2008. Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Review of Palaeobotany and Palynology.* 149, 187–201.

Burn, M.J., Mayle, F.E., Killeen, T.J., 2010. Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South America. *Palaeogeography, Palaeoclimatology,Palaeoecology.* 295, 1–18.

Clark, J.S., Lynch, J., Stocks, B.J., Goldammer, J.G., 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. *The Holocene.* 8, 19-29.

Cochrane, M.A., Ryan, K.C., 2009. Fire and fire ecology: Concepts and principles. In: Cochrane, M.A., (eds) Tropial fire ecology: Climate Change, Land Use and Ecosystem Dynamics. Springer, pp. 25-55.

Cohen, A.S., 2003. Paleolimnology: The History and Evolution of Lake Systems, Oxford University Press.

Colinvaux, P.A,, De Oliveira, P.E,, Moreno, J.E., 1999. Amazon Pollen Manual and Atlas, Harwood Academic Publishers, Amsterdam.

Croudace, I.W., Rindby, A,, Rothwell, R.G., 2006. ITRAX: description and evaluation of a new multi-function X-ray core scanner. In: Rothwell, R.G., (Ed.), New Techniques in Sediment Core Analysis. The Geological Society of London, London, pp. 51–63.

Dezzeo, N., Chacón, N., Sanoja, E., et al., 2004. Changes in soil properties and vegetation characteristics along a forest-savanna gradient in southern Venezuela. *Forest Ecology and Management*. 200, 183–193.

Eden, M.J., 1974. Paleoclimatic influences and the development of savanna in southern Venezuela. *Journal of Biogeography*. 1, 95-109.

Fölster, H., 1986. Forest–savanna dynamics and desertification processes in the Gran Sabana. *Interciencia.* 11(6), 311–316.

Fölster, H., Dezzeo, N., Priess, J., 2001. Soil–vegetation relationship in base-deficient premontane moist forest–savanna mosaics of the Venezuelan Guayana. *Geoderma.* 104, 95–113.

Frost, T.M., 2001. Terrestrial, Algal, and Siliceous Indicators. In: Smol. J.P., Birks, H.J., Williams, M., (eds) Tracking Environmental Change Using Lake Sediments. Volume 3. Kluwer Academic Publishers, pp.253-264.

Gómez, E., Picó,n G., Bilbao, B., 2000. Los incendios forestales en Iberoamérica. Caso Venezuela. In: Vélez-Muñoz, R., (eds) La defensa contra incendios forestales, Fundamentos y experiencias.McGraw-Hill, Madrid.

Gosling, W.D., Mayle, F.E., Tate, N.J., et al., 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Review of Palaeobotany and Palynology.* 153, 70–85.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology.* 25, 101–110.

Hernández, L., Fölster, H., 1994. Vegetación en transición. *Scientia Guayanae.* 4, 118-144.

Hernández, L ., 1999. Fisionomía y estructura de bosques submesotérmicos y mesotérmicos. In: Hernández, L., (eds) Ecología de la altiplanicie de la Gran Sabana(Guayana Venezolana) II. Estructura, diversidad, crecimiento y adaptación en bosques de las subcuencas de los ríos Yuruaní y Alto Kukenán. Scientia Guayanae.Volume 9. Ediciones Tamandúa. Caracas, pp. 5–34.

Herrera, L.F., Urrego, L.E., 1996. Atlas de polen de plantas útiles y cultivadas de la Amazonia colombiana, Tropenbos Colombia, Colombia.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., et al., 2012a. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters.* 15, 759–768.

Hoffmann, W.A., Jaconis, S.Y., Mckinley, K.L .,et al., 2012b. Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries: Flammability of savanna-forest boundary. *Austral Ecology.* 37, 634–643.

Huber, O., 1986. La vegetación de la cuenca del río Caroní. *Interciencia.* 11(6), 301–310.

Huber, O., 1995a. Geographical and physical features. In: Steyemark, J.A., Berry, P.E., Holst, B.K., (eds) Flora of the Venzuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden. Press. St. Louis, pp. 1-62.

Huber, O., 1995b. Vegetation. In: Steyemark, J.A., Berry, P.E., Holst, B.K., (eds) Flora of the Venzuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden. Press. St. Louis, pp.97-160.

Jeltsch, F., Weber, G.E., Grimm, V., 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology.* 161, 161-171.

Jones, H.T., Mayle, F.E., Pennington, R.T., Killeen, T.J ., 2011. Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. *Review of Palaeobotany and Palynology.* 164, 223–237.

Kingsbury, D., 2001. Impacts of land use and cultural change in a fragile environment: indigenous acculturation and deforestation in kavanayén, Gran Sabana, Venezuela. *Interciencia.* 26, 327–336.

Krammer, K., Lange-Bertalot, H., 1986–1991.Süsswasserßora von Mitteleuropa, (4 volumes). Gustav Fischer Verlag: Stuttgart.

Leal, A., Berrío, J.C., Raimúndez, E., et al., 2011. A pollen atlas of premontane woody and herbaceous communities from the upland savannas of Guayana, Venezuela. *Palynology*. 35, 226–266.

Leal, A., Bilbao, B., Berrío, J.C., 2013. A Contribution to Pollen Rain Characterization in Forest-Savanna Mosaics of the Venezuelan Guayana and Its Use in Vegetation Reconstructions from Sedimentary Records. *American Journal of Plant Sciences.* 4, 33–52.

Ledru, M.P.,1993. Late Quaternary environmental and climatic changes in central Brazil. *Quaternary Research.* 39,90–98.

Ledru, M.P., Salgado-Labouriau, M.L., Lorscheitter, M.L., 1998. Vegetation dynamics in southern and central Brazil during the last 10,000 yr BP. *Review of Palaeobotany and Palynolog*y. 99,131–142.

Marchant, R., Almeida, L., Behling, H., et al., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Review of Palaeobotany and Palynology.* 121, 1–75.

Mayle, F.E., Power, M.J., 2008. Impact of a drier Early-Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society B.* 363, 1829–1838.

Mayle, F.E., Iriarte, J., 2012. Integrated palaeoecology and archaeology e a powerful approach for understanding pre-Columbian Amazonia. *Journal of Archaeological Science*. http://dx.doi.org/10.1016/j.jas.2012.08.038

Meyers, P.A., Lallier-Vergés, E.,1999. Lacustrine sedimentary organic matter records of Late Quaternary paleoclimates. *Journal of Paleolimnology*. 21, 345-372.

Montoya, E., Rull, V., Nogué, S., et al. , 2009. Paleoecología del Holoceno en la Gran Sabana, SE Venezuela: Análisis preliminar de polen y microcarbones en la Laguna Encantada. *Collectanea Botanica* . 28, 65–79.

Montoya, E., Rull, V., 2011. Gran Sabana fires (SE Venezuela): paleoecological perspective. *Quaternary Science Reviews*. 30, 3430–3444.

Montoya, E., Rull, V., Stansell, N.D., et al., 2011a. Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron. *Journal of Quaternary Science.* 26, 207–218.

Montoya, E., Rull, V., Nogué, S., 2011b. Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE Venezuela): Palynological evidence from El Paují record. *Palaeogeography, Palaeoclimatology, Palaeoecology.* 310, 413–426.

Montoya, E., Rull, V., Stansell, N.D., et al., 2011c. Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quaternary Research.* 76, 335–344.

Murphy, B.P., Bowman, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna?. *Ecology Letters.* 15, 748–758.

Oliveira-Filho, A.T., Ratter, J.A., 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. In: Paulo S. Oliveira; Robert J. Marquis. (Org.). The Cerrados of Brazil: ecology and natural history of a Neotropical savanna. New York: Columbia University Press. p. 91-120.

Pessenda, L.C.R., Gouveia, S.E.M., Ribeiro, A., et al., 2010. Late Pleistocene and Holocene vegetation changes in northeastern Brazil determined from carbon isotopes and charcoal records in soils. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 297, 597–608.

Pinheiro, M.H.O., Monteiro, R., 2010. Contribution of the discussions on the origin of the cerrado biome: Brazilian savanna. *Brazilian Journal of Biology.* 70(1), 95-102.

Pivello, V.R., 2011. The Use of Fire in the Cerrado and Amazonian Rainforests of Brazil: Past and Present. *Fire Ecology.* 7:1, 24-39.

Roubik, D.W., Moreno, J.E., 1991. Pollen and Spores of Barro Colorado Island, Missouri Botanical Garden, Missouri.

Rull, V., 1987. A note on pollen counting in palaeoecology. *Pollen et Spores.* 29, 471–480.

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

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

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

Rull, V., 2007. Holocene global warming and the origin of the Neotropical Gran Sabana in the Venezuelan Guayana. *Journal of Biogeography.* 34, 279–288.

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

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

Schubert , C., Huber, O., 1989. The Gran Sabana: Panorama of a region. Cuadernos LAGOVEN, Caracas.

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

Warrier, A.K., Shankar, R., 2009. Geochemical evidence for the use of magnetic susceptibility as a paleorainfall proxy in the tropics. *Chemical Geology.* 265, 553–562.

Wright, HE., Mann, DH., Glaser, P.H., 1984. Piston corers for peat and lake sediments. *Ecology.* 65, 657–659.

Ziegler, M., Jilbert, T., de Lange, G.J., Lourens, L.J., Reichart, G.J., 2008. Bromine counts from XRF scanning as an estimate of the marine organic carbon content of sediment cores. *Geochemistry, Geophysics, Geosystems*, 9, Q05009, doi:10.1029/2007GC001932.

Chapter II:

Vegetation changes in the uplands of the Gran Sabana (SE Venezuela) during the Late Glacial: insights of the origin of grassland

2.0. Abstract

The study of biotic responses to past abrupt climate changes provides useful information to anticipate potential ecological responses for future climate changes. Two examples of abrupt climate changes occurred at the onset (cooling) and termination (warming) of the Younger Dryas (YD; 12,850-11,650 cal yr BP). In the Gran Sabana (GS), the origin of the treeless savanna appears to have occurred during the YD/early Holocene, though such inferences have been based on only two records. Here, a palaeoecological study of a new sequence of the Late Glacial age is presented, which comprises the interval between 12,725 and 9520 cal yr BP. The main aims of this study were to (1) analyse the vegetation responses to the abrupt climate changes during the period studied, and (2) evaluate the hypotheses that intend to explain the origin of the open savanna. Between 12,725 and 12,385 cal yr BP, the sequence has pollen counts which are too low to infer vegetation changes during this interval. The reconstruction of vegetation dynamics suggests the following trends: (1) mosaic vegetation formed by forests, *helechales* and savanna (12,385-12,070 cal yr BP); (2) abrupt vegetation change towards grassland occurred in ~12,070 cal yr BP,this vegetation type remained in the area; and (3) grassland with local meadow (10,440-9520 cal yr BP), similar to the plant community surrounding the location nowadays. Very low pollen abundances at the onset of the YD, in combination with poor age control at the beginning of that climatic event, hindered the analysis of vegetation responses to the abrupt YD cooling. It was interpreted that changes in mosaic vegetation (12,385-12,070 cal yr BP) were driven by climate and fire. The abrupt origin of grassland was suggested to have been caused by the synergistic action between rapid warming at the end of the YD, drier climate than the present, fire and availability of fuel loads. In the case of human activities since the YD, human induced fires could have played an additional role in this synergism. Considering the future scenario of warming and higher occurrence of fires in South America, the forest replacement by grassland at the YD-Holocene transition could be considered as a potential past analogue of the current and future environmental setting for the GS region. Nevertheless, the available evidence is still insufficient to make such a conclusive statement.

2. 1. Introduction

Abrupt climate changes (ACC) occur when the climate system is forced to shift to a new climate state at a rate that is determined by the climate system itself. The shift occurs faster than the cause, taking place over a few decades or less, and persists for at least a few decades (NRC, 2002). As a result, an ACC has the potential to severely affect natural systems (NRC, 2013). This is mainly due to the fact that some biotic communities might not be able to keep up with its pace, and thereby, ecosystems may change in unpredictable ways. It has long been argued that it is essential to develop an understanding of biotic responses to past abrupt changes (Birks, 2012) preserved in palaeoecological records, as a model for anticipating potential ecological responses to future climate changes (Rull et al., 2015a). Two examples of ACC occurred within the Quaternary record: at the onset and at termination of the Younger Dryas (YD; 12,850-11, 650 cal yr BP, Rasmussen et al., 2006). Both examples are explained below.

As the Earth (more specifically the northern hemisphere) was slowly warming during the Bølling/Allerød (B/A) interstadial (14,600-12,850 cal yr BP, Rasmussen et al., 2006), the YD halted the transition to today’s relative warming in many parts of the world abruptly. The YD constitutes a cooling reversal phase associated with dry conditions that took place just before the beginning of the current interstadial, the Holocene (last 11,650 yr). In the Neotropical region, the main bulk of evidence of the YD has been found in marine (Lea et al., 2003) and high mountain records (e.g., northern and central Andes, Fig. 2.1a). In this second region, the YD has been interpreted as a decrease of temperature between 1-4ºC compared to the present and by a general pattern of increased aridity at the beginning of the YD chron (Islebe et al., 1995; Stansell et al., 2010; Rodbell et al., 2009; Rull et al., 2010; Thompson et al., 1998; Van der Hammen and Hooghiemstra, 1995; Van’t veer et al., 2000). The vegetation response, when noticeable, to the YD’s cooling consisted of a downslope shift of the upper forest line (Islebe et al., 1995; Rull et al., 2010, 2005; van der Hammen and Hooghiemstra, 1995; Van’t veer et al., 2000). Similarly, in some lowland regions located close to hilly areas in the Amazon (Fig. 2.1a), a downslope migration of some montane floral elements also seems to have taken place during the YD chron, consistent with a maximum cooling between 4-5ºC (Bush et al., 2004; Colinvaux et al., 1997; Ledru et al., 2001; Li and Colinvaux, 1985). However, research on this topic is scarce in lowlands and uplands characterised by roughly flat topographic features. To date, there is no documentation of any vegetation responses to rapid cooling in these ecosystems, so the question whether plant species were sensitive to the YD’s abrupt cooling is still open to debate. Hence, studies on new sequences from these ecosystems would help establish vegetation responses constrained by flat topography, a piece of scarcely explored field research.

At the end of the YD, the global climate warmed at a rate of around 4ºC/century and lasted few decades (Jackson and Overpeck, 2000). This past global warming trend roughly matches with the higher warming scenario of 5.5ºC/century by 2100 proposed by the latest IPCC reports (Stocker et al., 2013). Additionally, the YD-Holocene warming acted on the same species that exist today (Vegas-Vilarrúbia et al., 2011). Following this, several researchers have proposed that YD-Holocene warming might constitute a perfect natural experiment for forecasting potential biotic responses to current and future climate warming (Amman, 2000; Birks, 2012; Cole, 2009; Vegas-Vilarrúbia et al., 2011; Willis et al., 2013), thus becoming a powerful past analogue for projection modelling. Hence, palaeoecological studies that cover this transition might provide insights and valuable information regarding the potential magnitude and directions of vegetation changes. After this rapid climate change, warming continued until approximately 10,500 cal yr BP (Haug et al., 2001), a period known as the Early Holocene Warming (EHW), but at a slower pace, indicative of non-abrupt behaviour.

Within the uncertainties of the consequences that global warming may have in the Neotropics, the expansion of savannas and the reduction of forests (savannisation) is a major concern (Stocker et al., 2013). In this sense, there is a debate regarding the drivers involved in the origin of current main extents of savannas (Berrío et al., 2012). One of the main savanna regions in northern South America is the Gran Sabana (GS) (Fig. 2.1b), located in southeastern Venezuela on a plateau of mid altitude and characterised by humid climate. To date, only two palaeoecological sequences from the GS have recorded the origin of treeless savanna (or grassland) from woody communities around YD/early Holocene, suggesting different environmental drivers as the main cause. Based on the available evidence of the two sequences, three hypotheses have been proposed to explain the origin of the savanna. On the one hand there is the climate hypothesis, which suggests that climate change in the form of warming was the most probable cause for the replacement of a cloud forest by open savanna around 10,200 cal yr BP (Rull, 2007). A second hypothesis contends that fire influenced the observed change, in this case from shrubland to treeless savanna as the dominant vegetation at the Pleistocene/Holocene boundary (~11,700 cal yr BP; Montoya et al., 2011). This hypothesis is supported by the fact that the shrubland decline coincided with the presence of first fires of high intensity/frequency. Finally, a third hypothesis about mixed origin (fire-warming) of the GS savannas has been suggested recently, supported by the combined results obtained from these two records (Montoya et al., 2011; Rull, 2009; Rull et al., 2013). Thus, the limited evidence indicates that the ecological processes that led to the origin of grassland in the GS are not completely understood. The study of a new sequence of the Late Glacial located in a flat topography region would add insightful information to assess the aforementioned hypotheses. Furthermore, it would allow the evaluation of vegetation responses to the abrupt climate changes during the onset of the YD and the transition to the Holocene, the latter as a potential past analogue for the future climate change in the GS.

This chapter reports a palaeoecological study of a peat bog from southern GS based on pollen and fern-spores analyses, supported by algal remains and charcoal particles. The period under study encompasses the Late Glacial (from 12,725 to 9520 cal yr BP), providing a new record for the GS region during this period of unstable climatic conditions. The aims of this study were to: (1) analyse the vegetation responses to the abrupt climate changes during the period studied; (2) evaluate the alternative hypotheses about the origin of the southern GS savanna; and (3) assess whether the origin of open vegetation located in the Fidencio basin could be considered a past analogue of the ongoing warming.

2. 2. Present-day environmental setting

2. 2.1. Regional features

The GS is an extended region (~10,800 km^2) located in southeastern Venezuela (Bolívar state), in the Venezuelan Guyana and between the Orinoco and Amazon basins (4º36'-6º37'N and 61º4'-74º2'W) (Fig. 2.1). The climate of the south of the GS has been described as submesothermic tropophilous, with an average annual temperature of approximately 18-22ºC and precipitation of 1600–2000 mm/yr. The GS is a high, undulating erosion surface that forms a plateau inclined from north (1350 m a.s.l) to south (700 m a.s.l) known as uplands, which are dominated by savannas. The GS also includes tabular mountains known as Tepuis (> 1500 m altitude) that constitute the highlands of this region (Huber and García, 2011). Soils in the GS are characterised by poor nutrient content, with low concentrations of phosphorus, calcium and nitrogen, and high concentrations of iron and aluminium oxides (Huber, 1995a).

In the Venezuelan Guayana region, the principal vegetation types are evergreen montane and gallery forests; but the majority of the GS uplands are covered by treeless savannas intermingled with forest patches forming grassland-forest mosaics (Huber, 1986). Three primary types of herbaceous vegetation occur in this region (Huber, 1995b): (1) treeless savannas; (2) shrub savannas; and (3) open savannas with *morichales*, which are mostly monospecific dense stands of the Arecaceae *Mauritia flexuosa* (locally known as *moriche*). *Mauritia* palm swamps are located in the south and centre of the GS, restricted to elevations up to 1000 m a.s.l. Other vegetation types in the GS landscape are montane rainforests (800-1500 m asl; Huber, 1995b; Hernández, 1999), shrublands, secondary woody communities and *helechales* (dense fern-dominated communities). A more detailed description of the vegetation composition is provided in previous studies (Huber 1995b). For the main taxa, refer to Table 2.1.

Fire currently plays a significant role in the landscape dynamics of the GS, with a frequency between 5000 and 10,000 fires per year (Gómez et al., 2000). Nearly 70% of detected fires start in savanna areas, but some fires cross the savanna-forest boundary (Bilbao et al., 2010), causing forest degradation (Dezzeo et al., 2004; Fölster, 1986; Fölster et al., 2001). The vast majority of these fires are of anthropogenic origin (Bilbao et al., 2010). Based on palaeoecological evidence, it seems that fire has been present in the GS at least since the Late Glacial. So far, the oldest evidence of fire in the GS dates back to around 12,400 cal yr BP, but at low occurrence. An increased fire intensity in ~11,700 cal yr BP was hypothesized as potential evidence of postglacial human occupation in the region (Montoya and Rull, 2011; Montoya et al., 2011).

2. 2.2. Study site

The Fidencio peat bog (4º40'N and 61º00'W; 860 m a.s.l) is located near the town of Santa Elena de Uairén in a private farm named "Hato Divina Pastora" (Fig. 2.2). The peat bog lies within an occasionally flooded grass savanna (*Paspalum*-dominated) with non-gramineous elements represented by *Xyris*, *Eriocaulon*, Cyperaceae and *Lycopodium*. The vegetation is grassland with local meadow and a few *Mauritia flexuosa* palms scattered in the landscape (Fig. 2.2).

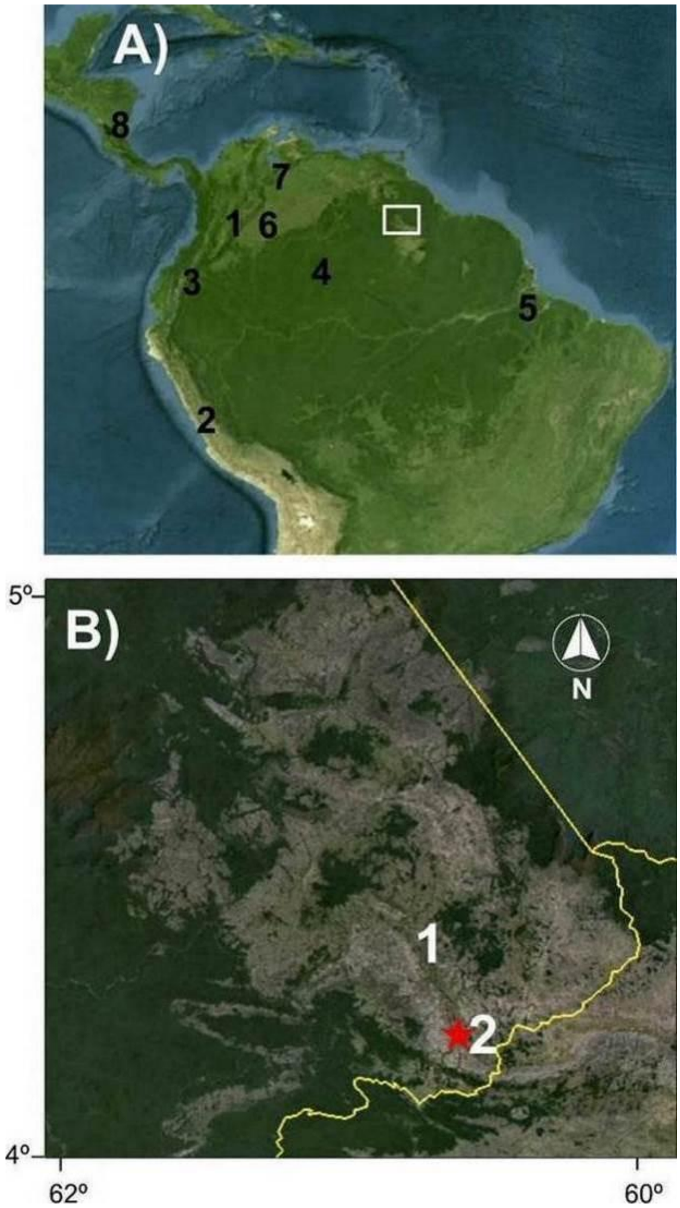


Figure 2.1. A) A modified image of Tropical America, from Google Earth. The location of the Gran Sabana in Northern South America is delimited by the white square. Numbers indicate the sites with palaeoecological information mentioned in the text, grouped here by location topography: Type I (Highlands): 1—Northern Andes; 2—Central Andes. Type II (Amazon lowlands located close to hilly areas): 3—Ecuadorian Amazon; 4—Northwestern Brazilian Amazon; 5—Northeastern Brazilian Amazon. Type III: (Lowlands in flat landscapes): 6—Eastern Colombian savannas; 7—Northern Venezuela; 8—Central American lowlands. **B)** A modified image of The Gran Sabana, from Google Earth. A red star indicates the coring site. Numbers indicate the sites with paleoecological information mentioned in the text: 1—Mapaurí, 2—Lake Chonita.

Plant formation	**Dominant taxa**
Forest –montane type (800-1500 a.s.l)	*Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignonaceae), *Anaxagorea* (Annonaceae), *Alexa* (Fabaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Simarouba* (Simaroubaceae), *Porouma* (Cecropiaceae), *Byrsonima* (Malpighiaceae), etc.
***Morichales* (also considered as savanna with palms)**	Large stands of the palm *Mauritia flexuosa* (Arecaceae), accompanied by the following plant formations: Grasses-*Hypogynium, Andropogon*, *Panicum* (Poaceae); Sedges-*Rhynchospora* and *Bulbostlylis* (Cyperaceae). Shrubs-*Miconia* (Melastomataceae), *Mahurea* (Calophyllaceae), *Piper* (Piperaceae).
Shrubland-sclerophyllous type	*Euphronia* (Euphroniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Byrsonima* (Malpighiaceae), etc.
Savanna	C_4 grasses-*Axonopus* and *Trachypogon* (Poaceae) Sedges-*Bulbostylis*, *Rhynchospora*, *Hypolytrum* and *Scleria* (Cyperaceae).

Table 2.1. Main plant communities and their dominant taxa in the GS (Huber, 1995b)**.**

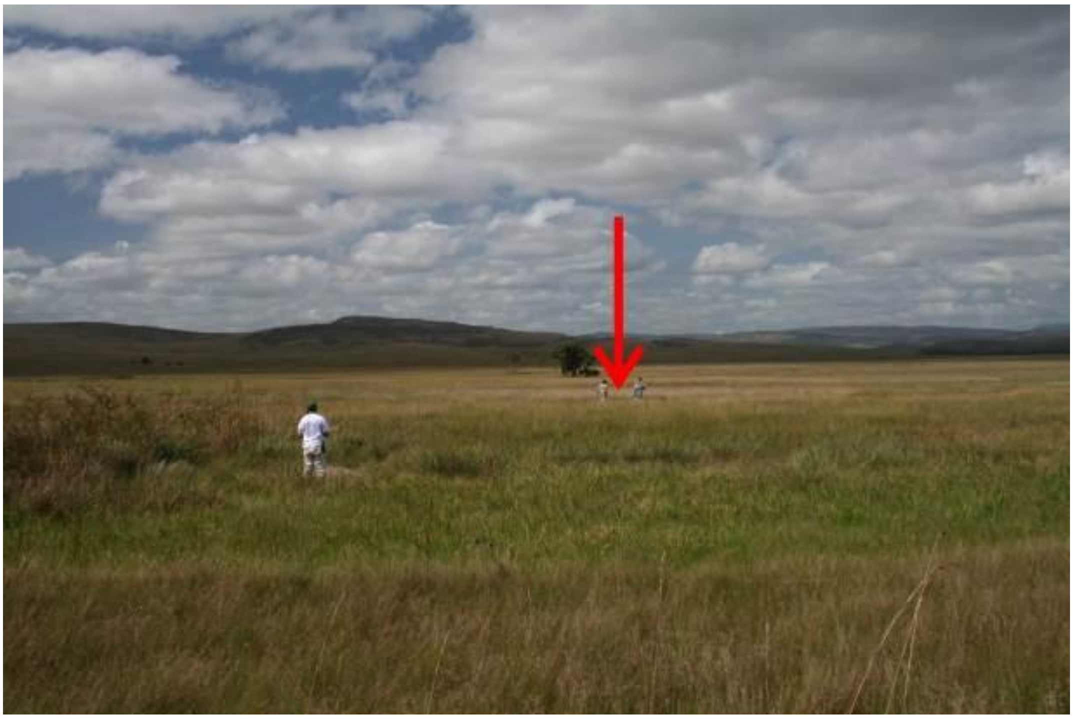


Figure 2.2. Image of grassland vegetation in Fidencio's area. There are a few *Mauritia flexuosa* palms scattered in the background landscape. The coring site is indicated by a red arrow. (Photo: E. Montoya).

2.3. Methodology

The core analysed here (PATAM3 A07; 321 cm long) was obtained in January 2007 and was recovered from a peat bog using a modified Livingstone squared-rod piston (Wright et al., 1984). Nine samples were taken along the core for AMS radiocarbon dating (analysed at Beta Analytic Inc, Florida). The radiocarbon dates were calibrated with the CALIB 6.0.1 and the IntCal13.14c database (http://calib.qub.ac.uk./calib/, last access on March 2014). The age-depth model was produced with the Clam R statistical package (Blaauw, 2010).The present study is focused on the detailed analysis and palaeoecological interpretation of the bottom of the sequence, ranging from 207 to 321 cm. Four radiocarbon samples are included within the interval discussed here (Table 2.2). The core (Fig. I.10) was photographed at intervals of 10 cm and a basic lithological description was carried out.

Laboratory number	Sample	Depth (cm)	Material	Age (yr ^{14}C BP)	Age (cal yr BP) 2σ	Age (cal yr BP) *WA
Beta-333197	PATAM3A_D1/7	27	Pollen residue	1050 ± 30	970-931	966
Beta-347768	PATAM3A_D1/14	48	Pollen residue	1970 ± 30	1948-1883	2326
Beta-347769	PATAM3A_D1/20	67	Pollen residue	4030 ± 30	4542-4423	4044
Beta-333198	PATAM3A_D1/27	87	Pollen residue	7220 ± 40	8052-7971	5559
Beta-333199	PATAM3A_D2/52	162	Pollen residue	7550 ± 40	8398-8349	8390
Beta-333200*	PATAM3A_D3/74	228	Pollen residue	**8910 ± 40**	10188-9909	10174
Beta-333201*	PATAM3A_D3/92	282	Pollen residue	**10350 ± 50**	12403-12005	12025
Beta-347770*	PATAM3A_D3/94	291	Pollen residue	**10680 ± 40**	12712-12726	12214
Beta-316279*	PATAM3A_D3/96	294	Pollen residue	**9610 ± 50**	11167-10767	12264

Table 2.2. AMS radiocarbon dates were used to construct the age-depth model. Asterisks mark the samples included in the interval under study, the corresponding dates are highlighted. WA: weighted average.

Thirty-eight volumetric samples (2 cm^3) were taken in the section studied, at 3 cm intervals. Additionally, a sample from the top of the core was analysed as an indicator of the pollen rain produced by the modern vegetation. The samples were processed using standard palynological techniques (KOH, HCl, acetolysis, HF digestion and dehydration; Faegri et al., 1989). *Lycopodium* tablets were added as exotic markers (batch 177,745, average of 18,584 ± 1853 spores/tablet) (Benninghoff, 1962; Stockmarr, 1971). The slides were mounted in silicone oil without sealing and stored in the same mounting medium. Counts were conducted until a minimum of 300 terrestrial pollen grains was obtained when possible. Pollen count was performed until diversity saturation was reached (Rull, 1987). The identification of pollen and spores was based on Roubik & Moreno (1991), Herrera & Urrego (1996), Colinvaux et al (1999), Rull (2003), Burn and Mayle (2008) and Leal et al (2011). Identified pollen and spores were classified according to the vegetation types previously described for the region (Huber, 1995b).

Pollen diagrams were plotted with the software *PSIMPOLL 4.26 (http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html)*. Due to the large difference between the total counts of terrestrial pollen of each sample, it was considered that interpretations of vegetation dynamics must be inferred from concentration values of pollen taxa, instead of percentages values as it is routinely done. Therefore, pollen diagrams were represented in concentration values (unit-cm^{-3}), whereas traditional percentage pollen diagrams are shown in the Appendices (A2.1, A2.2 and A2.3). The zonation for the pollen diagrams was performed using the Optimal Splitting by Information Content (OSIC) method, and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Given the low number of pollen grains found in some samples, only samples with total counts above 150 terrestrial pollen grains were used in the zonation analysis. That is, six samples corresponding to the interval between 321 and 301 cm of core depth were excluded from the zonation analysis and were represented as an independent zone called FID-0. Only pollen types exceeding 1% abundance were used for zonation. The identification of pollen assemblages was based on comparisons with modern samples from previous studies (Leal., 2013; Rull, 1999) and the known autecology of the taxa (Burn and Mayle, 2008; Burn et al., 2010; Marchant et al., 2002). Pollen of aquatic plants (e.g., *Utricularia*, *Myriophyllum*), semi-aquatic plants (e.g., Cyperaceae, *Sagittaria*), and algal remains (e.g., *Botryococcus*, *Spirogyra*, *Mougeotia*, *Bulbochaete*) were counted on pollen slides and plotted in terms of concentration values. Charcoal counts were also carried out using the same pollen slides and were classified according to two different size classes defined by Rull (1999) for this study area with further modifications:

-Type I (smaller microcharcoal particles of 5–100 μm) consist of windborne charcoal dispersed over long distances and represents regional fire events (Clark, 1998; Blackford, 2000).

-Type II (larger microcharcoal particles >100 μm) are indicative of local fire events because they are not transported far from the fire source (Clark, 1998; Leal, 2010).

In order to evaluate potential relationships between environmental drivers and pollen taxa, we firstly estimated the gradient length of the response of pollen taxa by a Detrended Correspondence Analysis (DCA). The response was higher than two standard deviation (SD) units, which means long gradient (unimodal response). Therefore, a Canonical Correspondence Analysis (CCA) was performed subsequently, with the R software (*http://www.r-project.org*). Data were root-square transformed and rare pollen was down weighted. The interval 321 to 301 cm was excluded due to the low pollen counts.

2.4. Results and interpretation of environmental changes

2.4.1. Chronology and Stratigraphy

The results of AMS radiocarbon dating (Table 2.2) were used to build the age-depth model for the sequence. The best fit was obtained with a smooth-spline model (Blaauw, 2010) and is shown in Fig. 2.3a. The sequence encompassed approximately the last 12,725 cal yr. However, the section under study corresponds to the bottom of the core (12,725-9520 cal yr BP) and is highlighted in Fig. 2.3b. Between 12,725 and ~12,000 cal yr BP (321-281 cm), the dates show a wide range of variability (Fig. 2.3b), which decreases progressively from the oldest date. Sedimentation rates ranged from 0.06 to 0.03 cm/yr and gradually decreased from the bottom to the top of the studied section (Fig. 2.3b). Mean sampling resolution is approximately 85 years (range= 51-113 years).

From the bottom to the top of the studied sequence, five lithological units have been established (Fig. 2.3b). The first lithological unit (321-300 cm) consists of light-grey silt with desiccation features and root scars, rich in macro plant remains. The second unit (located between 300 and 284 cm) consists of mottled dark brown silt with a light-grey silt layer in its central part (290-293 cm). Plant remains are abundant. The two mottled layers contain large charcoal remains (Fig. 2.3b). The third lithological unit is composed of dark brown silt (284-260 cm). According to photos (Fig. I.10) and the texture of sediments, the transition between the second and third lithological units is considered gradual (Fig. 2.3b). The fourth lithological unit is present from 260 cm to 230 of core depth and is characterised by dark brown clay. Finally, the fifth unit (230-207 cm) is made up of dark brown clay with abundant and large plant fragments.

The sediments' lithological features in combination with the presence of plant macro remains allowed relating potential sedimentological processes to the previously defined lithological units (Fig. 2.3b), englobed into three main events as explained below:

Event 1. Occurrence of soil (lithological unit 1 and the lower half of the unit 2: 321-290 cm) approximately between 12,725 and 12,195 cal yr BP (Fig. 2.3b). A first soil was present during the lithological unit 1 (321-300 cm: 12,725-12,367 cal yr BP). The root scars probably correspond with the rooting system which existed at that time. A second soil formed by mottled dark brown silt (lower part of the second lithological unit: 300-293 cm) might have been established between 12,367 and 12,250 cal yr BP. Finally, a waterlogged soil appears to have been formed during the middle part of the lithological unit 2 (293-290 cm; 12,250-12,195 cal yr BP). As a working hypothesis it is proposed that dry conditions prevailed during the soil phases, with a slight increasing moisture trend. Wind may have eroded the soils, rendering them of silty condition.

Event 2. Transition to the lacustrine system is likely to have started in 12,195 cal yr BP (mid of lithological unit 2: 290 cm) (Fig. 2.3b), and finished with the complete establishment of a lake in approximately ~11,975 cal yr BP (beginning of lithological unit 3: 280 cm). Wetter conditions were probably responsible for the deepening of the water lamina; however, the texture of the sediments suggests that the lake would have remained shallow.

Event 3. The lake began to fill up progressively in roughly 11,350 cal yr BP (onset of fourth lithological unit: 260 cm), which resulted in a peat bog establishment around 10,245 cal yr BP (start of the fifth unit: 230 cm) that continued until the top of the section studied here (207 cm, ~9520 cal yr BP).

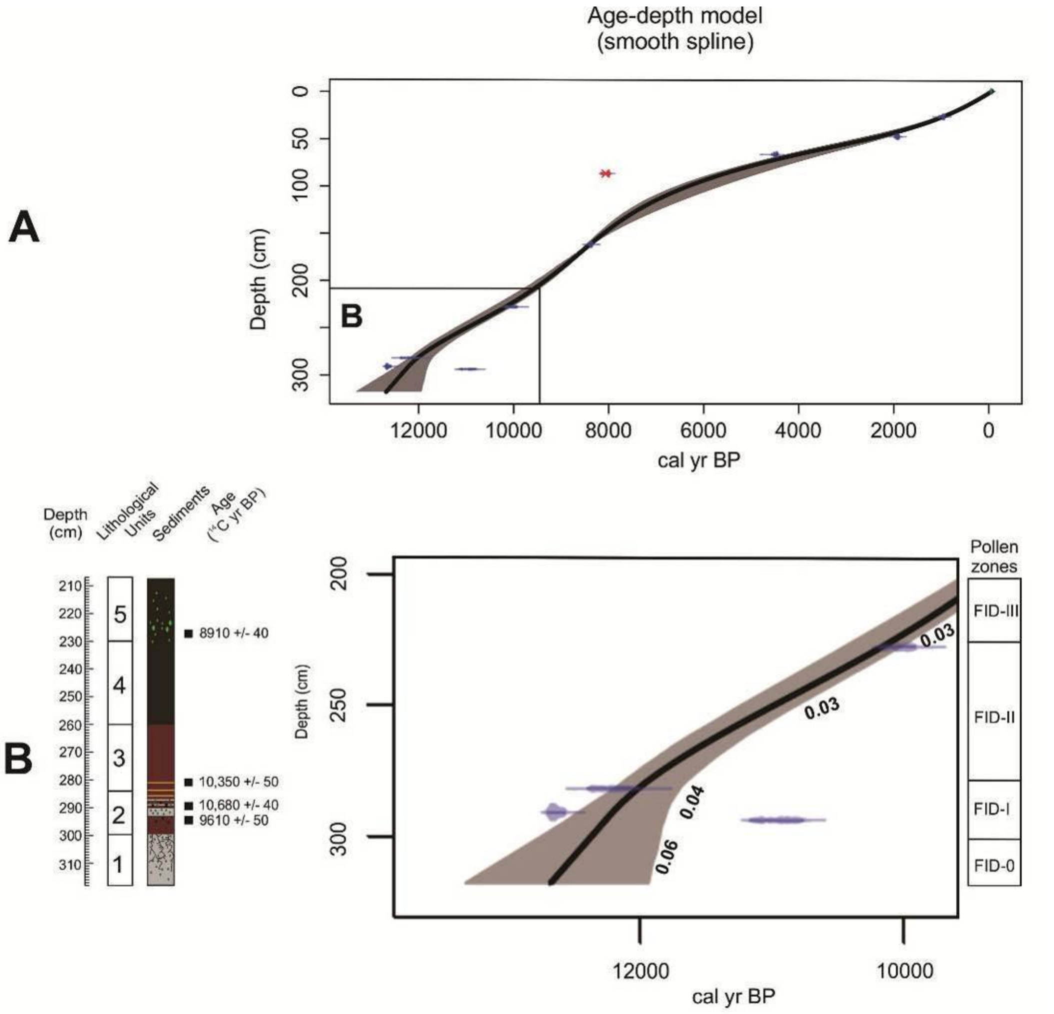


Figure 2.3. A) Age-depth model of Fidencio record (core PATAM3A 07).The period under study is indicated by the square. **B)** Age-depth model and sediment description of the interval between 321 and 207 cm of the core (present study). Four radiocarbon samples are included within this interval (Table 2.2). The values of average sedimentation rate are represented. Pollen zones are delimited.

2.4.2. Modern pollen sample

Sediments from the top 10 cm of the core were taken as a mixed sample in the field. Thus, a subsample from this mixture would have low chronological accuracy. Instead, a sample located at a depth of 11cm of the core was taken as the youngest available sample to be used as an indicator of the modern vegetation, corresponding with an estimated age of 330 cal yr BP. The sediments of this sample are peat. The main taxa and charcoal particles are represented in terms of concentration values (Fig. 2.4). The results show that herbs dominate the pollen assemblage significantly (Fig 2.4), in which the most abundant element is Poaceae (~$35*10^3$ grains*cm^{-3}). Other non-gramineous elements are *Xyris*, Polygalaceae and Cyperaceae (Fig. 2.4). Pollen grains from woody taxa show very low abundances, notably dominated by *Brosimum*. Algae exhibit relatively low concentrations (~$7*10^3$ remains*cm^{-3}), represented by *Mougeotia*. Smaller charcoal particles (type I=5-100µm, proxy for regional fires) show remarkably higher values (~$50*10^3$ particles*cm^{-3}) than the larger ones (type II= >100 µm, proxy for local fires; ~10^3 particles*cm^{-3}) (Fig. 2.4). The percentage values diagram is shown in the Appendix A2.1.

The pollen assemblage suggests that the vegetation near Fidencio's site was grassland with local meadow approximately 330 yr ago, which was affected by a relatively high occurrence of fires. This vegetation is likely to be similar to the current floristic description (section 2.2.2).

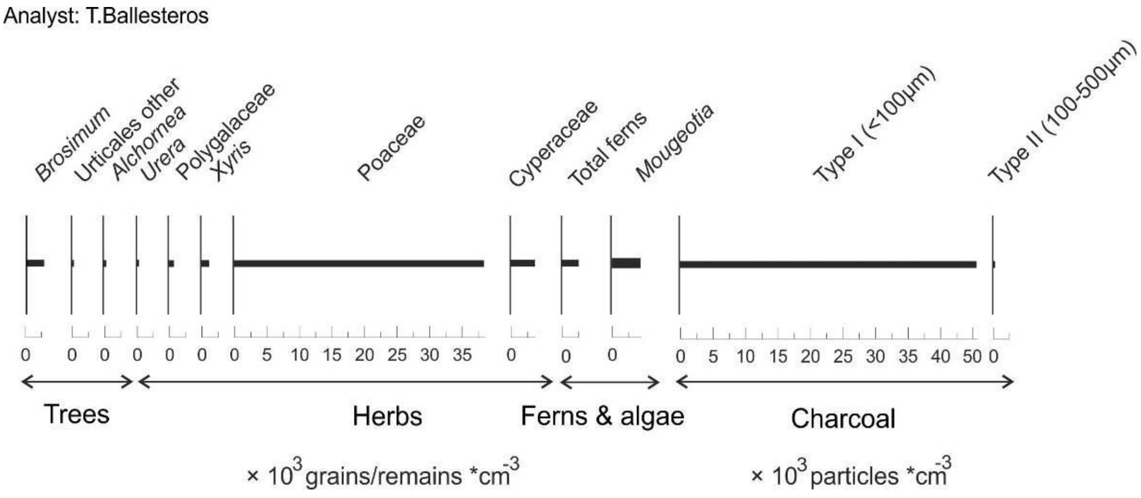


Figure 2.4. Diagram of the modern sample of the Fidencio location, showing the abundance of main taxa and charcoal particles, expressed in concentrations.

2.4.3. Late Glacial pollen record

The stratigraphic variations allowed the division of the pollen diagram into four zones (Fig. 2.5). FID-0 (12,725-12,385 cal yr BP) covers the initial part of the YD cold phase. FID-I (12,385-12,000 cal yr BP) comprises the mid part of this climatic event. Because of the trends' variations of several proxies, FID-I is subdivided into two subzones, FID-IA (12,385-12,260 cal yr BP) and FID-IB (12,260-12,000 cal yr BP). The third zone is FID-II (12,000-10,440 cal yr BP) and encompasses the end of the YD and the first part of the early Holocene (EWH period), and therefore, the YD-Holocene transition for Northern South America, according to Haug et al. (2001). Finally, FID-III (10,440-9520 cal yr BP) relates to the last part of the early Holocene covered in this study. The description of these pollen zones and interpretation of environmental dynamics are shown below. The percentage values diagrams are displayed in the Appendices A2.2 and A2.3.

FID-0 (321-301 cm; 12,725-12,385 cal yr BP; 6 samples)

The very low concentrations of total terrestrial pollen grains (<$30*10^3$ pollen grains*cm^{-3}) in these 6 samples and their correspondence with the first lithological unit (Figs. 2.5 and 2.6), allowed the consideration of them as an independent section. The lower half is almost barren of palynomorphs, but they progressively increase towards the top the zone, especially fern spores (~$60*10^3$ spores*cm^{-3}) and to a lesser extent pollen of woody taxa (trees and shrubs: ~$13*10^3$ grains*cm^{-3}), primarily represented by *Dimorphandra*, Meliaceae and *Cyrilla* (Figs. 2.5 and 2.6). Aquatic elements exhibit very low values along this zone, being almost absent in its lower half (Fig. 2.6). These elements, which are mainly cosmopolite alga *Mougeotia* (Zygnematacea), peak in the upper half of the section (Figs. 2.6 and 2.7). Type I charcoal particles are present throughout the zone at low values but suddenly peak at the top (Fig. 2.5).

The virtual absence of palynomorphs and algae (Fig. 2.6) might suggest the occurrence of arid conditions during this interval, which could have caused subaerial desiccation of the biological proxies studied, preventing their preservation. Additionally, the root scars on the grey sediments (lithological unit 1) might suggest that pollen from the upper sediments (lithological unit 2) could have percolated through them and filled these channels (Fig. 2.6). Thus, the pollen record found here might not have been produced during this interval; instead, it may have been the result of contamination with younger material. Based on these two potential scenarios, any possible interpretation of the biological proxies' data of this section has been avoided.

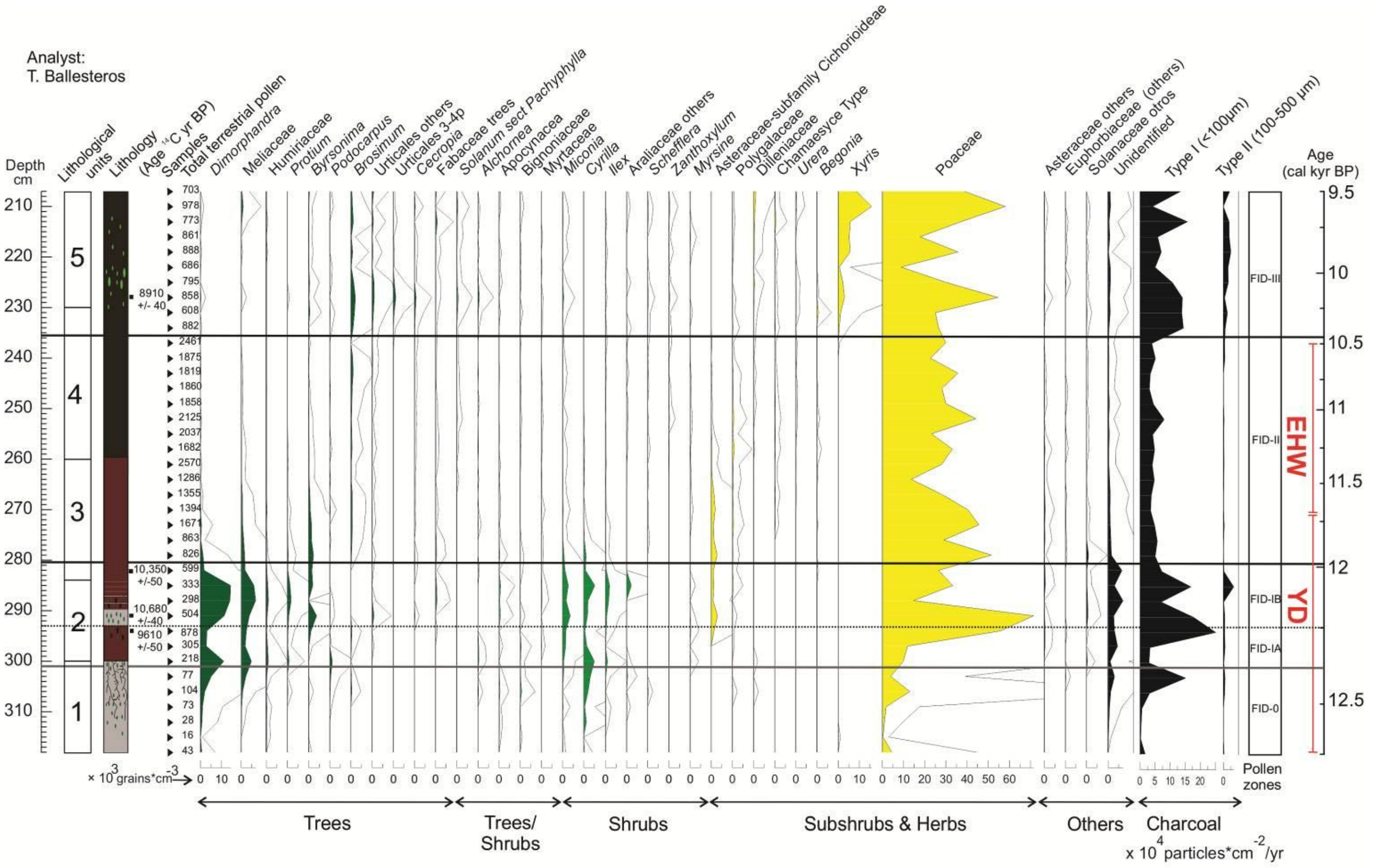


Figure 2.5. Diagram showing pollen taxa and charcoal particles expressed in concentration and influx values respectively. Solid lines represent x 10 exaggeration. Upper and lower bounds of the Younger Dryas (YD) and Early Holocene Warming (EHW) events for Northern South America are indicated, according to Haug et al.(2001).

Concerning fires, the first presence is reported in ~12,725 cal yr BP, but at low intensity/frequency. High fire occurrence took place around 12,450 cal yr BP. These ages represent the oldest fire record found in the GS so far, and among the first pieces of fire evidence obtained in the Neotropics (other Late Pleistocene fires reported: Behling, 2001; Montoya et al., 2011; Salgado-Labouriau, 1997; Salgado-Labouriau et al., 1998).

FID-I (301-280.5 cm; 12,385-12,000 cal yr BP; 7 samples)

This interval corresponds with the second lithological unit and the transition to the third lithological unit (Fig. 2.5). The concentration of total terrestrial pollen grains is on average $60*10^3$ pollen grains*cm^{-3} (Fig. 2.6). Variations of pollen assemblages are explained in two subsections, which reflect the vegetation dynamics.

First subsection, **FID-IA** (301-293 cm; 12,385-12,260 cal yr BP; 3 samples) coincides with the mottled brown silty soil (Fig. 2.5). FID-IA is represented by low concentration values of woody taxa (up to $13*10^3$ grains*cm^{-3}) and fern spores (~$5*10^3$ spores*cm^{-3}) (Fig. 2.6), which show a decreasing trend. Herbaceous pollen exhibits low values and increases dramatically at the top of the subsection (~$57*10^3$ grains*cm^{-3}). Algae remains show very low counts (~10^3 remains*cm^{-3}; Fig. 2.6), although they display a slight increasing trend compared with FID-0. Type I charcoal particles remain low in comparison with the peak observed at the top of the previous zone, and increase remarkably near the top of this subsection.

The second subsection, **FID-IB** (293-280.5; 12,260-12,000 cal yr BP; 4 samples) is characterised by remarkably increased concentration of pollen from woody plants (~$31*10^3$ grains*cm^{-3}, e.g. *Dimorphandra,* Meliaceae, *Protium, Byrsonima*, *Miconia*, *Cyrilla, Ilex*) and ferns. The herbaceous curve is characterised by a fluctuating pattern, peaking at the beginning of the zone and showing higher abundances than in previous subsection (Fig. 2.6). Algae values are higher than in FID-IA. The algae *Mougeotia* and *Bulbochaete* peak (Fig. 2.7), coinciding with the grey-silt layer (Fig. 2.6). Despite not reaching the high counts of charcoal particles found at the top of FID-IA, the general trend of charcoal values is higher in FID-IB than in the previous subsection (Fig. 2.6). Pollen grains from woody taxa decrease significantly (~$9*10^3$ grains*cm^{-3}) near the top, coinciding roughly with peaks of type I and type II charcoal particles (Fig. 2.5).

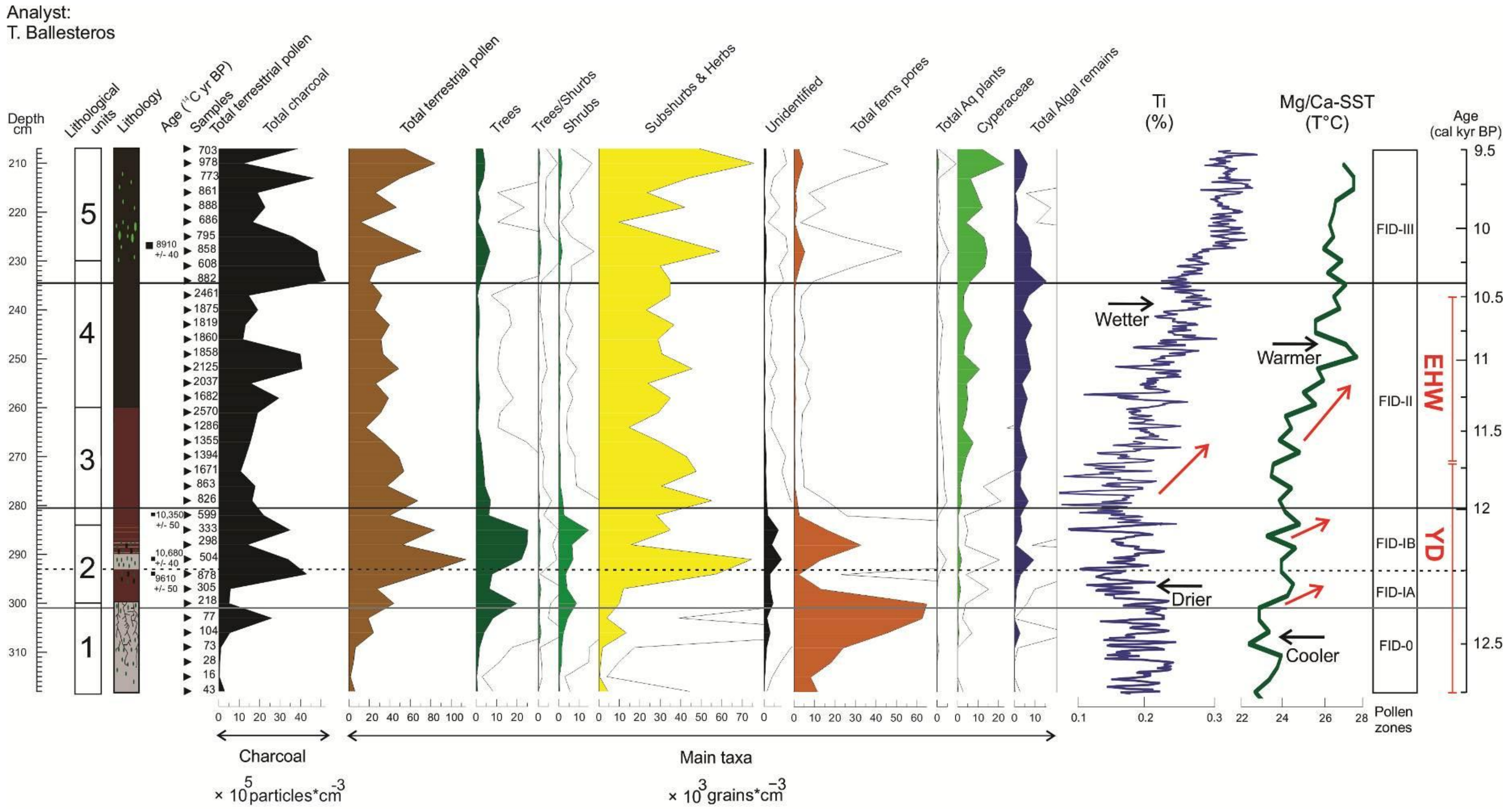


Figure 2.6. Diagram showing the concentration values of vegetation previously described for the region (trees,shrubs, herbs) and of aquatic elements (algae, aquatic and semi-aquatic plants) and total charcoal particles. Regional climate trends for northern South America (from Cariaco basin) are also plotted: Titanium curve (Ti) has been extracted from Haug et al. (2001) and indicates variations of hydrological cycle, whereas temperature reconstruction from Foraminifera Mg/Ca indicates variations in sea surface temperature (SST), and has been extracted from Lea et al. (2003). Both Cariaco curves have been downloaded from NOAA (http://www.ncdc.noaa.gov/data-access/paleoclimatology-data). Intervals defining the YD and EHW follow Figure 2.5.

FID-I zone (12,385-12,000 cal yr BP) covers approximately the mid part of the YD chron recorded in the high latitudes of the northern hemisphere. The variations of pollen assemblages observed seem to represent the dynamics of forest patches in mosaic with *helechales* and savanna. The most representative elements of the forests are generalist taxa that are common in a wide range of altitudes (from lowlands to uplands) (Berry et al., 1995a,b,c,d, e).

The available evidence did not allow us to determine the age of establishment of forests and *helechales*. At the beginning of **FID-IA**, forests and *helechales* may have formed patchily distributed plant communities that showed a decreasing trend towards the end this subinterval. Instead, grassy vegetation expanded, probably favoured by the canopy openness (Lehmann et al., 2011; Murphy and Bowman, 2012). Algae data and the lithological change provide evidence that the water balance was slightly higher than in FID-0, but still dry (Fig. 2.6). Climate on a regional scale appears to have been dry (Haug et al., 2001) and remarkably warmer (SST ~+2°C, Lea et al., 2003) than in the interval encompassed by the previous zone (Fig. 2.6). Factors other than climate can affect the growth of plant communities, such as fires, nutrient deficiency, availability of seed banks, light conditions, diseases, plagues, etc. These factors may have also played a part in the decrease of forest-*helechales* patches. Unfortunately, few of them are possible to assess from the palaeo-record, and evidence only exists for two of the aforementioned factors. In the case of fires, charcoal particles indicate that fire occurrence was not high at the time of low abundance of forests and *helechales* (Fig. 2.6). Regarding taxa composition, *Dimorphandra*-the dominant taxon of the forest patches (Fig. 2.5)- is a plant that conducts N_2-fixation (Fonseca et al., 2013). Furthermore, ferns promote nutrient storage in soils. Thus, the presence of ferns and *Dimorphandra* suggests that nutrient deficiency might not have been a limiting factor. Therefore, fires and nutrient deficiency might be dismissed as potential causes. In view of the available results, it is proposed that the cumulative impact of dry and warmer climate might have led to the reduction of the mosaic vegetation and the subsequent expansion of grassy vegetation.

At the beginning of **FID-IB,** increased soil moisture, inferred from the lithological change and aquatic taxa, related to wetter conditions could have promoted the growth of local forest patches at the expense of the grass layer (Fig. 2.6; Beckage et al., 2009; Lehmann et al., 2011). The *helechales* increased while the fires simultaneously dropped halfway through the subinterval FID-IB (Fig. 2.6). The ferns community was probably composed of pioneer plants that colonised land cleared by fire disturbance, as reported in other palaeoecological studies of the GS (chapter 1; Rull, 1999). The provenance of type I charcoal particles is traditionally considered regional (dispersed over kilometres). Nevertheless, the small size of the water body and previous studies in the GS about transport-deposition of charcoal particles (Leal, 2010) suggest that these particles may correspond with extra-local fires (the fire source occurs some meters from the coring site), which exhibited higher occurrence than in previous subintervals. Both extra-local (type I particles) and local fires (type II particles, in situ fires) peaked near the end of FID-IB (Fig. 2.5), occurring approximately at the same time as the onset of forest retraction around 12,070 cal yr BP. Based on this inference, it is hypothesized that fires might have contributed to forest retraction. Temperatures on a regional scale have been inferred to be warmer at the end of this subinterval (Lea et al., 2003), becoming the warmest interval of the whole pollen zone FID-I (Fig. 2.6). Therefore, the interplay between higher fire occurrence and warmer conditions could have facilitated the shift of forest-savanna mosaic dynamics in favour of grassland at the end of FID-I (Murphy et al., 2012, Accatino and De Michele, 2013). In summary, dynamics of mosaic vegetation in Fidencio appear to have been driven by climate during the entire FID-I-period and additionally by fire during FID-IB.

FID-II (280.5-235.5 cm; 12,000-10,440 cal yr BP; 15 samples)

This interval coincides with the third and fourth lithological units (Fig. 2.5). The concentration of total terrestrial pollen grains is on average $60*10^3$ pollen grains*cm^{-3}. The concentrations of herbaceous elements are higher than in the previous pollen zone and range between 15 and $55*10^3$ pollen grains*cm^3 (Fig. 2.6), significantly dominating the pollen assemblage. Terrestrial herbs are almost entirely represented by Poaceae (Fig. 2.5). Woody elements are represented by few taxa, primarily *Byrsonima* in the lower half of the zone (Fig. 2.5). The concentrations of Cyperaceae (semi-aquatic plants) and algae (*Mougeotia*, *Spirogyra* and *Bulbochaete*) are higher than in the previous zone (Fig. 2.7). The influx of type-I charcoal particles is evidently lower than in the previous section, but still has high values (~$5*10^4$ particles*cm^{-2}/yr; Fig. 2.5). Type II charcoal particles are virtually absent, but start to increase near the top of the zone (Fig. 2.5). The regression analysis between herbs and charcoal provides an adjusted-R^2 of 1 and a p-value <0.01.

The pollen assemblage indicates that grassland dominated the Fidencio's area during this period. The lithological change observed at the end of the previous interval continued in this period, indicating the establishment of a lacustrine system, which seems to have been shallow according to the porous nature of the sediments. The presence of standing-water algae (e.g. *Bulbochaete* and *Mougeotia*; Fig. 2.7) agrees with this inference. The development of a lacustrine system and the regional trend towards increased moisture (Fig. 2.6) indicate that climate in the study region was wetter than in the previous period (FID-I). This fact possibly contributed to the decrease in the fire regime (Fig. 2.6). The lake started to progressively fill with sediment from 11,350 cal yr BP. Shallowness of the lake in combination with regional increased precipitation (Fig. 2.6) may have enabled the deposition of terrestrial material in the water lamina, which may have caused the filling process. It is interpreted that wetter and warmer conditions (Fig. 2.6) may have favoured high production of grasses, contributing to the filling process locally. On an extra-local scale (and probably semi-regional), positive feedback between fuel loads (grasses) and fires would have formed during this period, likely maintaining the grassland condition (Lehmann et al., 2011; Murphy and Bowman, 2012).

FID-III (235.5-207 cm; 10,440-9520 cal yr BP; 10 samples)

This section corresponds with the last part of the fourth lithological unit and the establishment of a peat bog that prevailed along the fifth lithological unit (Fig. 2.5). The concentration of total terrestrial pollen grains is on average, $48*10^3$ pollen grains*cm^{-3}. Terrestrial herbs continue dominating the pollen assemblage with concentrations between 75.7 and $10*10^3$ pollen grains*cm^{-3} (Fig. 2.6) primarily consisting of Poaceae, and to a lesser extent *Xyris* (Fig. 2.5). Semi-aquatic Cyperaceae increase during this zone (Fig. 2.6). Woody elements increase slightly in the lower half (up to 6.8 $*10^3$ pollen grains*cm^{-3}); the increase is attributed to Urticales primarily, and to a lesser extent, *Cecropia*, *Solanum sect. Pachyphylla* and *Miconia* (Figs. 2.5 and 2.6). Fern spores follow a similar trend to that of woody taxa. Algal remains are more abundant at the lower half of the zone (Figs. 2.6 and 2.7). Smaller charcoal particles increase remarkably and remain high throughout the zone with slightly lower values during the middle of the section (Fig. 2.5). Larger charcoal particles exhibit an increasing trend (Fig. 2.5).

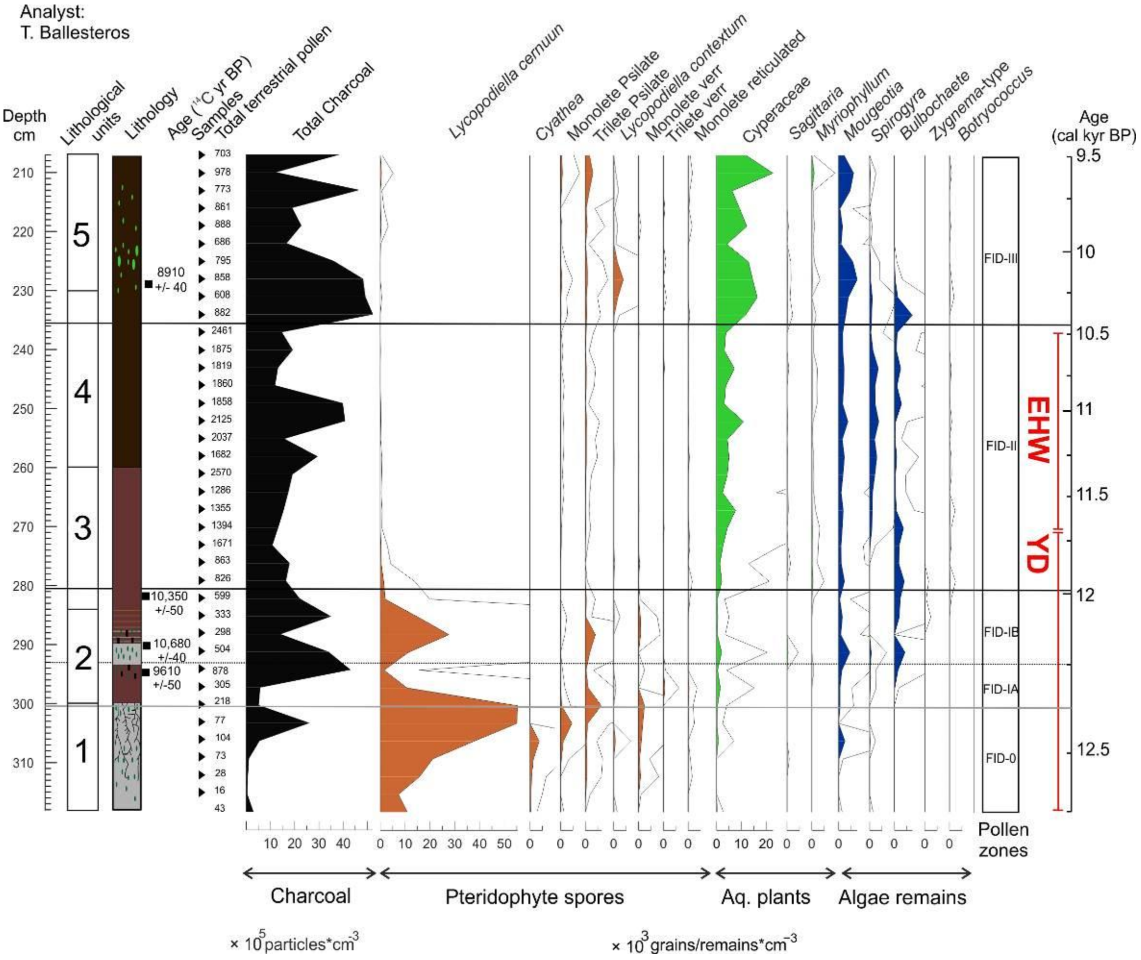


Figure 2.7. Diagram showing concentrations of aquatic and semi-aquatic plants, pteridophyte spores and algae remains. Solid lines represent x 10 exaggeration. Intervals defining the YD and EWH follow Figure 2.5.

The occurrence/increase of non-gramineous herbs (e.g., *Xyris*, Cyperaceae) suggests that local meadow developed within the open landscape. The presence of *Xyri*s, a plant commonly found in peat bogs in the GS (Berry et al., 1995f), agrees with the lithological change. Increased herbaceous plants under warmer climate (Fig. 2.6) may have promoted the continuity of the feedback between fuel loads and fires (Fig. 2.5). Scarce forest patches and *helechales* seem to have established in the area, displaying a fluctuating trend (Fig. 2.6). At the beginning of this period, algae exhibited higher counts than in the previous zone (Figs. 2.6 and 2.7), suggesting that increased moisture could have played a part in the growth of small forest patches regionally (Figs. 2.5 and 2.6). However, although the regional humidity continued to increase (Fig. 2.6), abundances of algae seem to have lowered around 10,000 cal yr BP (Figs. 2.6 and 2.7). This could be due to the filling of the water lamina with organic material and the establishment of the peat bog. Non-gramineous herbs are likely to have encroached and covered the surface of the peat bog (Figs. 2.5 and 2.6). Fires were remarkably higher during this period. Other factors (excluding moisture level) probably influenced the high fire regime.

2.4.4. Data analysis of environmental gradients*: Canonical Correspondence Analysis (CCA)*

The environmental proxies used are algae and charcoal, which have been interpreted as indicators of local water balance and fires respectively. In addition, samples (each corresponding with a depth of the core) and all taxa are included in the analysis, although only the main taxa are indicated. Fig 2.8 shows the results of the CCA along the biplot. Axis 1 explains 72.8% of the total variance, and Axis 2 27.21%. Negative values of Axis 1 are highly represented by algae, whereas charcoal has more influence on negative values of Axis 2. The angle between algae and charcoal indicates that both variables are uncorrelated. This result suggests that the level of water balance could not have induced/impaired fire ignition, unlike what it is reported in the literature of fires, which states that the moisture content of fuel source affects the ignitions rates (Cochrane and Ryan, 2009). Hence, other driver(s) (e.g., warmer temperatures, human-induced ignition) may have influenced fires occurrence.

A careful analysis of the samples distribution along Axis 1 (Fig. 2.8) reveals that they are clustered coinciding with the pollen zones defined in the diagram (Fig. 2.5), according to their association level with local water balance. Samples of pollen zones FID-II and FID-III together with aquatic plants and Cyperaceae fall in the left quadrants, whereas pollen zone FID-I and its main taxa are situated in the right quadrants. This suggests that the mosaic vegetation of FID-I occurred under drier conditions, unlike open vegetation (FID-II, FID-III), which seems to have happened during intervals of higher water balance. These results agree with those inferred from the pollen diagrams (Fig. 2.6).

Concerning Axis 2, samples are located according to their relationship with fire occurrence. Samples of pollen zone FID-III and *Xyris* are located in the lower quadrants. Pollen zones FID-II and FID-I are situated in the upper quadrants. Thus, grassland with local meadow (FID-III) may have been associated with high intensity/frequency of fires, whereas grassland (FID-II) and mosaic vegetation (FID-I) appear to be uncorrelated with that fire regime; instead, they may correlate with lower intensity/frequency of fires. The palynological results partially support these inferences.

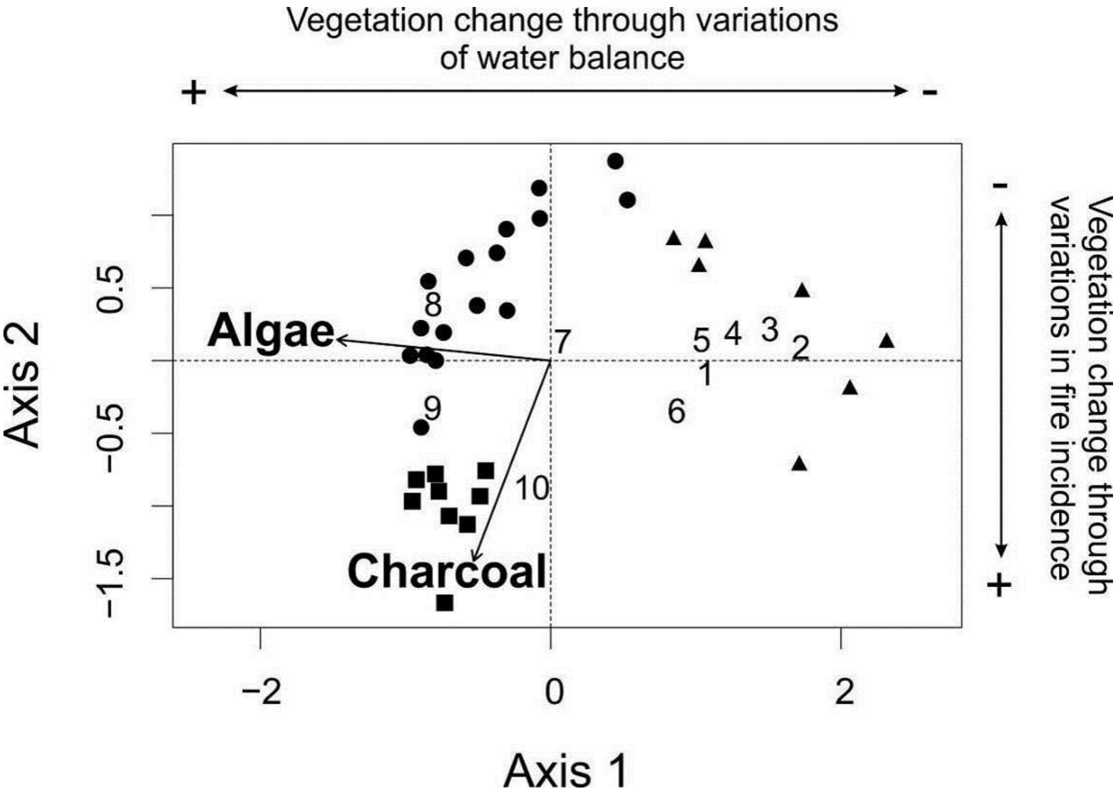


Figure 2.8. Biplot of Canonical Correspondence Analysis (CCA). Samples from FID-0 pollen zone are not included. Representation of samples according to their pollen zone: ▲ FID-I; ●FID-II; and ■ FID-III. Main taxa are indicated. Taxa abbreviations: 1: Humiriaceae, 2: *Dimorphandra*, 3: *Cyrilla*, 4: *Protium*, 5: Meliaceae, 6: Ferns, 7: Poaceae, 8: Aquatic plants, 9: Cyperaceae, 10: *Xyris*.

2.5. Discussion

2.5.1. Potential vegetation responses to YD's rapid cooling reversal

The studied sequence yields very low counts of palynomorphs between 12,725 and 12,385 cal yr BP (FID-0), which prevented us from knowing the vegetation responses at the onset of the YD. In addition, it was not possible to relate any potential vegetation shifts to the abrupt start of the YD due to the poor age control at the bottom of the sequence (Fig. 2.3b).

In the GS region, there is another sequence of Late Glacial age (maximum age around 15,000 cal yr BP); Lake Chonita (Montoya et al., 2011), which is approximately 2 km away from Fidencio (Fig. 2.1b). Lake Chonita sequence was barren of palynomorphs until ~12,700 cal yr BP, when pollen began to increase markedly. High pollen values from woody taxa indicate that a shrubland dominated by *Bonyunia* (Loganiaceae) occupied the basin of the lake between 12,700 and 11,700 cal yr BP, coinciding with the YD chron (Montoya et al., 2011). The absence of palynomorphs until 12,700 cal yr BP prevented the authors from inferring whether the shrubland was present before that date. To add, it was not possible to determine whether the vegetation changed to the *Bonyunia*-dominated shrubland during the Bølling-Allerød/YD transition. Therefore, based on the palynological evidence to date, it was not possible to discern vegetation responses to the YD's abrupt cooling in the flat areas of the GS. With regard to future research, it is proposed that the following factors are necessary to determine the vegetation responses to the YD's cooling reversal in the GS: incorporation of local independent proxies for temperature, the study of more Late Glacial age sequences, performing higher sampling resolution and obtaining better control age.

The knowledge of vegetation responses to the YD's rapid cooling is also limited in other Neotropical savanna areas characterised by flat topographic conditions (e.g., northern Venezuela, Guatemalan lowlands and eastern Colombian savannas). This is partially due to the lack of sedimentary records with accurate control age during the YD chron (Behling and Hooghiemstra, 1999; Curtis et al., 1999; Leyden, 1985; Correa-Metrio et al., 2012; Hillesheim et al., 2005). Among the limited evidence, in northern Venezuela and Guatemalan lowlands the presence of grassland and xeric vegetation has been associated with the dry climate typical of the YD for the northern hemisphere (Fig. 2.1a; Curtis et al., 1999; Leyden, 1985; Correa-Metrio et al., 2012; Hillesheim et al., 2005). In eastern Colombian savannas (*Llanos Orientales*, Fig. 2.1a), there is evidence of increased gallery forests during the YD, driven by higher available moisture (Berrío et al., 2012). In the GS, the available records (including this study) suggest that climate appears to have been dry, but with an increasing moisture trend from the middle of the YD chron onwards. The GS records coincide with those of the *Llanos Orientales* on the presence of woody communities during the first part of this climatic event. The differences of moisture balance between northern (Guatemalan lowlands and northern Venezuela, dry conditions) and southern locations (eastern Colombian savannas and the GS, wetter trend) may be explained by the position of the Intertropical Convergence Zone over the American continent (Fig. 2.1a; Haug et al., 2001). Future palaeoecological researches are encouraged to be aimed at assessing vegetation responses to the YD's rapid cooling in Neotropical areas characterisded by flat topography. In doing so, it would be necessary to include the methodological requirements mentioned previously.

2.5.2. Origin of grassland during the YD/Holocene transition

Dynamic mosaic vegetation formed by forests, *helechales* and savanna dominated the area nearby Fidencio at least between ~12,385 and 12,070 cal yr BP (Fig. 2.6). Rapid substitution of forested areas by grassland took place in ~12,070 cal yr BP, which constitutes the origin of grassland vegetation in the studied area. Even though the vegetation replacement occurred approximately at the same time as the increase in the fire regime (Fig. 2.6), high occurrence of fires was already present in Fidencio's area (unlike previous GS records; Montoya et al., 2011; Rull, 2007; Rull et al., 2015b) without causing diminution of the forest cover. This result is very important because it is the first piece of evidence about the presence of intensive/frequent fires before the origin of grassland in the region. Therefore, the results do not support the idea that the origin of open vegetation came into existence solely because of fires, as modern studies have suggested for current savanna extension (Dezzeo et al. 2004). Moreover, *Dimorphandra*, which is the most abundant tree of the forest in FID-I, is a fire resistant taxon found in annually burnt savannas (Muniz da Silva and Batalha, 2008). Therefore, the strong diminution of the *Dimorphandra*-dominated forest caused only by fire action appears to be unlikely; though, the occurrence of fires could have played a role within a synergy of several environmental factors.

In Fidencio's area, the transition to lacustrine system might indicate a slight increasing trend of moisture from ~12,195 cal yr BP (Fig. 2.6). On a regional scale, though moisture began to increase in ~12,000 cal yr BP, climate was still dry (Fig. 2.6; Haug et al., 2001; Stansell et al., 2010). Therefore, the changes regarding the sediment nature and the progressive (though small) increase in the algal record might suggest that the forest replacement by grassland in Fidencio coincided with a trend towards slightly higher available moisture compared to the beginning of the YD. In Lake Chonita's area, the presence of first fires of high intensity/frequency occurred in ~11,700 cal yr BP under dry climate, though slightly wetter than that of the Bølling-Allerød, coincided with the dramatic change from shrubland to treeless savanna (Montoya and Rull, 2011; Montoya et al., 2011; Rull et al., 2013). Therefore, Fidencio's dry climate in spite of an increase in moisture during the origin of open vegetation was also observed in Chonita record (Montoya et al., 2011); suggesting that the climatic trend probably occurred within a basin scale. Rull et al., (2015b) proposed that drier climate compared to present values contributed to increase in vegetation flammability, and thereby favouring the propagation of fires. Following this, the interplay between YD's dry climate and fire was suggested as the most plausible explanation for the onset of savannisation in the south of the GS. The results of Fidencio partially agree with the scenario proposed by Rull et al. (2015b), in the sense that the role played by fires in the savannisation was apparently less important in Fidencio than in Chonita. The other available record of the origin of treeless savanna is from Mapaurí peat bog (Fig. 2.1b), located at the bottom of a tepui slope. In Mapaurí (Fig. 2.1), it was interpreted that local climatic dryness may have been involved in the replacement of cloud forests by open savanna in ~10,200 cal yr BP (Rull, 2007). In summary, the available evidence in the GS suggests that local moisture might have contributed to the origin of open vegetation (Rull et al., 2015b).

Regional paleoclimatic records suggest an early termination of the YD's cooling in northern South America. It was proposed that the warming trend started between ~12,650 and 12,300 cal yr BP (Fig. 2.6; Lea et al., 2003; Stansell et al., 2010), approximately 1000-650 yr prior to the high latitudes of the northern hemisphere (11,600 cal yr BP, Rasmussen et al., 2006). Therefore, the early start of the warming trend might have had an adverse effect on the maintenance of forest patches in Fidencio. This effect was hypothesized for Mapaurí, where warming was considered as the most probable cause of the cloud forest-open savanna turnover (Rull, 2007). This forest could have migrated upward along the tepuian slope (Rull, 2007), where it is found nowadays. However, the generalist condition of taxa that comprised the Fidencio forests might have enabled them to withstand the rise in temperature. It is recognised that the rapid warming at the termination of the YD was characterised by a global increase in the incidence of fires (Daniau et al., 2010). Based on that, it is proposed that the regional rise in temperature may have contributed to occurrence of severe fires in Fidencio around 12,070 cal yr BP (Fig. 2.6), and thus, the synergy between warming and fire may have been influential in the origin of grassland (Montoya et al., 2011; Rull, 2009; Rull et al., 2013).

It has been suggested that GS paleofires could be of anthropogenic nature (Montoya and Rull, 2011; Rull, 2009; Rull et al., 2015b). The emergence of human communities is said to be associated with extensive use of fire (McBrearty and Brooks, 2000). Data derived from archaeological records in South America provide reliable evidence that this continent started to be populated between 15,000 and 13,500 cal yr BP (Bueno et al., 2013; Dillehay, 1999; Meltzer, 1997). Therefore, humans may have arrived in Venezuela around those dates. Modern fires are certainly man-made in the GS (Bilbao et al. 2010).

As a result, it seems unlikely that the paleofires in Fidencio (Figs. 2.5 and 2.6), higher in magnitude than the modern ones (Fig. 2.4), were originated simply from natural sources. Thus, in the case of sporadic human activities since the YD, paleoindians could have contributed to fire ignition, becoming an external and indirect influence on the origin of grassland and its posterior maintenance (Rull et al., 2015b; Rull et al., 2013). Unfortunately, to date there are no archaeological studies in the GS. Therefore, in order to test this human hypothesis, interdisciplinary palaeoecological and archaeological studies should be carried out in the region.

Rull et al. (2013, 2015b) hypothesized that the most likely cause of the origin of grassland-dominated landscape in the GS was the synergy between rapid warming at the end of the YD, fire, drier climate than the present, availability of fuel loads (grasses) and potential human activities. In Fidencio, savanna vegetation existed before the origin of grassland (Figs 2.5 and 2.6). Therefore, the evidence of Fidencio's sequence agrees with the hypotheses formulated by Rull et al. (2013, 2015b). It appears that the aforementioned synergism was strong enough to destabilise the forests, leading the origin of grassland vegetation in Fidencio's area. In order to fully comprehend the ecological process of the origin of open vegetation, it is strongly recommended to add in future studies independent local proxies for temperature and moisture.

2.5.3. Vegetation change at YD-Holocene transition as a potential past analogue for global warming

According to the IPCC's Fifth report, temperature is expected to increase by between 3-6ºC while rainfall is projected to decrease by between 25-50% in northern South America by the end of this century (Magrin et al., 2014; Stocker et al., 2013). Concerning the GS, the region will probably experience a milder temperature increase of between 2-3 ºC. An assessment of threatened ecosystems in South America (SA) by Jarvis et al. (2010) concluded that current grasslands and savannas are being highly threatened due to excessively frequent fires, which will intensify in the future according to climatic models (Stocker et al., 2013).

As explained in the previous section, rapid warming, fire, (natural and/or man-fire) and availability of grasses probably occurred during the Pleistocene-Holocene transition. At present, the GS vegetation is under high fire regime, high regional availability of fuel beds (Bilbao et al., 2010), and the regional climate is warming rapidly. Therefore, the GS environmental setting of the transition to the Holocene shares similarities with the current situation. Based on this fact, it is suggested that the forest replacement by grassland at the YD-Holocene transition could be considered as a potential past analogue of the current and future environmental setting for the GS region.

Neoecological studies suggest that current forests of the GS have low resilience to fire practices (Fölster et al., 2001). Hence, considering three particular conditions: (1) the future scenario of warming and higher occurrence of fires for SA, (2) the current environmental setting of the GS, and (3) the palaeoeocological and neoecological evidence, it is prognosticated that grassland vegetation could expand in the course of this century similarly to what was observed historically. Therefore, the remaining forest patches in the GS would irreversibly reduce. Even though the available evidence is still insufficient to make a conclusive statement, the results shed some light on this topic.

2.6. Conclusions

The Fidencio palynological sequence, recovered from a mid-altitude savanna region, shows the presence of mosaic vegetation with forest patches, *helechales* and savanna during the middle of the YD chron. Vegetation dynamics during this interval were probably driven by temperature, moisture and fire, in close relationship with the regional climate trends. In this sequence, very low pollen counts between 12,725 and 12,385 cal yr BP hindered the analysis of vegetation responses to the YD's abrupt cooling.

The results of Fidencio's sequence agree with the hypotheses proposed previously (Rull et al., 2013, 2015b), which state that the most likely cause of the origin of grassland was the synergy between rapid warming, drier climate than present, fire (natural and/or anthropogenic), and the availability of fuel loads. This multifactorial synergism may have affected the survival of forests, leading the substitution of forest patches to open vegetation (Rull et al., 2013).

The forest replacement by grassland at the YD-Holocene transition could be considered as a potential past analogue of the current and future environmental setting for the GS region. This suggests that grassland vegetation might expand similarly to what was observed historically. Nevertheless, the available evidence is still insufficient to make such a conclusive statement.

2.7. Acknowledgements

I wish to thank to Fidencio Montáñez (owner of the Hato Divina Pastora) for his interest and good will during our work and Sandra Nogué, Nathan Stansell and Broxton Bird for their participation in the fieldwork. I acknowledge Maarten Blaauw for this contribution to improve the age-depth model and Santiago Giralt for his help to improve the sediments description and interpretation

2.8. Funding

This work was supported by the Spanish Ministry of Science and Innovation (projects CGL2006-00974 and CGL2009-07069/BOS to V. Rull), the BBVA Foundation (project BIOCON-08-031 to V. Rull), the Spanish Council for Scientific Research (CSIC, project 200830I258 to V. Rull), and the Foundation for the future of Colombia-COLFUTURO, which provided a scholarship-loan to Tania Ballesteros.

2.9. References

Accatino, F., De Michele, C., 2013. Humid savanna-forest dynamics: A matrix model with vegetation-fire interactions and seasonality. *Ecological Modelling*. 265, 170-179.

Ammann, B., 2000. Biotic responses to rapid climatic changes: Introduction to a multidisciplinary study of the Younger Dryas and minor oscillations on an altitudinal transect in the Swiss Alps. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 159. 191-201.

Beckage, B., Platt, W.J., Gross, L.J., 2009. Vegetation, fire and feedback: a disturbance mediated model of savannas. *The American Naturalist*. 174, 805-818.

Behling, H., 2001. Late Quaternary environmental changes in the Lagoada Curuça region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. *Vegetation History and Archaeobotany*. 10, 175-183.

Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the LGM from El Piñal and Carimagua. *Journal of Paleolimnology*. 21, 461-476.

Bennett, K.D. 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytol*. 132, 155–170.

Benninghoff, W.S., 1962. Calculation of pollen and spore density in sediments by addition of exotic pollen in known quantities. *Pollen et Spores*. 4, 332-333.

Berrío, J.C., H. Wouters, H., Hooghiemstra, H., Carr, A.S. & Boom, A., 2012. Using paleoecological data to define main vegetation dynamics along the savanna-forest ecotone in Colombia: implications for accurate assessment of human impacts. In: R. Myster (ed.), Ecotones between forest and grassland. P. 209-228. Springer, New York.

Berry, P.E., Holst, B.K.,Yatskievych, K., 1995a. *Protium*, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 3, Missouri Bot. Gard. Press, St. Louis, pp. 702-718.

Berry, P.E., Holst, B.K.,Yatskievych, K., 1995b. *Dimorphandra*, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 4, Missouri Bot. Gard. Press, St. Louis, pp. 58-62.

Berry, P.E., Yatskievych, K., Holst, B.K., 1995c. Humiriaceae, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 5, Missouri Bot. Gard. Press, St. Louis, pp. 623-640.

Berry, P.E., Yatskievych, K., Holst, B.K., 1995d. Meliaceae, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 6, Missouri Bot. Gard. Press, St. Louis, pp. 528-549.

Berry, P.E., Yatskievych, K., Holst, B.K., 1995e. *Miconia*, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 6, Missouri Bot. Gard. Press, St. Louis, pp. 387-467.

Berry, P.E., Yatskievych, K., Holst, B.K., 1995f. *Xyris*, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 9, Missouri Bot. Gard. Press, St. Louis, pp. 526-574.

Bilbao, B.A., Leal, A.V., Méndez, C.L., 2010. Indigenous Use of Fire and Forest Loss in Canaima National Park, Venezuela. Assessment of and Tools for Alternative Strategies of Fire Management in Pemón Indigenous Lands. *Hum. Ecol*. 38, 663–673.

Birks,H.J.B., 2012. Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. *International Journal of Biodiversity Science, Ecosystem Services & Management*. 8(4), 292–304.

Blaauw, M., 2010. Methods and code for “classical” age-modelling of radiocarbon sequences. *Quat. Geochronol*. 5, 512–518.

Blackford, J., 2000. Palaeoclimatic records from peat bogs. *Trends in Ecology & Evolution*. 15, 193-198.

Bueno, L., Scmidt, A. & Steele, J., 2013. The Late Pleistocene/Early Holocene archaeological record in Brazil, A geo-referenced database. *Quaternary International.* 301, 74-93.

Burn, M.J., Mayle, F.E., 2008. Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Rev. Palaeobot. Palynol*. 149, 187–201.

Burn, M.J., Mayle, F.E., Killeen, T.J., 2010. Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South America. *Palaeogeogr. Palaeoclimatol. Palaeoecol*. 295, 1–18.

Bush, M.B., De Oliveria, P.E., Colinvaux, D.A, Miller, D.C., Moreno, J.E., 2004. Amazonian palaeoecological histories: one hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 214, 359-393.

Clark, J.S., Lynch, J., Stocks, B.J., Goldammer, J.G., 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. *The Holocene*. 8, 19-29.

Cochrane, M.A., Ryan, K.C., 2009. Fire and fire ecology: Concepts and principles. In: Cochrane MA (eds) Tropial fire ecology: Climate Change, Land Use and Ecosystem Dynamics. Springer, pp. 25-55.

Cole, K., 2009. Vegetation response to early Holocene warming as an analogue for current and future changes. *Conservation Biology*. 24, 29-37

Colinvaux, P.A., Bush, M.B., Steinitz-Kannan, M., Miller, M.C., 1997. Glacial and postglacial pollen records from the Ecuadorian Andes and Amazon. *Quaternary Research*. 48, 69-78.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., 1999. Amazon Pollen Manual and Atlas, Harwood Academic Publishers, Amsterdam.

Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, SH., Brenner, M., Hodell, D.A., Escobar, J., Guilderson, T., 2012.Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews*. 38, 63-75.

Curtis, J.H., Brenner, M., Hodell, D.A., 1999. Climate change in the Lake Valencia Basin, Venezuela, approximately 12,500 yr BP to present. *The Holocene*. 9, 609-619.

Daniau, A.L., Harrison, S.P., Bartlein, P.J., 2010. Fire regimes during the Last

Glacial. *Quaternary Science Review*. 29, 2918-2930.

Dezzeo, N., Chacón, N., Sanoja, E., Picón, G., 2004. Changes in soil properties and vegetation characteristics along a forest-savanna gradient in southern Venezuela. *For. Ecol. Manag*. 200, 183–193.

Dillehay, T.D., 1999. The late Pleistocene cultures of South America. *Evol. Anthropol. Issues News Rev*. 7, 206–216.

Faegri, K., Kaland, P.E., Krzywinski, K., 1989.Textbook of pollen analysis. IV edition. Blackburn, New Jersey.

Fölster, H., 1986. Forest-savanna dynamics and desertification process in the Gran Sabana. *Interciencia*. 11, 311-316.

Fölster, H., Dezzeo, N., Priess, J., 2001. Soil–vegetation relationship in base-deficient premontane moist forest–savanna mosaics of the Venezuelan Guayana. *Geoderma*. 104, 95–113.

Fonseca, M.B., de L. Carolino, M.M.S.S., Dias, T., Cruz, C., França, M.G.C., 2013. Early growth of Brazilian tree *Dimorphandra wilsonii* is also threatened by African grass *Urochloa decumbens*. *J. Plant Interact*. 9(1), 92-99.

Gómez, E., Picón, G., Bilbao, B., 2000. Los incendios forestales en Iberoamérica. Caso Venezuela, in: Vélez-Muñoz, R. (Eds.), La defensa contra incendios forestales, Fundmentos y experiencias., McGraw-Hill, Madrid.

Haugh, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward Migration of the Intertropical Convergence Zone Through the Holocene. *Science*. 293, 1304-1308.

Hernández, L., 1999. Fisionomía y estructura de bosques submesotérmicos y mesotérmicos, in: Hernández, L. (Eds.), Ecología de la altiplanicie de la Gran Sabana(Guayana Venezolana) II. Estructura, diversidad, crecimiento y adaptación en bosques de las subcuencas de los ríos Yuruaní y Alto Kukenán.,Scientia Guayanae,Volume 9. Ediciones Tamandúa, Caracas, pp. 5–34.

Herrera, L.F., Urrego, L.E., 1996. Atlas de polen de plantas útiles y cultivadas de la Amazonia colombiana, Tropenbos Colombia, Colombia.

Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F., Aristegui, D., Buck, D.G., Guilderson, T.P., Rosenmeier, M.F., Schnurrenberger, D.W., 2005. Climate change in lowland Central America during the late deglacial and early Holocene. *Journal of Quaternary Science*. 20(4), 363-376.

Huber, O., 1986. La vegetación de la cuenca del río Caroní. *Interciencia*.

11(6), 301–310

Huber, O., 1995a. Geographical and physical features, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 1. Introduction. Missouri Bot. Gard. Press, St. Louis, pp. 1-62.

Huber, O., 1995b. Vegetation, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 1. Introduction. Missouri Bot. Gard. Press, St. Louis, pp.97-160.

Huber, O., García, P., 2011. The Venezuelan Guayana region and the Study areas: Geo-ecological characteristics, In: Introduction. Missouri Bot. Gard. Press, St. Louis, pp 97-160.

Islebe, G.A., Hooghiemstra, H., Van der Borg, K., 1995. A cooling event during he Younger Dryas Chron in Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 117, 73-80

Jackson, S.T., Overpeck, J.T., 2000. Reponses of plant populations and communities to enviromental changes of the late Quaternary. *Palaeobiolog*y. 26(suppl.), 194-220.

Jarvis, A., Touval, J.L., Schmitz, M.C., Sotomayor, L., Hyman, G.G., 2010. Assessment of threats to ecosystems in South America. *Journal for Nature Conservation*. 18(3), 180-188.

Lea, D.W., Pak, D.K., Peterson, L.C., Hughen, K.A., 2003. Synchroneity of tropical and high-latitude Atlantic temperatures over the last Glacial Termination. *Science*. 301, 1361-1364.

Leal, A.V., 2010. Historia holocena de la vegetación y el fuego en bordes sabana/bosque y turberas de la Gran Sabana Venezolana. PhD Thesis, Sartenejas, Venezuela.

Leal, A., Berrío, J.C., Raimúndez, E., Bilbao, B., 2011. A pollen atlas of premontane woody and herbaceous communities from the upland savannas of Guayana, Venezuela. *Palynology*. 35, 226–266.

Leal, A., Bilbao, B., Bibiana, B., Berrío, J.C., 2013. A Contribution to Pollen Rain Characterization in Forest-Savanna Mosaics of the Venezuelan Guayana and Its Use in Vegetation Reconstructions from Sedimentary Records. *Am. J. Plant Sci*. 04, 33–52.

Ledru, M.P., Cordeiro, R.C., Landim, J.M., Martin, L., Mourguiart, P., Sifeddine, A., Turcq, B., 2001. Late-glacial cooling in Amazonia inferred from pollen at Lagoa Caçó, Northern Brazil. *Quaternary Research*. 55, 47-56.

Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A., Bond, W.J., 2011. Deciphering the distribution of the savanna biome. *New Phytologist*. 191, 197-209.

Leyden, B.W., 1985. Lake Quaternary aridity and Holocene moisture fluctuations in Lake Valencia Basin. *Ecology*. 66(4), 1279-1295.

Liu, K-B., Colinvaux, P.A., 1985. Forest changes in the Amazon Basin during the last glacial maximum. *Nature*. 318, 556-557.

Magrin, G.O., J.A. Marengo, J.-P. Boulanger, M.S. Buckeridge, E. Castellanos, G. Poveda, F.R. Scarano, and S. Vicuña, 2014: Central and South America. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1499-1566.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-Garćia, S., Hooghiemstra, H., Ledru, M.-P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Rev Palaeobot Palynol*. 121, 1–75.

McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of Human Evolution*. 39, 453-563.

Meltzer, D.J., 1997. Anthropology: Monte Verde and the Pleistocene Peopling of the Americas. *Science*. 276, 754–755.

Montoya, E., Rull, V., 2011. Gran Sabana fires (SE Venezuela): a paleoecological perspective. *Quat. Sci. Rev*. 30, 3430–3444.

Montoya, E., Rull, V., Stansell, N.D., Bird, B.W., Nogué, S., Vegas-vilarrúbia, T., Abbott, M.B., Díaz, W.A., 2011. Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron.*J. Quat. Sci*. 26, 207–218.

Muniz da Silva, D., Batalha, M.A., 2008. Soil-vegetation relatioships in cerrados under different fire frequencies. *Plant Soil*. 311, 87-96.

Murphy, B.P., Bowman, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna?. *Ecology letter*. 15, 748-758.

NRC (National Research Council), 2013. Abrupt impacts on climate change: Anticipating Responses. The National Academy Press, Washington.

NRC (National Research Council), 2002.Abrupt Climate Change: Inevitable surprises.

The National Academy Press, Washington.

Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.-L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E., Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. *J. Geophys. Res*. 111(D6), 27.

Rodbell, D.T., Smith, J.A, Mark, B.G., 2009. Glaciation in the Andes during the late Glacial and Holocene. *Quaternart Science Reviews*. 28, 2165-2212

Roubik, D.W., Moreno, J.E., 1991. Pollen and Spores of Barro Colorado Island, Missouri Botanical Garden, Missouri.

Rull, V., 1987. A note on pollen counting in palaeoecology. *Pollen et Spores*. 29, 471-480.

Rull, V., 1999. A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela. *J. Quat. Sc*i. 14, 137–152.

Rull, V., 2003. An illustrated key for the identification of pollen from Pantepui and the Gran Sabana (Eastern Venezuela Guayana). *Palynology*. 27, 99–133.

Rull, V., Abbott, M., Polissar, P.J., Wolfer, A, P., Bezada, M., Bradley, R.S., 2005. 15,000-yr pollen record of vegetation change in the high altitude tropical Andes at Laguna Verde Alta, Venezuela.*Quaternary Research*. 64, 308-317.

Rull, V., 2007. Holocene global warming and the origin of the Neotropical Gran Sabana in the Venezuelan Guayana. *J. Biogeogr*. 34, 279–288.

Rull, V., 2009. On the use of palaeoecological evidence to assess the role of humans in the origin of the Gran Sabana (Venezuela). *Human Ecology*. 37, 783-785.

Rull, V., Stansell, N.D., Montoya, E., Bezada, M., Abbott, M., 2010. Palynological signal of the Younger Dryas in the tropical Venezuelan Andes.*Quaternary Science Reviews*. 29, 3045-3056.

Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T., Safont, E., 2013. Ecological palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. *Perspect. Plant Ecol. Evol. Syst*. 15, 338–359.

Rull, V., Vegas-Vilarrúbia, T. & Montoya, E., 2015a. Neotropical vegetation responses to Younger Dryas climates as analogs for future climate change scenarios and lessons for conservation. *Quaternary Science Reviews*. doi, 713 10.1016/j.quascirev.2015.03.003

Rull, V., Montoya, E., Vegas- Vilarrúbia, T., Ballesteros, T., 2015b. New insights on palaeofires and savannisation in northern South America. *Quaternary Science Reviews.* 122,158-165.

Salgado-Labouriau, M.L., 1997. Late Quaternary paleoclimate in the savannas of South America. *Journal of Quaternary Science*. 12(5),371-379.

Salgado-Labouriau, M.L., Barberi, M., Ferraz-Vicentini, K.R., Parizzi, M.G., 1998. A dry climatic event during the Late Quaternary of tropical Brazil. *Review of Palaeobotany and Palynology*. 99,115-129.

Stansell, N.D., Abbott, M.B., Rull, V., Rodbell, D.T., Bezada, M., Montoya, E., 2010. Abrupt Younger Dryas cooling in the northern tropics recorded in lake sediments from the Venezuelan Andes. *Earth and Planetary Science Letter*. 293, 154-163

Stocker, T.F., Quin, D., Plattner, G.K., Tignor, M.M.B., Allen, S.K., Boschung, J., Nailes, A., Xia, Y., Bez, V., Midgley, P.M., 2013. Climate change 2013. The Physical Science Basis, workinh group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen et spores*. 13, 615-621.

Thompson, L.G., Davis, M.E., Thompson, E.M., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.N., Mikhalenko, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J., Francou, B., 1998. A 25,000-year tropical climate history from Bolivian ice cores. *Science*. 282, 1858-1864.

Van der Hammen, T., Hooghiemstra, H., 1995. The Abra Stadial, a Younger Dryas equivalent in Colombia. *Quaternary Sciene Reviews*. 14, 841-851

Van't Veer,R., Islebe, G.A., Hooghiemstra, H., 2000.Climatic change during the Younger Dryas chron in norhtern South America: a test of the evidence. *Quaternary Science Reviews*. 19, 1821-1835.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E., 2011. Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. *Quat. Sci. Rev*. 30, 2361–2388.

Willis, K.J., Bennett, K.D., Burrough, S.L., Macias-Fauria, M., Tovar, C., 2013. Determining the response of African biota to climate change: using the past to model the future. *Philosophical Transactions of the Royal Society B.* 368, 20120491

Wright, H.E., Mann, D.H., Glaser, P.H., 1984. Piston corers for peat and lake sediments. *Ecology.* 65, 657–659.

Chapter III:

Long-term evaluation of vegetation resilience and regime shifts in a savanna region (the Gran Sabana, SE Venezuela)

3.0. Abstract

Evaluation of regime shifts and ecosystem's resilience is crucial to achieve suitable ecosystem management plans. This approach needs long-term observations of ecosystems, which constitutes a piece of scarcely explored field of research. In this chapter, the Gran Sabana was considered as an appropriate case of study to assess regime shifts and resilience, due to its long history of vegetation changes under fire incidence. Two palaeoecological records were analysed: Lake Encantada (chapter 1, 8700 cal yr BP-the present) and Fidencio peat bog (chapter 2, 12,385-9520 cal yr BP). The regime shifts were evaluated in terms of variations of the tree cover within savanna, based on palynological analysis. The main results suggest that vegetation in the Lake Encantada's basin was resilient during specific time intervals to different levels of fire disturbance on a centennial timescale. It is proposed that the interplay between particular abiotic (medium to high levels of available moisture, selective burning) and biotic (medium-high degree of diversity, high Rates of Recovery -RRs-) factors could have contributed to the resilience of past forests. On the other hand, the interplay of a number of factors such as repetitive fires, low available moisture, decrease in diversity and low RRs, probably contributed to loss of resilience. Concerning Fidencio's sequence, the evidence indicates that forests of the interval studied were not resilient. The process of regime shift was characterised by a remarkable decreasing trend of diversity, which could have played an important role in reducing forest resilience. Loss of resilience in both locations studied could be considered as a phenomenon highly associated with expansion and domination of grasses.

3.1. Introduction

The study of ecological patterns and processes in the long-term, rather than palaeoenvironmental reconstructions, is the core of the so-called ecological palaeoecology (Birks, 2012; Rull, 2010, 2012, Seddon, 2014a). Conservationists, managers and restorers (represented by scholars, policy makers, stakeholders and society) have begun to acknowledge the importance of long-term ecological studies in developing conservation and management strategies in order to face climate change and achieve ecosystem sustainability (Birks, 2012; Froyd and Willis, 2008; Gillson and Marchant, 2014; Vegas-Vilarrúbia et al., 2011). Several authors coincide in some topics in which ecological palaeoecology can be used in developing conservation/management strategies, related to: **(1)** determination of baselines and natural ecosystem variability; **(2)** climate change; **(3)** cultural landscapes; **(4)** resilience and ecological thresholds; **(5)** biological invasions; and **(6)** management of novel ecosystems (Froyd and Willis, 2008; Willis et al., 2007a,b; Willis et al., 2010). In chapters 1 and 2, some aspects of the topics 1, 2 and 3 were evaluated. The knowledge regarding resilience and threshold responses (topic 4) is becoming of great international relevance for understanding biotic responses to environmental disturbances and thereby improving management decisions (Gil-Romera et al., 2010; Gillson and Ekblom, 2009). Acknowledging the importance of this topic, this chapter gives a step further and attempts to evaluate resilience and threshold responses in a long timescale. Definitions and applications of these concepts in ecosystem management are explained below.

First of all, it is worth remembering that an ecosystem state is as a quasi-stable ecological condition in which ecosystem properties/conditions (e.g., woody vegetation abundance) fluctuate within certain boundaries (Gillson and Ekblom, 2009). Resilience has been defined in the ecological literature in two different ways: **Engineering resilience** is a measure of the rate at which an ecosystem approaches steady state after a perturbation, that is, the velocity of return to the pre-disturbance state (Folke et al., 2004; Groffman et al., 2006; Gunderson. 2000). This concept is referred by some authors as *recovery* (Standish et al., 2014). **Ecological resilience** (also called *ecological robustness* or *resistance*) is the capacity of a system to absorb disturbance and reorganise without changing to another state, i.e., retaining the same function, structure, identity, and feedbacks (Holling, 1973; Walker et al. 2004). The concept of resilience therefore encompasses *recovery* and *resistance*. Several biodiversity elements (e.g., response diversity, functional redundancy, species richness) appear to enhance resilience (Elmqvist et al., 2003; Folke et al., 2004; Mori et al., 2013; Sasaki et al., 2015). This ecological concept considers the existence of multi stable states and non-linear responses. In this sense, resilience is not considered static; instead, it is dynamic and governed mainly by a combination of two factors: disturbance itself (amount, intensity, spatial-temporal scales) and traits of ecosystems at the time of disturbance. Thus, an ecosystem can have high resilience at one moment and low resilience at another, or be resilient to some disturbances but not to others. Hence, the study of resilience is of great significance to ecosystem management because it helps to predict biotic responses to different disturbances and infer feedback processes (Standish et al., 2014). The knowledge obtained of factors that promote decrease or increase in resilience is valuable information to consider when designing management strategies (resilience-based management, Sasaki et al., 2015).

Ecological thresholds are tipping-points (abrupt change at a specific time) or tipping-zones (gradual shift or transition) at which an ecosystem changes from one ecosystem state to another alternative one (Huggett, 2005). This ecological change to alternative states is known as **regime shift** (Holling, 1973), which implies changes in function, ecological properties and services of an ecosystem (Folke et al., 2004; Holling, 1973; Scheffer et al., 2001). In order to forestall undesirable regime shifts (e.g., from oligotrophic to turbid lake conditions), the identification of ecological thresholds is of particular interest to managers and policy makers because of their potential to define limits of acceptable change an ecosystem can withstand (i.e., within natural variability). In doing so, it is fundamental to understand first the ecological processes of threshold crossing.

Resilience and regime shifts are notoriously difficult to identify and assess in nature, especially when the timescales studied are too short (decades, neo-ecological time) to cover the complete range of ecosystem variability (Biggs et al., 2009). Therefore, short observations of natural systems provide only a snapshot and may give a misleading impression of the ecological conditions or trends (Gillson and Marchant, 2014). For instance, the use of biodiversity measurements has largely been limited to short-term studies (Sasaki et al., 2015); such limitation restricts the understanding of the potential contribution of diversity to resilience. Despite this awareness, in ecological studies resilience and threshold responses continue being mostly evaluated by manipulation experiments (short-term) and mathematical models (Biggs et al., 2009, Dakos et al., 2015; Dearing et al., 2014; Hirota et al., 2011; Veraart et al., 2012; Wang et al., 2012). In the case of terrestrial ecosystems, experimental tests of thresholds responses associated with disturbances are particularly rare because most of the organisms more commonly studied are of slow growth and long-lived (e.g., forest plant taxa), rendering logistic limitations (Standish et al., 2014). Hence, resilience and regime shifts of vegetation are more likely to be observed over timescales of centuries to millennia (Gillson and Marchant, 2014).

Even though resilience and threshold responses are key areas in which palaeoecological archives can contribute to conservation/management goals (Seddon et al., 2014a; Willis et al., 2010), there are a few palaeoecological studies about these topics (Bhagwat et al., 2012; Blarquez and Carcaillet, 2010; Cole et al., 2015; Gil-Romera et al., 2010; Seddon et al., 2011, 2014a). Particularly in the case of savannas, despite the existence of several long-term ecological studies, few have evaluated resilience and regime shifts, and are restricted to African savannas (Gil-Romera et al., 2010; Gillson and Ekblom, 2009). The paucity of research on these topics is probably the main reason why management plans in savannas are based on computational modelling and rangeland ecosystems (Calabrese et al., 2011). Therefore, long-term studies of resilience and regime shifts in savannas located in other geographical regions (e.g., South America) can provide additional scientific basis for their ecological management. Savanna ecosystems are characterised by the coexistence of trees and herbs (Accatino et al., 2013). Therefore, variations in the proportions of trees within the grass layer allow the identification of several sub-states of savanna. The knowledge of how tree cover changed in the past might help to improve present management strategies (Gillson and Duffin, 2007). In addition, to perform palaeoecological studies in savannas that can contribute to their sustainable management, two questions must be answered: (1) what makes savannas more or less resilient to disturbances? And (2) what are the processes of regime shifts that characterise the transition from one sub-state of savanna to another one?

This chapter evaluates resilience and regime shifts in savanna areas of the Gran Sabana region (GS; Fig. 3.1a). The abruptness observed in some forest-savanna turnovers (Montoya et al., 2011a,b,c; Rull 2007, 1999, 1992) suggests the existence of several thresholds in southern GS for the last ~13,000 yr (Rull et al., 2013), which have driven a long-term savannisation process in the region (Rull et al., 2013, 2015). During the 13,000-year period, the GS has been mostly under strong fire disturbance (Chapters 1 and 2; Rull et al., 2013; Montoya and Rull, 2011). Thus far, two palaeoecological studies have mentioned the degree of resilience in the GS, specifically forest resilience to fire (chapter 1; Rull, 1992). Chapter 1 suggests that forest patches were resilient to burning during middle Holocene. Rull (1992) proposed that after the removal of forests around middle-late Holocene, the small forests resulting had low resilience to fires. Several studies have analysed the relationships between vegetation and climate (Montoya et al., 2011a,b,c; Rull 2007, 1999, 1992), but how climate has influenced resilience has not been studied. Therefore, the evaluation of resilience and regime shifts are areas of research that promise useful information to be incorporated into conservation and management plans of the GS. Here, the evaluation of resilience and regime shifts was performed using the two palaeoecological sequences previously analysed in this thesis: Lake Encantada (chapter 1, 8700 cal yr BP-the present) and Fidencio peat bog (chapter 2, 12,385-9520 cal yr BP) (Fig. 3.1b).

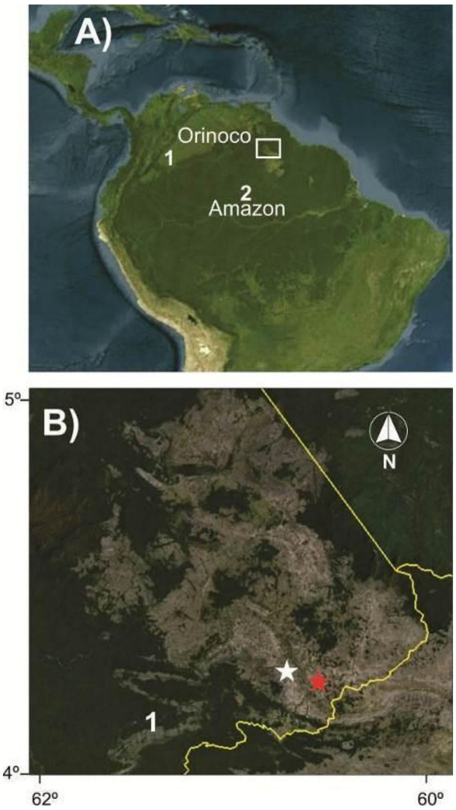


Figure 3.1. A) A modified image of Tropical America, from Google Earth. The location of the Gran Sabana in Northern South America is delimited by the white square. Numbers indicate the sites with palaeoecological information mentioned in the text. Lowlands: 1—*Llanos Orientales* of Colombia; 2—Northern Amazonia. **B)** A modified image of The Gran Sabana, from Google Earth (accessed in June 2015). The stars indicate the locations studied: Lake Encantada with a white star and Fidencio peat bog with a red star. Number indicates the sites with paleoecological information mentioned in the text: 1—El Paují.

3.2. Case of study: The Gran Sabana region

3.2.1. Environmental setting

The Gran Sabana (GS) is located in southeastern Venezuela between Orinoco and Amazon basins (Huber and Febres, 2000) (Fig. 3.1a). This region is a high, undulating erosion surface that forms a plateau inclined from north (1350 m a.s.l) to south (700 m a.s.l) known as midlands or uplands (Huber and García, 2011). The climate of southern GS has been described as submesothermic tropophilous, with average annual temperature of 18-22ºC and precipitation of 1600–2000 mm/yr (Huber, 1995). In this region of ~10,820 km^2, approximately 60% of the area is covered by grasslands (Huber and Febres, 2000). The remaining area is comprised of forests, shrublands, secondary woody communities and *helechales* (dense fern communities), forming mosaics with the herbaceous vegetation. Soils are mostly savanna oxisols, which are highly weathered, and poor in nutrients (especially P, N and Ca), highly acidic (pH 4-5), with very low cation exchange capacity and reduced water retention (Dezzeo et al., 2004; Fölster et al., 2001). Fire currently plays a key role in vegetation dynamics, with an alarming frequency between 5000 and 10,000 fires per year (Gómez et al., 2000). The vast majority of fires are of anthropogenic origin (Bilbao et al., 2010), ignited by the local indigenous inhabitants. Fires in grassland-forest borders are scarcely controlled and cause major concern about further grassland expansion. More detailed description of environmental setting is provided in the Introduction of this thesis.

3.2.2. *Resilience of current woody communities*

Current forests patches are at high risk of degradation and disappearance by repetitive burning. Neoecological studies suggest that GS forests have low resilience to fire and the soil status is an influential factor of this phenomenon (Fölster et al., 2001). Modern fires are usually of low height, smouldering the organic surface layer. Due to the concentration of fine roots of trees in this layer, the tree mortality because of fires is near 100% (Fölster et al., 2001), causing slow regrowth and preventing the storage of nutrients in the system (Fölster et al., 2001). This slow process can lead to a progressive decrease of the forest extent, which is replaced by annual herbs and thus a more open savanna landscape. This process is coupled with increased soil degradation in terms of reaching critical points of water stress, Al-Fe toxicity and nutrient content. Therefore, current savannisation seems to be a synergistic process in which anthropogenic (man-made fires) and edaphic drivers interact, providing very low resilience to forest communities. Hence, in order to prevent conversion of the remaining forest patches into grassland, it seems urgent to implement an appropriate management plan that averts further loss of resilience.

3.2.3. Palaeoecological evidence

Recently, Rull et al. (2013) reviewed the available palaeoecological evidence in southern GS spanning the last 13,000 yr. The authors concluded that several savanna-forest turnovers have occurred in this region of the GS. Climate and fire have not played the same role as forcing factors along the temporal scale studied, displaying different importance in specific intervals. During the Late Glacial, woody communities were replaced by open savanna, probably under fire and warming influences in interplay with other environmental factors (chapter 2; Montoya et al., 2011a; Rull, 2007; Rull et al., 2015, 2013). Rainforest patches extent notably increased at expenses of savanna areas during the middle Holocene (~7000-5000 cal yr BP), despite recurrent fires (Chapter 1; Montoya et al., 2009, 2011b). However, the fires were of less intensity/frequency than during the Late Glacial (Montoya et al., 2011a,b; Rull et al., 2013). In this case, wet climate likely promoted this vegetation change (Montoya et al., 2011a). Between 5000 and 4000 cal yr BP, a clear shift to open vegetation is likely to have occurred (Chapter 1; Montoya et al., 2011b; Rull, 1992). The areas near El Paují (Fig. 3.1) and Lake Encantada (Chapter 1) were therefore dominated by savanna-forest mosaic. This vegetation change took place under higher moisture availability, so climatic explanation of this vegetation shift is unlikely. Forest burning appears to be the main cause of the observed forest retraction (chapter 1; Montoya et al., 2011b). However, in other locations this vegetation shift has been explained in terms of temporal droughts (Rull, 1992). Remarkable savanna expansion that resulted in the establishment of treeless savanna occurred in most locations approximately 2000 yr ago, driven probably by increased fire occurrence (Montoya et al., 201b,c; Rull, 1999, 1992). The drastic reduction of forests was attributed to their low resilience (Rull, 1992). Edaphic factors may have promoted this phenomenon. In some locations, the aforementioned vegetation opening was accompanied by the establishment of *morichales*, probably also related to increased fire occurrence (chapter 1; Montoya et al., 2011c). The role of climate seems to have been secondary during the last two millennia (Rull et al., 2013).

3.3. Methodology

3.3.1. Coring sites

Lake Encantada (core PATAM4C 07)

The study site (4º 42’ 37.44” N - 61º 05’ 03.29” W; 857 m elevation) is located within the private farm called “Hato Santa Teresa” (Fig. 3.1b). The lake is surrounded currently by grassland (also called treeless savanna) with scattered *morichale*s. The core (PATAM4C 07; 2.13 m long) was obtained in the deepest part of the lake (2.6 m water depth) using a modified Livingstone squared-rod piston core (Wright et al., 1984). The sequence encompasses most of the Holocene (~9700 cal yr-the present). However, the palaeoecological analysis was focused on the last 8700 yr because of the absence of biological proxies prior to this time (bottom of the sequence; chapter 1). More information about the paleoecological study and methods can be found in chapter 1.

Fidencio peat bog (core PATAM3A 07)

The study site (4º40‘N and 61º00’W; 860 m elevation) is located within the farm called “Hato Divina Pastora”. The site is characterised currently by an extended grassland. The sequence studied (PATAM3A 07; 3.21 m long) was extracted with a Livingstone squared-rod piston (Wright, 1984) from the deepest part of the peat bog. The age of core comprises the last 12,725 cal yr BP, but the palaeoecological analysis was focused on the late Glacial, from 12,385 to 9520 cal yr BP. Before 12,385 cal yr BP (bottom of the core) very low counts of palynomorphs likely due in part to preservation problems prevented us from making reliable ecological interpretations (chapter 2). More information about the paleoecological study and methods are included in chapter 2.

3.3.2. Paleoecological methodology

It is worth noting that the two locations evaluated have had savanna vegetation in their background, even when forest patches were extensive (chapters 1 and 2). Therefore, evaluation of regime shifts corresponds to variations in the proportion of trees to herbs that led different sub-states of savanna. In doing so, I implemented two complementary approaches. Firstly, pollen counts were used to calculate the woody/non-woody pollen ratio (WP/NWP) after classifying the taxa into woody (trees and shrubs) and non-woody (herbs and sedges) types. This ratio is indicative of vegetation cover (Bhagwat et al, 2012) and can be used to differentiate between forest (dominance of tree cover), savanna (co-dominance of woody and non-woody cover) and grassland (dominance of herbaceous cover). In addition to the WP/NWP ratio, the pollen sum that reports pollen percentages of trees (arboreal pollen, hereafter AP%), shrubs and grasses was included. Because Cyperaceae (sedges) are comprised of terrestrial, semi-aquatic and aquatic plants in the GS, this family was excluded from the pollen sum, and their percentage values were shown separately.

The basins evaluated are relatively small (<50 m diameter, chapters 1 and 2); hence, it was expected that both basins represent local and extra local histories of vegetation and fires. As it was explained in chapter 1, presence of wind-transported pollen from tree taxa (e.g. Urticales) might have been sourced extra-locally from neighbouring forests.

A criterion widely used to recognise regime shifts is an *abrupt qualitative change* in the state of an ecosystem (Biggs et al., 2009; Dakos et al., 2015; Folke et al., 2004; Hirota et al., 2011). In palaeoecological studies, regime shifts are manifested as *jumps* in the palynological sequences (Vegas-Villarrúbia et al., 2011). In this study, jumps in the AP% and WP/NWP of Encantada and Fidencio pollen diagrams were used as indicative of a noticeable shift in the level of tree cover, which suggests change towards alternative sub-states of savanna (regime shift, e.g., from forest-savanna mosaic to open savanna with forest patches). Savannas can be classified by AP%. The numerical criteria used here to define the sub-states of savanna are found in Table 3.1, based on surface pollen assemblages of the GS (modern samples; Leal et al., 2013; Rull, 1999). The identification of sub-states of savanna along the sequence using the criteria exposed in Table 3.1 allowed confirming the visual examination of the jumps in the palynological records.

Vegetation type	**AP%**
Open savanna with small and scattered forest patches (or grassland)	<20%
Savanna-forest mosaic (or open savanna with forest patches)	21-35%
Forest-savanna mosaic (forest interspersed within savanna)	36-55%
Dense forest patches within savanna	56-70%

Table 3.1. Savannas classification based on AP% (arboreal pollen %). Modified from Leal et al. (2013) and Rull (1999).

Algae remains (proxy used to infer changes in available moisture) and charcoal particles (proxy of fire occurrence) were used as environmental factors, which were represented by concentration values (units*cm^{-3}).

3.3.3. Ecological parameters

Pollen diversity was represented using the Shannon-Wiener index, species richness and species evenness. The calculation of diversity indices were performed using R software (http://www.r-project.org).

The Shannon-Wiener Index (*H'*) takes into accounts both abundance and evenness of species present in each sample (Margalef, 1957). For a given number of taxa, the value of a diversity index is maximised when all taxa are similarly abundant.

Formula 1: Shannon-Wiener Index (*H'*)

$$H' = \sum_{i=1}^{S} pi \ln pi$$

Where *pi* is the proportion of each taxa belonging to the i^{th} type; *S* quantifies the total number of species found in the community.

Species richness can be simply assessed as a count of species in a given community. For the purpose of this study, palynological richness was estimated as the total number of taxa present in a community and was calculated as the total number of pollen taxa within a sample. Due to the variances in pollen production and diagenetic processes, the pollen assemblage does not always accurately reflect the richness of the parent vegetation (Bush, 1995; Goring et al., 2013; Odgaard, 2001). For example, Poaceae has high pollen production, is wind-borne (Brown et al., 2007), and is well represented stratigraphically in both sequences (chapters 1 and 2). Consequently, Poaceae might mask rare taxa. Therefore, in order to prevent a bias in favour of abundant pollen taxa that underestimate those of low production/preservation and/or animal dispersal, it was considered more appropriate the use of a richness metric that standardises the taxa abundances. In doing so, the Chao-1 index (S_1) was utilised (Chao, 1984; Gotelli and Colwell, 2011).

Formula 2: Chao-1 Index (S_1)

$$S_1 = S_{obs} + \frac{F1^2}{2F_2}$$

Where S_{obs} is the number of species in a palynological sample; F_1 is the number of rare taxa (i.e. singletons, the number of taxa with only a single occurrence in the sample) and F_2 is the number of species with more than a single occurrence in the sample. If a sample contains many singletons, it is likely that more undetected rare taxa exist, and the Chao-1 therefore will estimate greater species richness.

Species evenness refers to how close in numbers the individuals of the species are in an ecological community, and therefore, it is a measure of how similar the community is numerically (Margalef, 1957; Mulder et al., 2004). In palynological studies, evenness describes the distribution of pollen taxa within the pollen assemblage (Keen et al., 2014). In this sense, an assemblage (i.e., palynological sample) with a dominant taxon or few dominant taxa (high number of pollen grains of the same type) shows low evenness, whereas an assemblage or pollen pool without a clear dominant taxon (pollen grains similarly/equally distributed amongst all taxa) represents high evenness (Smith and Wilson, 1996). Evenness was calculated using the Pielou's evenness index (J; Pielou, 1966):

Formula 3: Pielou's evenness index (J)

$$J = \frac{H'}{H'\max} = \frac{H'}{\ln S}$$

Where S represents the total number of taxa found in the community, *H'* is the number derived from the Shannon diversity index and *H'max* is the maximum value of *H'*, equal:

Formula 4: Maximum value of *H'*

$$H'\max = -\sum_{i=1}^{S} \frac{1}{S} \ln\frac{1}{S} = \ln S$$

Pielou's evenness index (J) is constrained between 0 and 1. The theoretical maximum value for J occurs if all species in the sample are equally abundant.

3.3.4. Data Analysis

Linear regression analyses were performed to evaluate the relationships between indicators of vegetation cover (WP/NWP and AP%) and diversity elements (*H'*, S_1, J) spanning the entire periods. Variables were square-root or log10 transformed to fulfil the assumptions of regression analysis.

Vegetation history of the GS informs about several vegetation turnovers in favour of savanna expansion at expenses of forest patches (Rull et al., 2013). Therefore, it seemed appropriate to conduct an analysis of forests recovery to complement the analysis of resilience. It has been suggested from mathematical models that the magnitude of recovery rates could be a robust indicator of the degree of resilience in different ecosystems (Dakos et al., 2012; Veraart et al., 2012).

Recently Cole et al. (2014) introduced the calculation of "Rate of Recovery" (RR), which constitutes a novel approach to analyse long-term trends in tropical forests recovery after disturbances, using fossil palynological data. According to these authors, forest recovery is described as the maximum increase in the percentage of forest pollen displayed in the pollen sum after a decline, before a stabilizing point or further decline. RRs are the percentages of forest (including trees and shrubs) recovered after disturbance in relation to their pre-disturbance level, in which time elapsed during the recovery is considered. Therefore, units of RRs are % recovery of forest taxa/year. The extension of forests pre-disturbance (Fpre), at-disturbance (Fmin) and post-disturbance (Fmax), expressed in %, and the period of recovery (Fmin-Fmax), expressed in years, are considered in the estimation of RR. Table 3.2 shows the calculation method of Cole et al. (2014).The authors defined disturbance (regardless the disturbance source) as events resulting in a loss of pollen of woody taxa, and include both catastrophic disturbances (>90% decline), and small perturbations (<10% decline), the latter excluding regime shifts. Here, RRs were calculated on all events of decline in percentage of forest taxa and its posterior recovery, observed from palynological results detailed in Chapters 1 and 2.

Variable	Description	Notation
Recovery Rate (% recovery/year)	Rate of increase in forest abundance relative to degree of disturbance-induced changes, that is, % increase in forest pollen abundance per year in relation to pre-disturbance level	**RR** $=(((F_{MAX}-F_{MIN})/(F_{PRE}-F_{MIN}))*100)/T_{REC}$
Forest abundance maximum pre-disturbance (%)	Percentage of forest pollen at maximum point pre-decline (that is, pre-disturbance forest pollen percentage)	$\mathbf{F_{PRE}}$
Forest abundance minimum at disturbance (%)	Percentage of forest pollen at minimum point during disturbance event	$\mathbf{F_{MIN}}$
Forest abundance at maximum recovery (%)	Percentage of forest pollen at point of maximum recovery (before a stablizing point or further decline)	$\mathbf{F_{MAX}}$
Time period of recovery (years)	Time period from maximum reduction to maximum recovery (from F_{MIN} to F_{MAX})	$\mathbf{T_{REC}}$

Table 3.2. Description or rate of recovery calculation from Cole et al . (2014)

3.4. Results and interpretations

3.4.1. Lake Encantada record (8700 cal yr BP-the present)

3.4.1.1. Regime shifts

The palynological sequence shows several jumps in AP% and WP/NWP (Fig. 3.2), which indicate that a few regime shifts could have occurred during the period studied. In this sense, values of these two parameters suggest that four regime shifts probably occurred along the sequence, accompanied by changes in algae, charcoal particles and in diversity parameters.

It is worth remembering that tree pollen taxa and charcoal particles were probably extra-locally sourced along this sequence (chapter 1), mainly between 173 and 32 cm (~8700 and 1800 cal yr BP).

Regime shift N°1 (142-133 cm; ~7720-7320 cal yr BP). Between 173 and 144 cm (~8700-7750 cal yr BP), the values of AP% are <20% (see pollen sum, Fig. 3.2), indicating vegetation of open savanna with small and scattered forest patches (or grassland, Table 3.1). The WP/NWP ratio is ~0.25. Subsequently, between 142 and 133 cm (~7720-7320 cal yr BP), the values of AP% and WP/NWP increase progressively to reach values of ~30% and 0.78 respectively (Fig. 3.2), which suggest a regime shift towards savanna-forest mosaic (Table 3.1).

Concerning RRs prior to the occurrence of the regime shift (between 163 and 153 cm; ~8243-8077 cal yr BP), the small forest patches retract and recover at a rate of 0.57%/yr (event 1, Tabla 3.3; Fig 3.2). The forests retract again at 143 cm (Fmin, event 2, Table 3.3; Fig. 3.2). During the interval of the regime shift, the forests recover at a rate of 1.49%/yr (event 2), while charcoal particles decrease (Fig. 3.2). The values of S_1 are roughly stable (Fig. 3.2). On the contrary, J increases from 0.34 to 0.62 (Fig. 3.2). *H*' follows the same increasing trend as J; however, less pronounced.

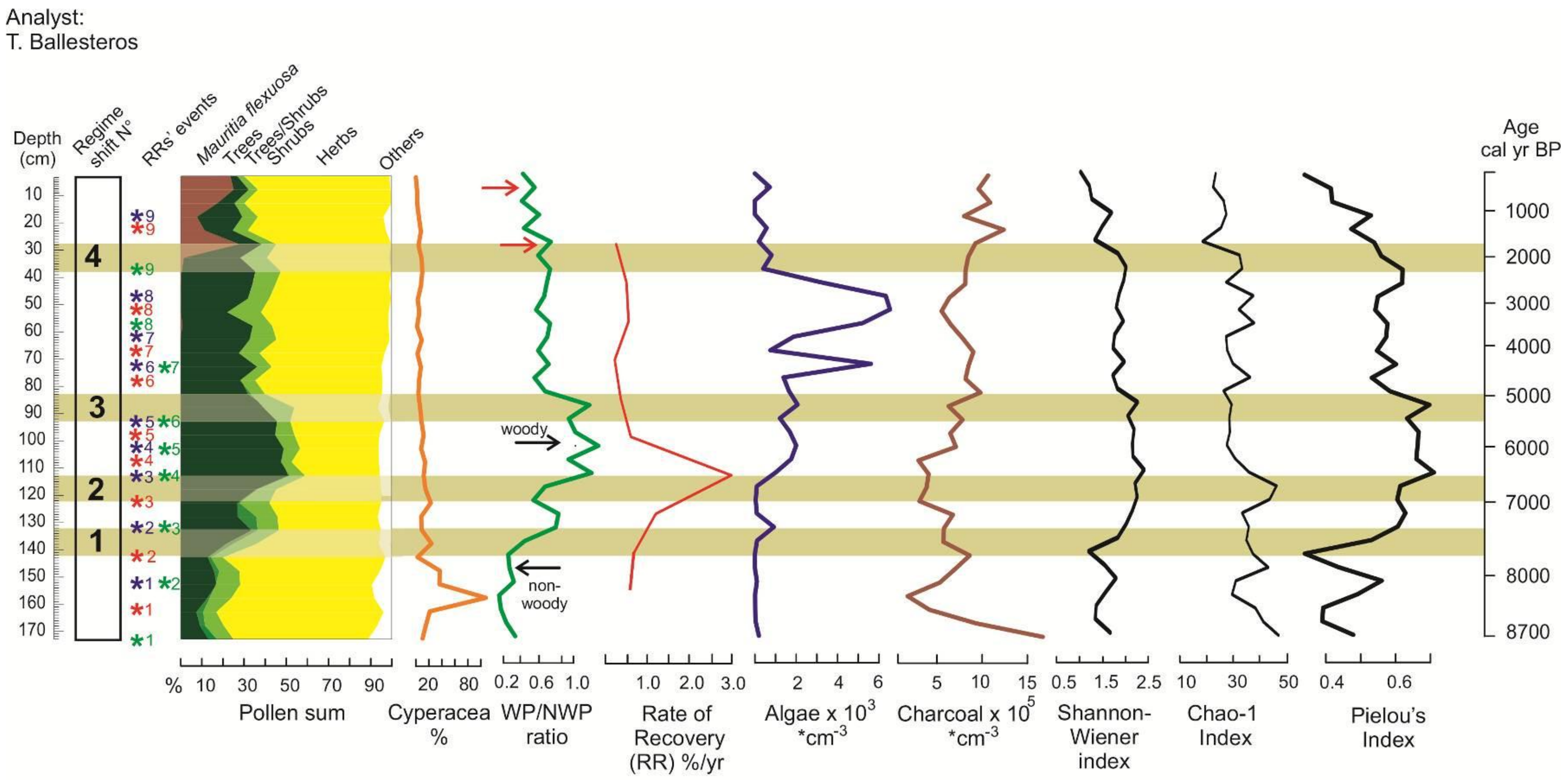


Figure 3.2. Diagram showing the variables analysed of the Lake Encantada record. Palynological sequence: pollen sum, Cyperaceae %, the WP/NWP ratio and the curve of RRs. The * indicate: * =Fpre, * =Fmin, * = Fmax, for each event (Table 3.3). Environmental factors; algae and charcoal particles, shown by their concentration values. Diversity indices: Shannon- Wiener, Chao-1 and Pielou's evenness. Ochre stripes represent the intervals of the regime shifts. Red arrows indicate peaks of *morichales* in the sequence.

	Event N°	F_{PRE} (%)	F_{MIN} (%)	F_{MAX} (%)	T_{REC} (yrs)	RR (%/yr)
Depth-Age*	**9**	42% 38-2190	18.5% 23-1300	29% 18-1006	294 *n*=2	**0.15**
Depth-Age*	**8**	42% 58-3380	35.95% 53-3084	43% 48-2786	298 *n*=3	**0.39**
Depth-Age*	**7**	40% 73-4265	36.53% 68-3973	41.02% 63-3679	294 *n*=2	**0.44**
Depth-Age*	**6**	51.75% 93-5160	34.44% 78-4553	40% 73-4265	288 *n*=2	**0.11**
Depth-Age*	**5**	53.6% 103-5918	47.91% 98-5660	51.75% 93-5160	274 *n*=2	**0.25**
Depth-Age*	**4**	52.14% 113-6420	46.51% 108-6171	53.6% 103-5918	253 *n*=2	**0.49**
Depth-Age*	**3**	35.35% 132-7276	34% 122-6884	52.14% 113-6420	467 *n*=2	**2.87**
Depth-Age*	**2**	22% 153-8077	19.62% 143-7717	35.35% 132-7276	441 *n*=3	**1.49**
Depth-Age*	**1**	22.66% 173-8700	11.87% 163-8243	22% 153-8077	166 *n*=3	**0.57**

Table 3.3. Values of the Rates of Recovery (RR) and those of the parameters included in their calculation (F_{PRE}, F_{MIN}, F_{MAX} and T_{REC}) for Lake Encantada. Each "event" represents a disturbance signal associated with loss of pollen of woody taxa and subsequent recovery identified in the diagram (Figure 3.2), and refers to the interval between F_{PRE} and F_{MAX}. *Depth is represented in cm and age in cal yr BP. *n* refers to the number of samples between F_{MIN} and F_{MAX}.

Higher fire occurrence might have contributed to the diminution of the woody cover before the regime shift (Fig 3.2). The lower fire incidence during the vegetation change could have influenced the expansion of the small forest patches towards another savanna sub-state characterised by higher levels of tree cover (Fig. 3.2). In addition, the increased RRs was likely related to the growth of forest taxa. The results also indicate that during the process of vegetation change, the taxa were more evenly distributed and the vegetation became more diverse. It is not dismissed that lower fire occurrence and/or higher taxa evenness may have influenced greater RRs. It is interpreted that the interplay between lower fire occurrence, higher diversity and RRs could have driven the regime shift.

Regime shift N°2 (122-113 cm; ~6885-6420 cal y BP). During this interval, the values of AP% increases from 22% to 44.5% (Fig. 3.2). The WP/NWP ratio also increases to 1.21. The percentage of herbs ranges between 31 and 41% (Fig. 3.2). Thus, the increase in tree cover and tree-herb proportion suggests a regime shift towards vegetation of rainforest-savanna mosaic (Table 3.1; chapter 1).

Fire disturbance probably influenced the decrease of forest patches at ~125 cm (Fig 3.2). Subsequently, during the interval of regime shift the forest patches recover noticeably at a rate of 2.87%/yr (event 3, Table 3.3). Charcoal particles decrease just before the vegetation transition, exhibiting lower concentrations than during the regime shift N°1 (Fig. 3.2). The values of algae are low and increase slightly at the end of the interval (Fig. 3.2). Concerning the diversity indices, S_1 increases at the beginning and then decreases in the upper part of the regime shift interval. J increases moderately at the end of the regime shift (0.6-0.71; Fig. 3.2).

Since taxa evenness increased after initiating the expansion of forest patches, the evidence suggests that the lower fire occurrence might have played a role in the remarkable increase in RRs (Fig. 3.2), possibly together with other factors not evaluated in this study. In this sense, greater RRs and weaker fire regime appear to have been drivers of the vegetation change. In addition, the expansion of tree cover might have been reinforced by slightly wetter conditions at the end of this process, as suggested by the algal remains' trends. The expansion of forest patches resulted in taxa abundances more homogeneous (Fig. 3.2).

Regime shift N°3 (93-83 cm; ~5400-4840 cal yr BP). AP% decreases progressively along this interval, until reaching values of ~30% (Fig. 3.2). WP/NWP also exhibits a decreasing trend, from 1.22 to 0.69. The decrease observed in the tree cover suggests that a regime shift towards savanna-forest mosaic occurred (Table 3.1). Therefore, the vegetation in the basin of this lake seems to have returned to similar levels of tree cover that there were between ~142 and 123 cm (~7720 and 6900 cal yr BP; Fig. 3.2).

Between 108 and 93 cm (~6200-5400 cal yr BP, prior to this regime shift), the rainforest patches show dynamics of retraction and recovery, though slight (Fig. 3.2). However, the RRs associated with these dynamics exhibit a marked decreasing trend (from 0.49 to 0.25%/yr, events 4 and 5, Table 3.3; Fig. 3.2). Charcoal particles increase from 103 cm (~6000 cal yr BP). Thus, higher fire occurrence could have contributed to the slight decreases in tree cover before the regime shift and the marked retraction of forest patches during the vegetation change. Algae increase slightly during the vegetation shift (Fig. 3.2). Thus, medium levels of available moisture seem not to have influenced the vegetation change. The evidence suggests that higher fire occurrence in combination with low RRs probably influenced the regime shift.

The first half of this vegetation transition is characterised by increase in J, which coincides with temporary increase in shrubs and WP/NWP (Fig. 3.2). However, J decreases from 0.69 to 0.58 in the upper half of the regime shift (Fig. 3.2). *H*’ roughly follows the same trend as J. These indices may indicate that when woody elements increased, the taxa abundances were more even distributed and the vegetation was more diverse. Nonetheless, when the forest cover decreased near to complete the vegetation shift, a few taxa (e.g., herbaceous) started to dominate and vegetation diversity dropped.

Regime shift N°4 (38-28 cm; ~2190-1600 cal yr BP). AP% declines significantly during this interval, from 31.6 to 10%. The arboreal elements of the AP% are comprised mainly of taxa characterised by wind-transported pollen (chapter 1). Therefore, neighbouring forests appear to have retracted severely. On the contrary, pollen abundance of the palm *Mauritia flexuosa* increases dramatically, from 1.4 to 26.6% (Fig. 3.2). This palm appears for the first time in the record and has been an important element of GS vegetation since then. The pollen of this palm has very low dispersion ability and is only found in soils below *morichales* (Leal et al., 2013; Rull, 1999). Thus, presence of *Mauritia* in the palynological record indicates local distribution of *Mauritia* swamps, likely bordering the lakeside (chapter 1). Unexpectedly, the

WP/NWP ratio exhibits an increase rather than a decrease around 26 cm (~1500 cal yr BP; Fig 3.2). This may be the due to the effect of *Mauritia*, which can skew the computation of this ratio. Based on the criteria used in Table 3.1, the results suggest the occurrence of a regime shift in the basin, from savanna-forest mosaic to grassland, and the appearance of local *morichales* (Table 3.1).

Between 78 and 48 cm (4553-2786 cal yr BP, prior to the regime shift), the forest patches within savanna show dynamics of retraction and recovery (Fig. 3.2), characterised by an increasing trend of RRs (events 6, 7 and 8, Table 3.3). High occurrence of fires and fluctuation of available moisture may have played a part in the forest retractions of the aforementioned events (Fig. 3.2). Charcoal particles remain stable during the regime shift (Fig. 3.2). The values of algae are very low, suggesting significantly lower available moisture. The three-diversity indices exhibit a noticeable decrease during the vegetation change, especially J (from 0.62 to 0.54; Fig. 3.2). After the establishment of grassland vegetation, this index continues decreasing until 0.3. Based on the available evidence, it can be interpreted that the interplay between lower available moisture, fire occurrence and reduced plant diversity could have influenced the vegetation shift towards grassland in the basin. Other factors not analysed in this study could be involved in the vegetation change, for the alternative hypotheses proposed see Chapter 1. The peak of charcoal at 24 cm (~1400 cal yr BP) and the forests decline of event 9 at 23 cm (Tabla 3.3; Fig. 3.2) suggest that fire may have played a part in the drop of RRs. The interpretation of factors and processes that influenced the establishment of *morichales* was provided in chapter 1 and elsewhere (Montoya et al., 2011c; Rull and Montoya, 2014; Rull et al., 2013).

3.4.1.2. Interplay between vegetation cover and diversity along the studied period

H' shows the highest values of the record (~*H'*=2.5) between 132 and 89 cm (~7320-5200 and cal yr BP), coinciding with the highest values of AP% and WP/NWP (Fig. 3.3). On the contrary, the lowest values (*H'*=1.1-1.8) are found in two intervals, 173-138 cm (~8700-7500 cal yr BP) and the first 31 cm of the top of sequence (~ last 1800 years), in which values of AP% and WP/NWP are the lowest. The regression analyses between AP% and *H'* (R^2= 0.76, *p-value*= $3.82*10^{-12}$) and between WP/NWP and *H'* (R^2= 0.80, *p-value*= $2.19*10^{-13}$) indicate significant positive association between levels of tree cover and diversity (Fig. 3.3).

S_1 (Fig. 3.3), exhibits a trend of higher values between 173-113 cm (~8700-6400 cal yr BP) and 77-28 cm (~4500-1600 cal yr BP). Lower values are observed in the interval 113-83 cm (~6400-4840 cal yr BP). In addition, the lowest values of S_1 are found in the first 26 cm of the top of sequence (~last 1600 years). The regression analyses between AP% and WP/NWP with S_1 indicate no relationship between tree cover and taxa richness. Therefore, the results indicate that the effect of richness on diversity was negligible.

J largely mimics the trends of AP% and WP/NWP (Fig. 3.2). This agrees with the regression analyses (Fig. 3.3), which shows highly significant coefficients of determination between AP% and J (R^2= 0.78, *p-value*= $1.29*10^{-12}$) and between WP/NWP and J (R^2= 0.83, *p-value*= $2.50*10^{-14}$). These statistical results suggest high positive association between levels of tree cover and taxa evenness. The highest values of J (~0.7) are found between 113-88 cm (~6400-5150 cal yr BP). J exhibits moderate values (~0.62) in the intervals 133-123 cm (~7300-6880- cal yr BP) and 73-33 cm (~4260-1900 cal yr BP). Finally, J decreases consistently in the first 35 cm of the top of sequence (~last 2000 years). These results suggest that along the studied period the abundance of taxa were more homogeneous when woody cover was higher, and vice versa. These results agree with those inferred from the pollen diagram. Hence, in Encantada’s basin pollen diversity seems to have been determined by taxa evenness.

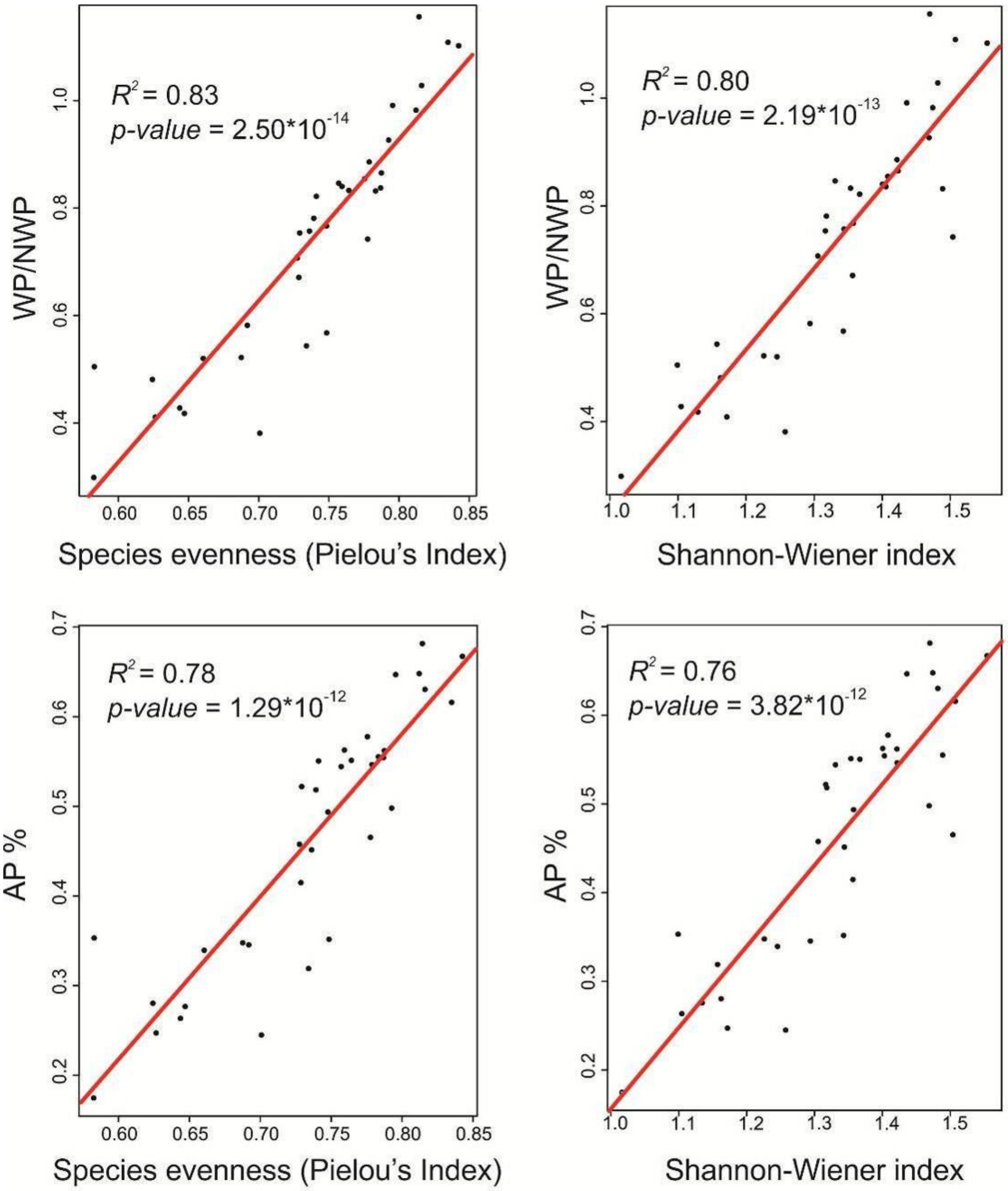


Figure 3.3. Linear regression analyses between indicators of vegetation cover (WP/NWP, AP%) and diversity parameters (Shannon-Wiener index, Pielou's evenness) for Lake Encantada sequence. Only significant analyses are shown.

3.4.2. Fidencio peat bog record (12,385-9520 cal yr BP)

3.4.2.1. Regime shift Nº1 (288-283 cm; ~12,177-12,050 cal yr BP)

Between 301 and 293 cm (~12,385-12,250 cal yr BP), AP% changes considerably from 45 to 14% (Fig. 3.4). At ~289 cm (~12,180 cal yr BP), AP% increases to similar previous values (~47%), exhibiting a recovery rate of ~0.85 % forest taxa/yr (event 1, Table 3.4). Because the insufficient accuracy of chronology at the bottom of the sequence (chapter 2), that value of RR is only indicative of the magnitude of forest recovery at that time. The changes in AP% between 301 and 289 cm suggest either very dynamic forest patches or a reversible regime shift, or both. Based on AP% values (Table 3.1), it can be interpreted that dense forest patches within savanna dominated the Fidencio's area around 289 cm (Fig. 3.4). Subsequently, AP% decreases from 47 to ~17% between 288 and 283 cm (~12,177-12,050 cal yr BP) (Fig. 3.4). During this interval, WP/NWP decreases from ~2.0 to 0.25. This remarkable change in tree cover suggests a regime shift from dense forest patches within savanna to grassland (Table 3.1). AP% does not increase to higher values of 20% in the remaining part of the studied section (until 207 cm, ~9520 cal yr BP). The WP/NWP ratio does not show any important change during this period either. Therefore, grassland vegetation remained in Fidencio's area at least until ~9520 cal yr BP (Fig 3.4).

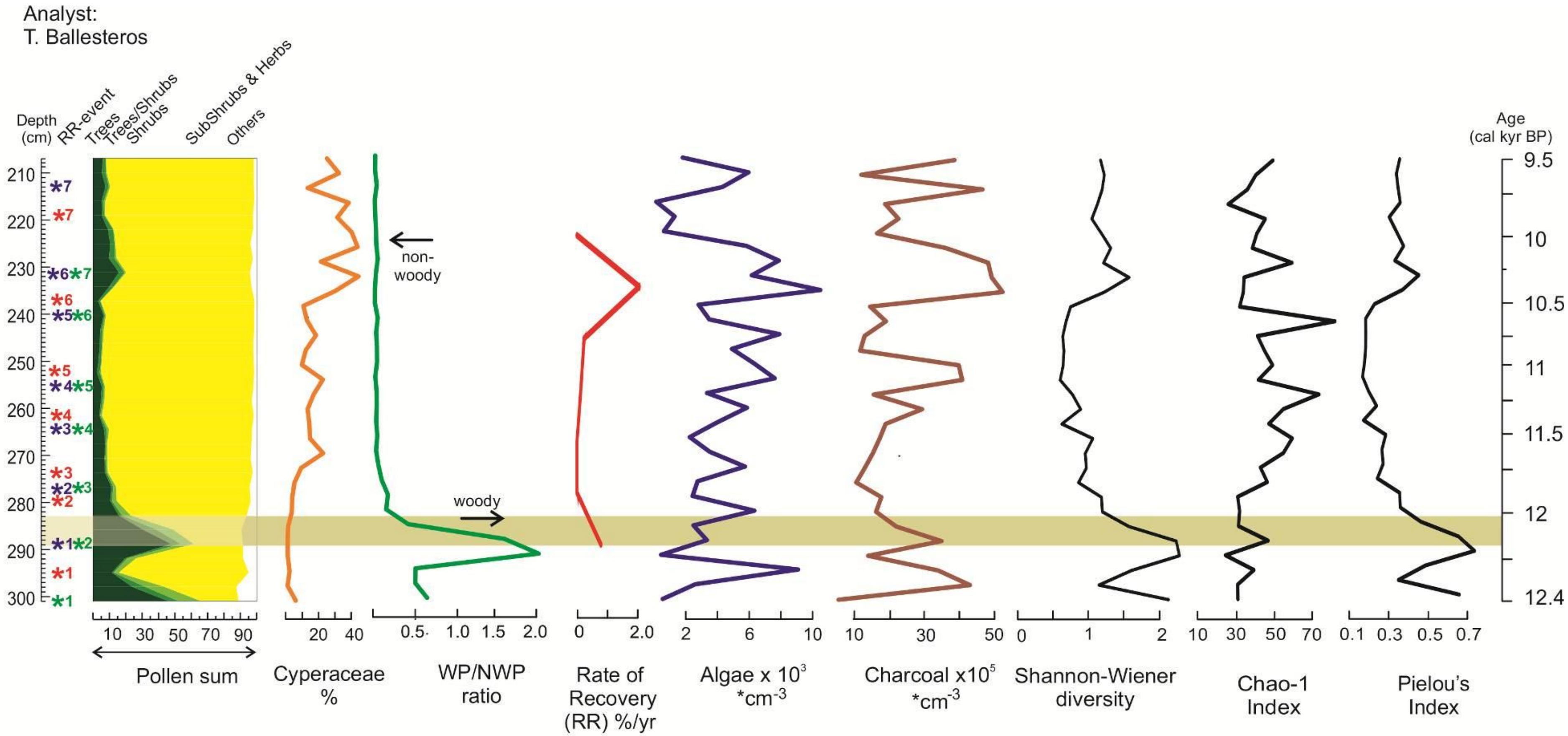


Figure 3.4. Diagram showing the variables analysed of the Fidencio record. Palynological sequence: pollen sum, Cyperaceae%, the WP/NWP ratio and the curve of RRs. The * indicate: *=Fpre, *=Fmin, *= Fmax, for each event (Table 3.4). Environmental factors: algae and charcoal particles, shown their concentration values. Diversity indices: Shannon- Wiener, Chao-1 and Pielou's evenness. The ochre stripe represents the interval of the regime shift. The results showed refer only to the interval analysed with pollen counts higher than 150 pollen grains (the bottom of the sediment is excluded, see Chaprter 2 for more information).

	Event N°	**F_{PRE} (%)**	**F_{MIN} (%)**	**F_{MAX} (%)**	**T_{REC} (yrs)**	**RR (%/yr)**
Depth-Age*	**7**	19% 231-10,279	7% 219-10,130	10% 213-9693	437 *n*=5	**0.05**
Depth-Age*	**6**	8% 240-10,608	5% 237-10,497	19% 231-10,279	218 *n*=3	**2.14**
Depth-Age*	**5**	7% 255-11,170	4% 252-11,059	8% 240-10,608	451 *n*=5	**0.29**
Depth-Age*	**4**	10% 264-11,490	5% 261-11,386	7% 255-11,170	216 *n*=3	**0.18**
Depth-Age*	**3**	16% 277-11,895	9% 274-11,810	10% 264-11,490	320 *n*=4	**0.05**
Depth-Age*	**2**	60% 289-12,177	14% 280-11,975	16% 277-11,895	80 *n*=2	**0.05**
Depth-Age*	**1**	65% 301-12,725	16% 295-12,850	60% 289-12,177	105 *n*=6	**0.85**

Table 3.4. Values of the Rates of Recovery (RR) and those of the parameters included in their calculation (F_{PRE}, F_{MIN}, F_{MAX} and T_{REC}) for Fidencio. Each "event" represents a disturbance signal associated with loss of pollen of woody taxa and subsequent recovery identified in the diagram (Figure 3.4), and refers to the interval between F_{PRE} and F_{MAX}.. *Depth is represented in cm and age in cal yr BP. *n* refers to the number of samples between F_{MIN} and F_{MAX}.

Algae increase slightly during the regime shift (Fig. 3.4), suggesting slightly wetter conditions occurred during the vegetation change. However, climate was still dry (chapter 2). It was proposed that moisture possibly played a part, though not substancial, in the vegetation shift towards grassland (chapter 2). Charcoal particles peak during the vegetation change (AP%, Fig. 3.4), which suggests that potential forest burning could have affected forest permanence. However, when this charcoal-peak is compared with the trend of WP/NWP (Fig. 3.4), the peak appears to have occurred just after the tree cover started to decrease. Therefore, it seems that fire did not trigger the retraction of dense forest patches.

After the dramatic reduction of dense forest patches observed (Fmin of 14% at 280 cm, ~11,975 cal yr BP, event 2, Table 3.4), the small forest patches recover at a rate of 0.05%/yr around 277 cm (~11,895 cal yr BP). During the condition of grassland, the small forest patches exhibit several dynamics of retraction and recovery (events 3, 4, 5, 6 and 7, Table 3.4; Fig. 3.4), which are related to very low RRs (<0.2%/yr). These dynamics were probably driven by the natural vegetation variability. However, event 6 is characterised by significant increase in RR around 231 cm (~10,279 cal yr BP), reaching values of 2.14%/yr (Table 3.4). Higher available moisture could have contributed to the expansion of forest patches (chapter 2; Fig. 3.2), and therefore, the temporary increase of RR.

3.4.2.2. Interplay between vegetation cover and diversity along the studied period

The highest values of *H'* (~2.27) coincide with the highest values of AP% and WP/NWP (Fig. 3.4). From 288 cm *H'* values decrease markedly (~0.84). The regression analyses between AP% and *H'* (R^2= 0.72, *p-value*= $1.15*10^{-9}$) and between WP/NWP and *H'* (R^2= 0.69, *p-value*= $4.55*10^{-9}$) indicate significant positive association between levels of tree cover and diversity (Fig. 3.5).

S_1 shows higher values from 278 cm, coinciding with low values of AP% and WP/NWP (Fig. 3.4). The regression analyses between both indicators of vegetation cover with S_1 indicate no relationship between tree cover and taxa richness.

J follows largely the same trend as *H*' (Fig. 3.4). The regression analyses confirm the high positive relationship between AP% with J (R^2=0.72 *p-value*= $8.13*10^{-10}$) and between WP/NWP with J (R^2=0.71 *p-value*= $1.82*10^{-9}$) (Fig. 3.5). Therefore, taxa evenness was likely the main driver of plant diversity in Fidencio's area, highly associated with changes in tree cover.

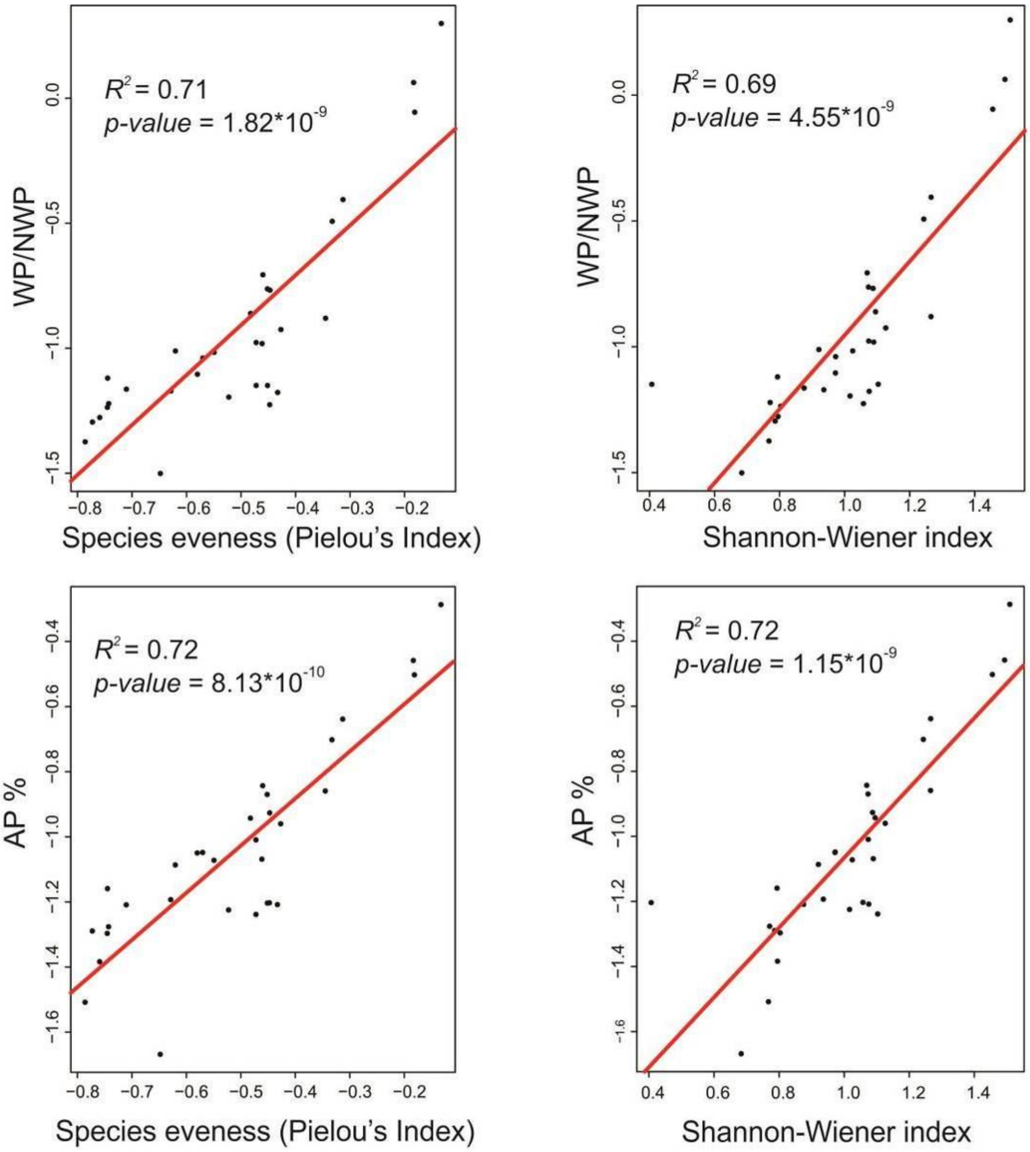


Figure 3.5. Linear regression analyses between indicators of vegetation cover (tWP/NWP , AP%) and diversity parameters (Shannon-Wiener index, Pielou's evenness) for Fidencio sequence. Only significant analyses are shown.

3.5. Discussion

3.5.1. Were the GS forests resilient to past disturbances? Factors that promoted resilience

The current vegetation of the GS, mainly the forests, has commonly been considered to have very low resilience to fire, which may have been influenced by the poor soil status (Dezzeo et al., 2004; Fölster et al., 2001). This lack of resilience seems to make forests susceptible to disturbances, thereby facilitating the replacement of forest patches by open savanna. In this subsection, the resilience of the forests patches of the GS will be tested through the evaluation of palaeoecological evidence and palynological diversity indices, which may suggest the existence of resilience. Evidence of this topic comes mainly from four intervals of the Lake Encantada record, which are discussed below.

Fire regime decreased and remained at moderate levels during the intervals 7720-7320 cal yr BP (regime shift N°1) and 6885-6420 cal y BP (regime shift N°2) (Fig. 3.2). During these intervals, the small forest patches could not only withstand moderate levels of fire disturbance but also responded to the reduction in fires expanding their extension (Fig. 3.2). Therefore, the forest patches can be considered as resilient during the aforementioned intervals. It is hypothesized that medium levels of diversity and high RRs contributed to resilience of vegetation (Fig. 3.2).

From ~6000 cal yr BP, fires increased and remained at high values and RRs decreased markedly (Fig. 3.2; Table 3.3). Some authors have proposed that rates of recovery in ecosystems become slower as the system comes closer to tipping points/zones (Cole et al., 2014; Dakos et al., 2015, 2012; Veraart et al., 2012). However, even though the behaviour of fires and the rates, vegetation of rainforests in mosaic with savanna remained until ~5400 cal yr BP and then changed to savanna-forest mosaic (Fig. 3.2). This result suggests that the vegetation was resilient to high fire regime for roughly six centuries (~6000-5400 cal yr BP; Fig. 3.2). During this period, two environmental factors could have contributed to resilience: high levels of taxa evenness and medium levels of available moisture (Fig. 3.2).

Finally, between 4600 and 2780 cal yr BP, despite the high fire regime, forests patches did not decrease noticeably and thus the vegetation remained in savanna-forest mosaic condition (Fig. 3.2). Thus, it can be interpreted that vegetation was resilient to intense fires. This period coincides with the highest values of algae of the entire record (Fig. 3.2). The indication of local wet climate fits with regional climate trends recorded in other localities of the Amazon basin (e.g., other locations in the GS, *Llanos Orientales* of Colombia and northern Amazonia; Montoya et al., 2011b; Rull, 1992; Behling and Hooghiemstra, 2000; Pessenda et al., 2010; Fig. 3.1a). Despite repetitive fires of high intensity/frequency, wet conditions must have prevented critical levels of forest burning. Moreover, higher available moisture could have contributed to the permanence of forests and enhanced the RRs (events 7 and 8, Table 3.3; Fig. 3.2). Another factor that may have contributed to resilience is the potential human-made selective burning (chapter 1); as a result, some areas would have been affected by fire and others not. Moderate levels of taxa evenness could have also played a role in the permanence of forests (Fig. 3.2). Based on the available evidence, it is suggested that three factors promoted the vegetation resilience between 4600 and 2780 cal yr BP: humid climate, equitable abundances of taxa and selective forest burning. Nevertheless, lack of information about human and cultural activities limited our ability to make a definite statement. Hence, to test the aforementioned hypothesis it is needed interdisciplinary palaeoecological-archaeological-anthropological studies.

This is the first palaeoecological study that evaluates and documents the existence of resilience of past forests communities in the GS. However, there is also evidence from other palaeoecological studies, though scanty. For instance, the pollen diagrams from El Paují record (located at the southernmost part of the GS, Fig. 3.1b) show long-term permanence of forest patches under continuous and moderate fire occurrence between 8250 and 5040 cal yr BP (Montoya et al., 2011b). During this interval, a regime shift was observed from open savanna with forest patches to forest-savanna mosaic (Montoya et al., 2011b). Although the study of resilience was not the aim of that investigation, it can be inferred that the forest communities in El Paují were resilient to fire. Thus, the results from Encantada's and El Paují's basins suggest that forests in the southern GS could have been resilient on a centennial timescale. The results from this study agree with the palaeoecological findings in African savannas about savanna vegetation is likely to have been resilient to disturbances on a centennial timescale (Gillson and Ekblom, 2009; Gil-Romera et al., 2010).

Previously, Rull (1992) suggested that diversity of past communities in the GS was more-equitability dependent than richness-dependent. This study supports this hypothesis (Figs. 3.2 and 3.3). In addition, the evidence shows that increase in plant diversity was associated positively with levels of tree cover. Higher values of the diversity parameters were associated with the presence of resilience. This inference supports the hypothesis derived from ecological studies in a wide range of ecoystems that states diversity elements (e.g., response diversity, functional redundancy, species evenness) help sustain resilience of ecosystems in the face of disturbances (Elmqvist et al., 2003; Folke et al., 2004; Mori et al., 2013; Sasaki et al., 2015). Bhagwat et al. (2012) studied resilience of Indian forests on a long timescale (last 7500 years) and suggested that in tropical ecosystems a tree-covered matrix, even if fragmented, is one key landscape condition that needs to be conserved because of its role in providing refugia for important elements of biodiversity and in maintaining resilience. Our results agree with Bhagwat et al. (2012). It is suggested that in Encantada's basin, the interplay between particular abiotic (e.g., higher available moisture, selective burning) and biotic (e.g., medium-high degree of taxa equitability, high RRs) factors could have promoted resilience of past forests communities.

3.5.2. Processes and factors that decrease resilience

Three intervals were observed (one in Fidencio and two in Lake Encantada) in which resilience decreased, thus leading to a regime shift characterised by lower levels of tree cover. In each case, different processes and drivers appear to have contributed to the decrease in resilience.

In Fidencio, the evidence suggests that dense forests did not have capacity to absorb disturbances and reorganise to retain the same function in the interval 12,177-12,050 cal yr BP. Therefore, the loss of resilience probably led the vegetation shift towards grassland vegetation. Chapter 2 hypothesized that the most likely cause of the vegetation shift was the synergy between warming, fire, drier climate than the present, availability of fuel loads and potential human activities, in agreement with similar forests declines found in other GS sequences (Rull et al., 2013, 2015). This synergism could have eroded the forest resilience. The inclusion of diversity analyses and calculation of RR provided additional evidence to better evaluate the abrupt forest reduction and resilience in Fidencio. The diversity indices show that the regime shift was characterised by remarkable decreasing trend of diversity and taxa equitability (Fig. 3.4). It is suggested that decreased diversity was involved in the synergism proposed. The results of Fidencio may indicate that decrease in diversity was probably a condition associated with loss of resilience. In addition, RRs appear to have been highly dependent of the extent of forest patches. Thus, small forest patches scattered in grassland seems to have had almost null recovery capacity, unless favourable environmental conditions (e.g. wetter conditions) contributed to their recovery (Fig. 3.4; Table 3.4).

As it was explained previously for basin of Lake Encantada, forests may have been resilient to fires initially in the interval between 6000 and 5400 cal yr BP. Nevertheless, the progressive rise in intensity and frequency of fires during the aforementioned period (Fig. 3.2) could have played a part in eroding gradually the resilience of forest patches, until ecological thresholds were reached in the interval 5400-4840 cal yr BP (regime shift N°3). Low RRs were probably associated with the loss of resilience (Fig. 3.2; Table 3.3). The marked reduction in taxa equitability around 5160 cal yr BP (Fig.3.2) may have contributed to reach a threshold more easily. It is proposed that stronger fire regime and low RRs were important drivers of the progressive loss of resilience. Decrease in taxa evenness might have accelerated/intensified this process (Fig. 3.2).

Continuing with Lake Encantada sequence, a number of factors destabilised the vegetation resilience from ~2190 cal yr BP onwards, leading its decreasing process. Available moisture decreased remarkably around ~2780 cal yr BP (Fig. 3.2). The hydrological balance agrees with that recorded from other GS sequences (Montoya et al., 2011c) and in northern South America (Haug et al., 2001). Diversity started to decrease around 2190 cal yr BP, wheras fire occurrence remained high at that time (Fig, 3.2, Table 3.3). It is suggested that the synergistic effect between a number of environmental factors such as drier climate, repetitive fires and decrease in diversity, could have contributed to the gradual reduction in resilience. In addition, this synergism probably promoted the establishment of the current grassland vegetation in the basin. The interplay proposed could have also driven the drop in RRs ~1000 years ago (event 9, Table 3.3). The small forest patches within grassland have not been able to recover since then. Instead, expansion of grassy vegetation has been accentuated (Fig. 3.2). Hence, the resilience of forest vegetation may have continued decreasing during the last 1000 years. Thus far, other palaeoecological studies in the GS have mainly studied the potential role of fires and climate in the recent savanna expansion (Montoya et al., 2011c; Rull, 1992, 1999; Rull et al., 2013), concluding that these factors have been determinant. This study provides extra evidence to evaluate this vegetation change.

The three intervals evaluated suggest that loss of forest resilience can be considered as a phenomenon highly associated with expansion and domination of grasses. This phenomenon can be explained by the dominance of grass layer and the resulting low diversity, which provides few elements (e.g., seed banks of forest taxa, microclimatic conditions, soil conditions) to maintain the resilience of forests. Sustainable management strategies of biodiversity and ecosystem services have increasingly acknowledged the importance of maintaining resilient ecosystems (Sasaki et al., 2015). Hence, the aforementioned finding provides evidence-based to design management practices aimed at preventing further loss of forest patches and/or conversion to grassland in the region.

The evidence from this study suggests that the environmental drivers (abiotic and biotic) have not played the same role as forcing factors of resilience trends along the temporal scales studied. Therefore, the different processes and drivers that built and/or eroded resilience indicate that relationships between environmental drivers and vegetation were not linear. Similar findings have been documented by palaeoecological studies in other savanna regions and other tropical ecosystems (Gillson and Ekblom, 2009; Gil-Romera et al., 2010; Seddon et al., 2014b). Hence, it is only by evaluating vegetation dynamics over long-term periods that the understanding of complex ecological processes in different savanna regions can be improved.

3.6. Conclusions

The 8700-year palaeoecological history of Lake Encantada suggests that forests in the basin were resilient to fires during several temporal intervals on a centennial timescale. It is proposed that the interplay between particular abiotic (medium to high levels of available moisture, selective burning) and biotic (medium-high degree of diversity, high RRs) factors could have contributed to resilience of past forests. On the other hand, the interplay of a number of factors such as repetitive fires, low available moisture, decrease in diversity and low RRs, probably contributed to loss of resilience. The aforementioned processes and drivers could have influenced the regime shifts towards increase or decrease of tree cover depending on the case.

Concerning the Fidencio record, the evidence indicates that forests of the interval studied (Late Glacial) were not resilient to a suite of disturbances. The decrease in diversity was a condition associated with loss of resilience.

Diversity of past communities in the two localities studied was more-equitability dependent than richness-dependent. Moreover, plant diversity was associated positively with levels of tree cover. Finally, loss of resilience could be considered as a phenomenon highly associated with expansion and domination of grasses.

3.7. References

Accatino, F., De Michele, C., 2013. Humid savanna-forest dynamics: A matrix model with vegetation-fire interactions and seasonality. *Ecol. Model*. 265, 170–179.

Behling H., Hooghiemstra. H., 2000. Holocene Amazon rainforest-savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science* .15, 687–695.

Bhagwat, S.A., Nogué, S., Willis, K.J., 2012. Resilience of an ancient tropical forest landscape to 7500 years of environmental change. *Biol. Conserv.* 153, 108–117.

Biggs, R., Carpenter, S., Brock, W.A., 2009. Turning back from the brink: Detecting an impending regime shift in time to avert it. *PNAS.* early edition, 1-6.

Bilbao, B. A, Leal, A.V, Méndez, C.L., 2010. Indigenous Use of Fire and Forest loss in Canaima National Park, Venezuela. Assessment of and Tools for Alternative Strategies of Fire Management in Pemón Lans. *Human Ecology.* 38, 663-673.

Birks, H.J.C., 2012. Ecological palaeoecology and conservation biology: controversies, challenges, and comprises. *International Journal of Biodiversity Science, Ecosystem Services and Management.* 8, 292-304.

Blarquez, O., Carcaillet, C., 2010. Fire, Fuel composition and resilience threshold in subalpine ecosystems. *Plos One*. 5(8), 312489.

Brown, A.G., Carpenter, R.G., Walling, D.E., 2007. Monitoring fluvial pollen transport, its relationship to cachtment vegetation and implications for palaeoenvironental studies. Review of Palaeobotany and Palynology. 147, 60-70.

Bush, M.B., 1995. Neotropical plant reproductive strategies and fossil pollen representation. *Am. Soc. Nat.* 145, 594–609.

Calabrese, J.M., Deffuant, G., Grimm, V., 2011. Bridging the Gap Between computational models and viability based resilience in Savannaecosystems. In: Deffuant, G., Gilbert, N. (Eds.) Variability and resilience of complex Systems: concepts, methods and case studies from ecology and society. Chapter 5. Springer, pp. 107-130.

Chao, A., 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*. 11, 265-270.

Cole, L.E., Bhagwat, S., Willis, K., 2015. Long-term disturbance dynamics and resilience of tropical peat swamp forests. Journal of Ecology.103, 16-30.

Cole, L.E.S., Bhagwat, S.A., Willis, K.J., 2014. Recovery and resilience of tropical forests after disturbance. *Nature communications*. DOI: 10.1038/ncomms4906

Dakos, V., Carpenter, S.R., Van Nes, E.H., Scheffer, M., 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. *Phil. Trans. R. Soc. B.* 370, 20130263.

Dakos, V., Carpenter, S.R., Brock, W.A., Ellison, A.M., Guttal, V., Ives, A.R., Kéfi, S., Livina, V., Seekell, D.A., van Nes, E.H., Scheffer, M., 2012. Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. *PLoS One*. 7, e41010,

Dearing, J.A., Wang, Rong, Zhang, Ke, Dyke, J. G., Haberl, Helmut, Hossain, Sarwar, Langdon, P.G., Lenton, Timothy, Raworth, Kate, Brown, S., Carstensen, Jacob, Cole, Megan, Cornell, Sarah, Dawson, Terence, Doncaster, C.P., Eigenbrod, Felix, Flörke, Martina, Jeffers, Elizabeth, Mackay, Anson, Nykvist, Björn and Poppy, G.M., 2014. Safe and just operating spaces for regional social-ecological systems. *Global Environmental Change.* 28, 227238.

Dezzeo, N., Chacón, N., Sanoja, E., Picón, G., 2004. Changes in soil properties and vegetation characteristics along a forest-savanna gradient in southern Venezuela. *For. Ecol. Manag*. 200, 183-193.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., et al., 2003. Response diversity and ecosystem resilience. *Front. Ecol. Environ*. 1, 488-494.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annu. Rev. Ecol. Syst.* 35, 557-581.

Fölster, H., Dezzeo, N., Priess, J., 2001. Soil-vegetation relationship in base-deficient premontane moist forest-savanna mosaics of the Venezuelan Guayana*. Geoderma.* 104, 95-113.

Froyd, C.A. Willis, J.K., 2008. Emerging issues in biodiversity and conservation management: The need for a palaeoecological perspective. *Quaternary Science Reviews.* 27, 1723-1732.

Gil-Romera, G., López-Merino, L., Carrión, J.S., González-Sampériz, P., Martín-

Puertas, C., López Sáez, J.A., Fernández, S., García Antón, M., Stefanova, V., 2010. Interpreting Resilience through Long-Term Ecology: Potential Insights in Western Mediterranean Landscapes. *The Open Ecology Journal.* 3*,* 43-53.

Gillson, L., Duffin, K.I., 2007. Thresholds of potential concerns as benchmarks in the management of African savannhs. *Phil. Trans. R. Soc. B.* 362, 309-319.

Gillson, L., Ekblom, A., 2009. Resilience and Thresholds in savannas: Nitrogen and Fire as drivers and responders of vegetation transition. *Ecosystems.* 12, 1189-1203.

Gillson, L., Marchant, R., 2014. From myopia to clarity: sharpening the focus of ecosystem management through the lens of palaeoecology. *Trends in Ecology and Evolution.* 29(6), 317-325.

Gómez, E., Picón, G., Bilbao, B., 2000. Los incendios forestales en Iberoamérica. Caso Venezuela. In: Vélez-Muñoz, R. (Eds.), La defensa contra incendios forestaes. Fundamentos y experiencias. McGraw-Hill, Madrid.

Goring, S., Lacourse, T., Pellatt, M.G., Mathewes, R.W., 2013. Pollen assemblage richness does not reflect regional plant species richness: a cautionary tale. *J. Ecol*. 101, 1137–1145.

Gotelli, N. J. and R. K. Colwell. 2011. Estimating species richness. Pages 39-54 in A. E. Magurran and B. J. McGill, editors. Frontiers in measuring biodiversity. Oxford University Press, New York

Groffman et al., 2006. Ecological Thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems*. 9, 1-13.

Gunderson L.H., 2000. Ecological resilience-in theory and application. *Annu. Rev. Ecol. Syst.* 31,425–39.

Haug, G., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward Migration of the Intertropical Convergence Zone Through the Holocene. *Science*. 293, 1304-1308

Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M., 2011. Global Resilience of Tropical forest and savanna to critical transitions. *Science.* 334, 235-235.

Holling C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1-23.

Huber, O., 1995. Geographical and physical features, in: Steyemark, J.A., Berry. P.E., Holst, B.K. (Eds.), Flora of the Venzuelan Guayana., Volume 1. Introduction. Missouri Bot. Gard. Press, St. Louis, pp. 1-62.

Huber, O., Febres, G., 2000. Guía ecológica de la Gran Sabana. Nature Conservancy, Caracas.

Huber, O., García, P., 2011. The Venezuelan Guayana Region and the Study Areas: Geo-ecological characteristics. In: Peatlands of the Western Guayana Highlands, Venezuela, Ecological Studies. Springer Berling Heiderbelg, Berlin, Heiderberg. pp 29-89.

Huggett, A.J., 2005. The concept and utility of "ecological thresholds" in biodiversity conservation. *Biol. Conserv*. 124, 301–310.

Keen, H.F., Gosling, W.D., Hanke, F., Miller, C.S., Montoya, E.,Valencia, BG., Williams, J.J., 2014. A statistical sub-sampling tool for extracting vegetation community and diversity information from pollen assemblage data. *Palaeogeography, Palaeoclimatology, Palaeoecology.* 408: 48-59.

Leal, A., Bilbao, B., Berrío, J.C., 2013. A contribution to pollen rain characterization in forest-savanna mosaics of the Venezuelan Guayana and its use in vegetation reconstructions from sedimentary records. *American Journal of Plant Sciences.* 4, 33-52.

Margalef, R., 1957.Teoría de la Información. Memorias de la Real Academia de Ciencias y Artes de Barcelona 23, 373-449.

Montoya, E., Rull, V., 2011. Gran Sabana Fires (SE Venezuela): A Paleoecological Perspective. *Quaternary Science Reviews.* 30, 3430-3444.

Montoya, E., Rull, V., Nogué, S., Díaz, W.A., 2009. Paleoecología del Holoceno en la Gran Sabana, SE Venezuela: Análisis preliminar de polen y microcarbones en la Laguna Encantada. *Collectanea Botanica,* 28, 65–79.

Montoya, E., Rull, V., Stansell, N.D., Bird, B.W., Nogué, S., Vegas-vilarrúbia, T., Abbott, M.B., Díaz, W.A., 2011a. Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron. *J. Quat. Sci*. 26, 207–218.

Montoya, E., Rull, V., Nogué, S., 2011b. Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE Venezuela): Palynological evidence from El Paují record. *Palaeogeogr. Palaeoclimatol. Palaeoecol*. 310, 413–426.

Montoya, E., Rull, V., Stansell, N.D., Abbott, M.B., Nogué, S., Bird, B.W., Díaz, W.A., 2011c. Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quat. Res.* 76, 335–344.

Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response determines the resilience of ecosystems to environmental changes. *Biol. Rev. Camb. Philos. Soc.* 88(2), 349-364.

Mulder, C. P. H.; Bazeley-White, E.; Dimitrakopoulos, P. G.; Hector, A.; Scherer-Lorenzen, M.; Schmid, B., 2004. "Species evenness and productivity in experimental plant communities". *Oikos* 107, 50–63Murphy, B.P., Bowmann, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna? *Ecology letters*. 15, 748-758.

Odgaard, B.V., 2001. Palaeoecological perspectives on pattern and process in plant diversity and distribution adjustments: a comment on recent developments. *Divers. Distrib*. 7, 197–201.

Pessenda, L.C.R., Gouveia, S.E.M., Ribeiro, A., et al.,2010. Late Pleistocene and Holocene vegetation changes in northeastern Brazil determined from carbon isotopes and charcoal records in soils. *Palaeogeography, Palaeoclimatology, Palaeoecology* . 297, 597–608.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol*. 13, 131-144.

Rull, V. 1992. Successional Patterns of the Gran Sabana (Southeastern Venezuela) Vegetation During the Last 5000 Years, and its Responses to Climatic Fluctuations and Fire. *J Biogeogr*. 19, 329-338.

Rull, V., 1999. A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela. *J. Quat. Sci.* 14, 137–152.

Rull, V., 2007. Holocene global warming and the origin of the Neotropical Gran Sabana in the Venezuelan Guayana. *J. Biogeogr*. 34, 279–288.

Rull, V., 2010. Ecology and Palaeoecology: Two Approaches, One Objective. *Open Ecol. J*. 3, 1–5.

Rull, V., 2012. Community ecology: diversity and dynamics over time. *Community Ecology.* 13(1), 102-116.

Rull, V., Montoya, E., 2014. *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a Neotropical context. *Quaternary Science Reviews*. 99, 17-33.

Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T., Safont, E., 2013. Ecological palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. *Perspect. Plant Ecol. Evol. Syst.* 15, 338–359.

Rull, V., Montoya, E., Vegas-Vilarrúbia, T., Ballesteros., 2015. New insights on palaeofires and savannisation in northern South America. *Quaternary Science*

Reviews. 122, 158-165.

Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M., Mori, A.S., 2015. Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecological Indicators.* 57, 395-408.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature.* 413, 591–596

Seddon, A.W.R., Froyd, C.A., Leng, M.J., Milne, G.A., Willis, K.J., 2011. Ecosystem Resilience and Threshold Response in the Galápagos Coastal Zone. *Plos One*. 6(7), 1-10.

Seddon, A.W, Anson W. Mackay., Ambroise G. Baker., H. John B. Birks., Elinor Breman., Caitlin E. Buck., Erle C. Ellis., Cynthia A. Froyd., Jacquelyn L. Gill., Lindsey Gillson., Edward A. Johnson., Vivienne J. Jones., Stephen Juggins., Marc Macias-Fauria., Keely Mills. Jesse L. Morris., David Nogués-Bravo., Surangi W. Punyasena., Thomas P. Roland., Andrew J. Tanentzap., Kathy J. Willis., Martin Aberhan., Eline N. van Asperen., William E. N. Austin., Rick W. Battarbee., Shonil Bhagwat., Christina L. Belanger., Keith D. Bennett., Hilary H. Birks., Christopher Bronk Ramsey., Stephen J. Brooks., Mark de Bruyn., Paul G. Butler., Frank M. Chambers., Stewart J. Clarke., Althea L. Davies., John A. Dearing., Thomas H. G. Ezard., Angelica Feurdean., Roger J. Flower., Peter Gell., Sonja Hausmann., Erika J. Hogan., Melanie J. Hopkins., Elizabeth S. Jeffers., Atte A. Korhola., Robert Marchant., Thorsten Kiefer., Mariusz Lamentowicz., Isabelle Larocque-Tobler., Lourdes López-Merino., Lee H. Liow., Suzanne McGowan., Joshua H. Miller., Encarni Montoya., Oliver Morton., Sandra Nogué., Chloe Onoufriou., Lisa P. Boush., Francisco Rodriguez-Sanchez., Neil L. Rose., Carl D. Sayer., Helen E. Shaw., Richard Payne., Gavin Simpson., Kadri Sohar., Nicki J. Whitehouse., John W. Williams and Andrzej Witkowski., 2014a. Looking forwards through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology.* 102, 256-0267.

Seddon, A.W.R., Froyd, C.A., Witkowski, A., Willis, K.J., 2014b. A quantitative framework for analysis of regime shifts in a Galápagos coastal lagoon. *Ecology.* 95(11), 3046- 3055.

Smith, B., Wilson, J.B., 1996. A consumer's guide to evenness indices. *Oiko*s. 76, 70–82.

Standish et al., 2014. Resilience in ecology: Abstraction, distraction, or where the action is? *Biological Conservation.* 177, 43-51.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E., 2011. Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. *Quaternary Science Reviews*. 30, 2361-2388.

Veraart, A.J., Faasen, E.J., Dakos, V., van Nes, E.H., Lürling, M., Scheffer, M., 2012. Recovery rates reflect distance to a tipping point in a living system. *Nature.* 481, 357-359

Walker, BH., Meyers, J.A., 2004. Thresholds in ecological and social-ecological systems: a developing database. *Ecol. Soc.* 9(2), 3.

Wang, Rong, Dearing, John A., Langdon, Peter G., Zhang, Enlou, Yang, Xiangdong, Dakos, Vasilis and Scheffer, Marten., 2012. Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature*. 492, 419-422.

Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, .B., Froyd, C.A., Myers, N.,2007a. How can knowledge of the past help to conserve the future? Biodiversity conservarion and the relevance of longterm ecological studies. *Philosophical Transactions of the Royal Society B.* 362, 175-186.

Willis, K.J., Gillson, L., Knapp, S., 2007b. Biodiversity hotspots through time: an introduction. *hilosophical Transactions of the Royal Society B. 362,* 169-174.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birks, H.J.B., 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol*. 25, 583–591.

Wright, H.E., Mann, D.H., Glaser, PH., 1984. Piston corers for peat and lake sediments. Ecology. 65, 657-659.

GENERAL DISCUSSION

The palaeoecological evidence provided by this thesis has been substantial to: (*i*) better understand the ecological processes and vegetation responses that have governed the vegetation changes in the two locations of humid savannas studied, (*ii*) forecast potential future vegetation responses, (*iii*) propose some guidelines for savannas management, and (*iv*) understand the usefulness of using different proxies (multiproxy approach) to refine interpretations. Here, the advances in the knowledge of savannas obtained from the aforementioned topics are discussed in more detailed.

1. Ecological processes that governed the alternative sub-states of savanna in the humid savannas studied. Potential applicability of palaeoecological evidence in management strategies

The results support the finding that fire alone has not been the main driver of vegetation dynamics in the GS (Montoya et al., 2011a,b,c; Rull, 2007; Rull et al., 2013). Instead, vegetation changes (either decreased or increased tree cover) have resulted from the interplay between fire with different sets of environmental factors (biotic and abiotic). Based on the interactions recognised, several ecological feedback processes have been identified. Concerning resilience, forests appear to have been resilient to fire disturbance during specific intervals, on a centennial timescale. It is proposed that the interplay between particular abiotic (medium to high levels of available moisture, selective burning) and biotic (medium-high degree of diversity, high Rates of Recovery-RR) factors could have contributed to resilience of past forests. The results and new findings are significant to better understand the ecology of savannas, due to the following reasons: **(*i*)** Fire is considered the factor that prevents the closure of canopy in humid savannas that otherwise would be allowed by rainfall abundance (Accatino and De Michele, 2013); **(*ii*)** There is not much ecological information for savannas, and therefore, feedback processes are still poorly understood (Gillson, 2004); and **(*iii*)** Forests in the GS have long been considered as plant communities of very low resilience to fire (Dezzeo et al., 2004; Fölster et al., 2001; Rull 1992). Consequently, the new evidence generated by studying past vegetation dynamics (e.g. interplay between vegetation and environmental drivers, vegetation responses) can have implications for conservation and management of humid savannas in general, and those of the GS in particular. In this section, major changes in vegetation and the feedback processes associated are discussed.

1.1. Vegetation changes towards increased forest patches within savanna

The evidence suggests that vegetation change of this type occurred in the basin of Lake Encantada during two periods (chapters 1 and 3), namely: (1) between ~7720-7320 cal yr BP, change from grassland to savanna-forest mosaic (open savanna with forest patches); and (2) from savanna-forest mosaic to forest-savanna mosaic between ~6885 and 6420 cal yr BP. There is not evidence of noticeable change towards greater tree cover in Fidencio's sequence after ~12,100 cal yr BP (chapters 2 and 3).

Between ~7720 and 7320 cal yr BP, the change from grassland to the alternative sub-state of savanna-forest mosaic could have been driven by the interplay between lower fire occurrence and higher diversity and RRs (chapter 3). Due to the potential disconnection-connection dynamics with the neighboring fluvial system proposed in chapter 1 (sedimentary interval B-2) for this period (see section 3 below), the effect of hydrological balance on the vegetation shift was not possible to discern based solely on the algae record.Additional palaeoecological evidence provided by a peat core (Fig. D1) extracted from the lakeside suggested that a similar vegetation change occurred locally during that period, which was associated with greater plant diversity (Montoya et al., 2009). Pollen diagrams from the GS records do not exhibit this type of vegetation change (Montoya et al., 2011a, b, c; Rull 1992, 1999, 2007). Hence, lack of evidence limited our ability to make a better assessment of the feedback process(es) involved in this vegetation shift. It has been suggested that in dry savannas, the change from grassland to wooded savanna was probably mediated by increased hydrological balance (Gillson and Ekblom, 2009). However, the limited evidence found in this thesis did not give us the opportunity to evaluate whether such phenomenon could also occur in humid savannas types like the GS.

In the period 6885-6420 cal yr BP, the interplay between decreased fires, greater RRs and slightly higher available moisture could have contributed to the vegetation change from savanna-forest mosaic to forest-savanna mosaic in Encantada's basin (chapters 1 and 3). The expansion of forest patches seems to have resulted in higher taxa evenness (chapter 3). Similar vegetation change occurred southernmost of the GS in El Paují area (near Amazon forests, Fig. D1) between 7715 and 5040 cal yr BP Montoya et al., 2011a). In this case, it was interpreted that the expansion of rainforests was probably promoted at first by fires developed in savanna. The authors observed a posterior increase in the hydrological balance once the forest was established, which might have influenced Paují's forests persistence (Montoya et al., 2011a). Therefore, it seems that different ecological processes might have operated in the vegetation change towards forest-savanna mosaic in the two localities with palaeoecological evidence of southern GS.

Simulations of global vegetation under fire exclusion show that vast areas of humid savannas in South America have the climate potential to form forests (Bond et al., 2005). Due to the occurrence of repetitive fires along the two sequences studied, this hypothesis could not be tested (chapters 1 and 2). In general, the evidence of the sequence of Lake Encantada indicates that only reduction in fires was not enough to promote alternative savanna sub-states characterised by increase in tree cover. This finding should be considered when designing management plans for the GS savannas, avoiding strategies aimed only at reducing fire occurrence. Encantada's results suggest that reduction in fires in interplay with other factors such as an increase in plant diversity and hydrological balance, and high RRs, was probably necessary to drive the expansion of forest patches (chapter 3). Therefore, considering the interplay previously explained, future management strategies in the GS should combine fire reduction with increase in RRs (e.g., by mechanisms of expression of seed banks) and diversity, and preferably being performed during wetter intervals. However, if RRs were highly dependent on decreased fire regime and whether increased diversity was the cause or consequence of higher levels of tree cover are research areas that deserve further study. Finally, the evidence of Lake Encantada suggests that higher hydrological balance in "humid savannas" possibly played a role in driving the expansion of the forest patches.

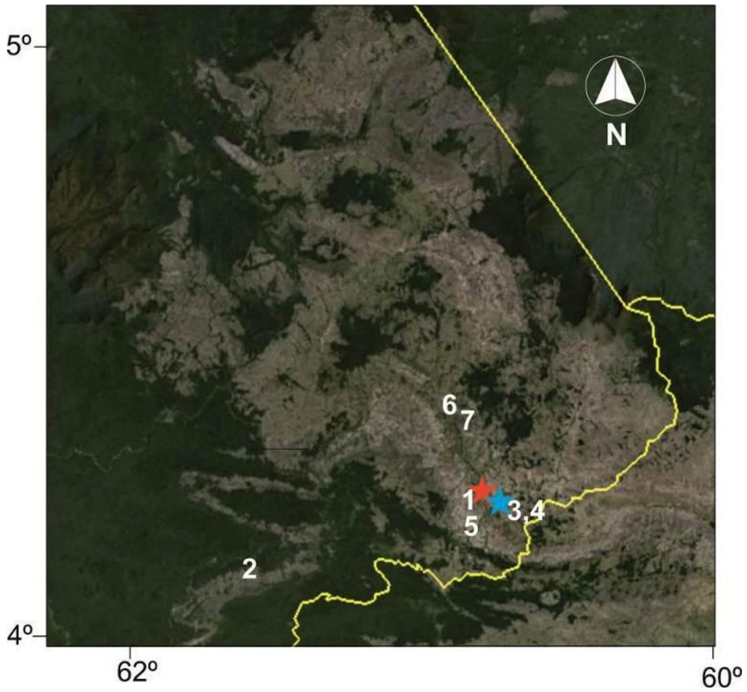


Figure. D1. An image of The Gran Sabana, modified from Google-Earth (accessed in May 2015). The sequences evaluated in this thesis: Lake Encantada with a red star and Fidencio peat bog with a light-blue star. Numbers indicate the sites with palaeoecological information mentioned in the text: 1—Encantada peat bog; 2—El Paují; 3—Lake Chonita; 4—Divina Pastora; 5—Santa Teresa; 6—Urué; 7—Mapaurí.

1.2. Vegetation changes towards more open vegetation

The sequence of Lake Encantada provides evidence of this type of vegetation change occurring during two periods (chapters 1 and 3): (1) between 5400 and 4840 cal yr BP, vegetation change from forest-savanna mosaic to open savanna with forest patches; and (2) change from savanna-forest mosaic to grassland between 2190 and 1600 cal yr BP. In Fidencio, a particular vegetation change from dense forest patches within savanna to grassland occurred around 12,100 cal yr BP (chapter 2). This change is considered to represent the origin of grassland in Fidencio's basin as the dominant vegetation type in the landscape. The three cases were apparently associated with reduction in resilience (chapter 3).

Between 5400 and 4840 cal yr BP, the change from forest-savanna mosaic to open savanna with forest patches in Encantada's basin was probably driven by the interaction of several factors such as increased fires, erosion, low RRs and decreased taxa evenness (chapters 1 and 3). Therefore, the synergy between these factors (abiotic and biotic) coud have contributed greatly to destabilise the interplay (medium levels of available moisture and high degree of taxa eveness; chapter 3) that maintained vegetation of forest-savanna mosaic for roughly one millennium (6400-5400 cal yr BP). Soil instability (erosion) was probably promoted by increase in fire occurrence (chapter 1). In the case of the biotic factors involved in the interplay, RRs possibly started the decreasing trend prior to the fire increase, and taxa evenness decreased roughly eight centuries after fires increased (~6000-5160 cal yr BP) (chapter 3). Hence, it is considered that fires could not have influenced the behaviour of the biotic factors analysed. It has been long considered that in humid savannas a negative feedback between fire (natural origin) and tree cover mediates transition between alternative ecosystem states (Hoffmann et al., 2012; Murphy and Bowman, 2012). The coexistence of wetter conditions, forest vegetation and fires during this period might be explained by land-use practices linked to fires (chapter 1). Thus, the potential anthropogenic origin of fires in Encantada could have made this feedback inoperable. Therefore, despite the presence of rainforest patches with medium levels of moisture, fires exhibited high occurrence (chapters 1 and 3). Evidence of similar vegetation change in the GS comes again from El Paují record around 5040 cal yr BP (Montoya et al., 2011a). In this sequence, only two environmental proxies were evaluated: fire and hydrological balance (Montoya et al., 2011a). Based on the available evidence, the authors suggested that the expansion of savanna could have been a consequence of forest burning, probably caused by humans (Montoya et al., 2011a). During the vegetation shift described, climate was wetter in Encantada and El Paují (chapters 1 and 3; Montoya et al., 2011a). Therefore, climate in the south of the GS seems not to have played a part in the retraction of forest patches (chapter 3; Montoya et al., 2011a). Instead, fire was probably an important driver of this vegetation shift.

In the interval between 2190 and 1600 cal yr BP, drier climate-fire and fire-erosion interactions probably contributed to the change from savanna-forest mosaic to grassland in Encantada's basin (chapters 1 and 3). Decrease in diversity was associated with this vegetation change (chapter 3). Thus far, the evidence from the studied savanna areas of the GS suggests that the reduction in forest patches that led the modern treeless savanna was the result of fire action (Lake Chonita, El Paují, Encantada peat bog; Fig. D1; Montoya et al., 2009; Montoya et al., 2011a,b; Rull et al., 2013), possibly in combination with drier climate (Divina Pastora, Santa Teresa, Fig. D1; Rull, 1992; Rull et al., 2013). The results from this thesis disagree with these inferences in the sense that drier conditions could have been as important as fire regime during this vegetation shift (chapter 3). Previous studies of the GS also suggest that the vegetation change described was characterised by continuous impoverishment of taxa (Encantada peat bog, Divina Pastora, Santa Teresa, Urué; Fig. D1; Montoya et al., 2009; Rull, 1992, 1999). The results of Encantada's basin agree with such decreasing trend in diversity.

The evidence from Lake Encantada suggests that the vegetation changes towards reduction in tree cover were driven by a multifactorial interplay: fire regime (repetitive fires or higher fire occurrence), erosion, decrease in taxa evenness and low RRs and hydrological balance. Erosion was likely promoted by fires, rather than by increased rainfall or droughts (chapter 1). Thus, the interplay between fire and erosion is an ecological process that should be considered in the study of dynamics of humid savannas. In dry savannas, the tree-grass dynamics is often attributed to water scarcity, which limits the growth of forest trees (Accatino and De Michele, 2013). The evidence from this thesis suggests that if availability of fuel loads is high, low hydrological balance could be an important stressor in humid savannas. Future studies should evaluate whether low available moisture is also an important stressor under reduced availability of fuel loads or extensive forest patches. In order to conduct management plans seeking to avoid loss of tree cover, the knowledge gained in this thesis informs that the interplay fire-erosion, moisture level, RRs and taxa evenness should be monitored.

1.2.1. Change from dense woody communities to treeless savanna during the Late Glacial: origin of open savanna

This vegetation change occurred during a period characterised worldwide by marked climate changes (Late Glacial) and has been registered in three locations of the GS (Fidencio, Lake Chonita, Mapaurí) (chapter 2; Montoya et al., 2011c; Rull, 2007). This vegetation shift is particularly important because it seems to be the origin of grassland in those locations (Rull et al., 2015a). In this subsection, a more detailed evaluation of the origin of grassland vegetation is presented.

In Fidencio (chapters 2 and 3, and Appendix A2.2), small savanna areas in mosaic with extensive woody patches probably existed between ~12,385 and 12,100 cal yr BP. Forest patches retracted significantly and grassy vegetation expanded around 12,100 cal yr BP (chapter 2). As a result, grassland vegetation established in the area, coinciding with a marked decrease in plant diversity (chapter 3). The origin of grassland as the dominant plant community occurred roughly four centuries before the oldest date reported in the region (11,700 cal yr BP in Lake Chonita's basin; Montoya et al., 2011c). It is worth noting that in Fidencio, high occurrence of fires was already present before the origin of open vegetation. In additon, fires increased just after the woody patches started to decline. Local available moisture was increasing; however, climate was still dry. The evidence presented in this thesis and the regional climate information available (moisture and temperature; Haug et al., 2001; Lea et al., 2003) for the period of savanna openning suggests that the synergy between several factors such as rapid warming at the end of the Younger Dryas, drier climate than the present, fire occurrence (natural and/or anthropogenic), availability of fuel loads (Rull et al., 2013) and decreased diversity, resulted in the origin of grassland in Fidencio. Therefore, our findings indicate that the origin of open vegetation was probably caused by a multifactorial synergism, which was not triggered only by fire occurrence nor increased burning. These findings are significant to better understand vegetation dynamics of humid savannas. Since the origin of open vegetation occurred first in Fidencio than in the Lake Chonita´s basin and Mapaurí (chapter 2; Montoya et al. 2011c; Rull, 2007), it is worth discussing whether the aforementioned synergism also influenced the vegetation turnover in the latter two locations.

In the basin of Lake Chonita, shrublands existed at least between ~12,700 and 11, 700 cal yr BP, which were replaced by treeless savanna under the influence of climate (global warming) and fire in ~11,700 cal yr BP (Montoya et al., 2011c). Fires occurred during the shrubland-interval, though at low frequency/intensity (Montoya et al., 2011c; Rull et al., 2015a). Subsequently, fires exhibited a significant increase during the vegetation change (Rull et al., 2015a). These results partially agree with those obtained in Fidencio. Hence, based on the results of Fidencio and Chonita, it is hypothesized that fire action alone did not trigger the origin of the open savanna in the south of the GS. Instead, fires seem to have played a part in the retraction of woody communities and further maintenance of grassy vegetation (Montoya et al., 2011c). Regarding the availability of fuel loads, the pollen sum in Chonita's sequence is represented by 10% of herbaceous pollen (Montoya et al., 2011c). This value indicates that savanna vegetation was not present at the exact Chonita's coring site before the origin of open savanna. It was suggested that grasses found in Chonita were probably a minor component of the regional vegetation and/or the shurbland understory (Rull et al., 2015a).

In Mapaurí peat bog (Fig. D1), the replacement of a cloud forest by grassland near the slope of a Tepui mountain was interpreted as the result of warming around 10,200 cal yr BP (Rull, 2007), coinciding with the Early Holocene Warming (Rull et al. 2015a, 2013). The Mapaurí vegetation shift was recorded at the same time as the presence of regional fires (Rull, 2009). The dramatic increase in regional fires during the interval of replacement of forests by open savanna suggests that fire would have played a significant role in the landscape shift of Mapaurí (Rull et al., 2013). In addition, this result would suggest that fires did not trigger the dramatic retraction of the cloud forest (Rull, 2007). At the beginning of forest decline, the percentage of herbaceous pollen (signicantly dominated by Poaceae) was approximately of 20% (Rull, 2007). In the GS, studies of modern pollen rain indicate that in forest areas Poaceae pollen may represent 1-25% of total pollen (Leal et al., 2013). Therefore, savanna vegetation is likely not to have existed at the exact Mapaurí's coring site before ~10,200 cal yr BP. Similarly to Chonita, the Poaceae pollen grains recorded in Mapaurí were probably sourced from neighbouring savanna areas or component of the forest understory.

The algal record of the three locations may indicate dry climate in spite of an increase in moisture during the origin of open vegetation (chapter 2; Montoya et al., 2011c; Rull, 2007). Therefore, the available evidence suggests that the synergy between fire, drier climate, warming and possibly availability of fuel loads could have influenced the replacement of woody vegetation by grassland in Fidencio, Chonita and Mapaurí. Absence of diversity analysis for the sequences of Chonita and Mapaurí prevented us from evaluating any potential role of diversity in driving the vegetation change described. Rull (2007) postulated two potential scenarios during the origin of open savanna during the Late Glacial: (1) savannas simply expanded from existing small savanna patches in the surrounding area, and (2) open savanna emerged as a new vegetation type in the region. In light of the available evidence, it is suggested that savannas could have expanded from existing small savanna areas rather than emerging as a new vegetation type. Finally, absence of independent proxies for temperature and moisture in the three locations studied limited our ability to make a better analysis of climate conditions in the GS during the Late Glacial (chapter 2), and therefore, better understand the origin of open vegetation.

1.3. Predominance of open savanna state

The evidence from Lake Encantada and Fidencio agrees with the hypothesis that the positive feedback between fire and herbs (fuel loads) is likely to have caused long-term predominance of open savanna condition in different periods (Lake Encantada: ~8700-7720 cal yr BP and the last ~1600 years; Fidencio: between ~12,000 and 9520 cal yr BP). It is recognised in other studies in the GS and elsewhere that this feedback maintains humid savannas in open condition (Accatino et al., 2013; Rull et al., 2013).

In the basin of Lake Encantada, this positive feedback was reinforced by drier conditions during the interval 2000 cal yr BP-the present (chapters 1 and 3). Furthermore, the synergistic action between fire and erosion appears to have been enhanced by open vegetation (chapter 1). However, in Fidencio the open savanna condition occurred under wet climate (chapter 2). It is interpreted that wetter and warmer conditions may have promoted high production of grasses to fuel the fires. In addition, human activites may have influenced the ignitions (chapter 2). In dry savannas, fires are limited by low production of herbs due to low available moisture. On the contrary, in humid savannas, and particularly in the GS, the availability of herbs seems not to have been a limiting factor. There were probably continuous fuel loads to burn, even during dry conditions. Thus, the feedback fire-herbs could have settled easily and maintained in humid savannas of the GS (at least the two locations studied) for long periods.

2. Potential future vegetation responses and their ecosystem management

Future vegetation responses to climate change have been scarcely studied in savanna ecosystems. In this thesis, it is proposed that the remarkable expansion of grassy vegetation observed during the Late Glacial could be considered as a potential past analogue of the current and future environmental setting for the GS region (chapter 2), as it has been proposed for other Neotropical locations (Vegas-Vilarrúbia et al., 2011, Rull et al., 2015a,b), and elsewhere (Cole, 2009). This means that the current grassland areas might expand in the near future similarly to what was observed historically. The palaeoecological evidence from the sequences of Lake Encantada and Fidencio indicates that decrease in tree cover within savanna has been highly associated with loss of diversity (mainly taxa evenness), decrease in resilience and RRs (chapter 3). Moreover, based on available evidence, it is suggested that future warmer and drier conditions forecasted for northern South America (Magrin et al., 2014) could promote a stronger positive feedback between fire, erosion and herbs. Interruption of this feedback (e.g. by limiting fires at the end of wet periods when there is high accumulation of grasses and climate is becoming drier) would permit managers to increase forest patches, which may cause increase in diversity and resilience (chapter 3). Therefore, the potential scenario: increasing grassy vegetation, stronger interplay fire-erosion-herbs and loss of diversity and resilience, is extremely important to be considered in adaptive management and restoration strategies for the GS region.

EDELCA managers (the regional hydro-electric company) has long pursued a strategy to detect, prevent and supress fires in the region, in an attempt to prevent loss of riverine forests (Sletto, 2008; Sletto and Rodríguez, 2013). However, ecological studies have shown that the *fire suppression strategy* is having unexpected consequences, most of them detrimental to the GS ecosystem (Bilbao et al., 2010; Stetto and Rodríguez, 2013). On the other hand, a few scholars have proposed that *fire management strategy* should be conducted in the region (Bilbao et al., 2010; Sletto, 2008; Sletto and Rodríguez, 2013). This strategy consists in the prevention of accumulation of fuel loads.. To do so, the authors propose that grasses should be burnt frequently. Fires should be small and be lit in the right time (e.g. rainy season). If not, dead and dry grasses would accumulate and lead to uncountrollable fires, which might enter forests. In this way, creation of savanna patches with different fire histories could be used to create firebreaks, which reduce the risk of wildfires and enhance habitat heterogeneity (Bilbao et al., 2010). This system of use of fire resembles the ancentral fire management used by local inhabitants of the etnia *Pemón* (Bilbao et al., 2010). Based on palaeoecological evidence and results from neoecological studies, it is proposed that *fire management* is the most appropriate strategy for the sake of vegetation conservation.

3. Use of different type of proxies to refine palaeoecological evidence

In sections 1 and 2, it was explained how the use of indicators additional to pollen grains and charcoal particles (e.g., diversity indices, magnetic susceptibility as erosion indicator and RRs) provided valuable information to evaluate vegetation dynamics. In this section, some results are explained in which the use of different geo-chemical proxies helped to refine interpretations, mainly of the aquatic systems.

In the case of Lake Encantada sequence (chapter 1), the geochemical proxies used and lithologological information handled by an expert geologist (collaborator of the research group) permitted us to assess the origin and ontogeny of the lake, that otherwise would had been practically impossible using only algal remains. The evidence suggests that the coring site experienced a change from fluvial sedimentary environment to a lacustrine one. Thus, the absence of lacustrine sediments older than 9700 cal yr BP was possibly not only due to drought (regional climate was dry at that time), but probably to flowing waters that impeded the sedimentation of any material. Moreover, the relationships between the XRF elements and lithology were crucial to identify potential intervals of connexion and disconnection with the fluvial system (between 8700 and 6700 cal yr BP). The available evidence suggests that riverine dynamics could have been driven by variations in drainage patterns rather than climate conditions (hydrological balance). If this was the case, any inference of available moisture during the fluvial phase could not be based just on the algal record. This finding can add evidence to support the hypothesis that states the GS has had an active hydrological system (e.g., anastomosing river; Schubert et al., 1986). Furthermore, this finding suggests that aquatic and terrestrial dynamics were driven by different factors during the aforementioned interval. Hence, both ecosystem compartments must be evaluated separately (chapter 1).

On the other hand, the nitrogen and carbon isotopes analysed in the same sequence provided useful information to evaluate the aquatic system, mainly $\delta^{15}N$ (chapter 1). Low values of $\delta^{15}N$ (<1‰) suggested that aquatic productivity was mostly ruled by nitrogen-fixing bacteria (e.g. interval B-2 and the last 1500 years). Thus, if the system was nutrient-limited, the analysis of algae based only on their abundances could lead to misleading interpretations of moisture conditions. For instance, low concentrations of algae may not mean in all cases dry conditions, but probably aquatic productivity not dominated by algae. These findings suggest that in the GS the analysis of composition-abundance of algae should be complemented with isotopic analyses. Moreover, this suggests that an independent proxy for humidity is necessary to include in paleoecological studies (e.g., $\delta^{18}O$ of aquatic cellulose; Buhay et al., 2012; Wolfe et al., 2007).

In Fidencio record (12,725-9520 cal yr BP, chapter 2), a detailed analysis of the lithology also permitted to assess the origin of the lake and the development of depositional environments. It was found that the environment surrounding the coring site changed, from terrestrial to lacustrine and then to peat bog (wetland). In a similar way to Lake Encantada's basin, variations of depositional environmental greatly influenced the surrounding vegetation. For instance, lacustrine environment was related with gallery forests, peat bog with meadows dominated by *Xyris*, and terrestrial soil characterised by the virtual absence of pollen of aquatic plants (chapters 2).

4. Research limitations and future studies

Although this research has reached its aims, I am aware of its limitations and shortcomings. I will describe them and explain how important they are. Finally, I propose possible future directions for palaeoecological research in the GS region.

4.1. Limitations

Study design limitations:

- The sampling resolution (3 and 5 cm) of both sequences (Lake Encantada and Fidencio) provided centennial to multi-centennial resolution of the samples. I have noticed that evaluation of vegetation responses (mainly during sensitive climate periods) requires higher sample resolution (decadal or annual in intervals of interest, if possible). Otherwise, rapid responses, the ecological processes involved and the exact timing of their occurrence cannot be identified. This lack of information limited us to achieve a better assessment of vegetation dynamics in the two sequences.

- Identification of the type of vegetation burnt. The charcoal analysis did not allow us to distinguish fires ignited in savanna areas from forest patches, nor what taxa were burnt. This information could have been of paramount importance to better evaluate the dynamics vegetation-fire.

- At the beginning of the study of Fidencio, magnetic susceptibility (MS) was the only available physico-chemical proxy for that sequence. MS could be a good indicator of soil erosion (Sandgren and Snowball, 2001). However, the information provided by this proxy was confusing. The geologist expert concluded that the evaluation of MS required the information of a suite of physico-chemical indicators and a more detailed analysis of lithology, which we did not have. Therefore, we decided not to include the results of MS in chapter 2. Since erosion could have been an important process in vegetation dynamics of Encantada's basin (chapter 1), the lack of a multiproxy approach for Fidencio's sequence prevented us from evaluating catchment processes and their potential influence in vegetation dynamics of Fidencio's basin.

Data limitations:

-Age control. This was an important limitation of Fidencio's sequence in the interval between 321 and 280 cm (ages reported by the available age-depth model ~12,725 and 12,000 ± 50 cal yr BP). Due to this limitation, it was not possible to relate the vegetation shifts to the abrupt start of the YD or determine whether vegetation shifts occurred during the Bølling-Allerød/YD transition.

Lack of complementary information:

-Pollen identification. Although new pollen atlases of the GS were available (Leal et al., 2011), some taxa were not fully identified yet or their identification level was not detailed (e.g., family level). Accurate identification of such taxa (e.g. Poaceae) would have permitted a better assessment of the ecology of communities composed by them.

- Independent proxies for temperature and hydrological balance. Analysis of vegetation responses in Fidencio (e.g., origin of grassland) to abrupt climate changes during the Late Glacial was limited by the absence of independent proxies of temperature and moisture. Concerning Encantada's sequence, the analysis of available moisture based on algae was limited in some cases by the fluvial-lacustrine dynamics and nutrient-limited system. Hence, an independent proxy for moisture would have been_useful to infer better the variations of hydrological balance.

- Since archaeological records are lacking in the GS, it was not possible to relate closely the fire regimes with human activities in both sequences, and thus discern between natural and man-made fires. Therefore, hypothesis about potential anthropogenic origin of grassland and land use patterns are still open to test (Rull, 2009; Montoya and Rull, 2011; Montoya et al., 2011a).

4.2. Future studies

Most previous palaeoecological studies in the GS share similar limitations (Montoya and Rull, 2011; Montoya et al., 2011a,b,c; Rull, 1992, 1999, 2007). Nonetheless, the aforementioned limitations could be overcome in future studies. With this aim, I would like to suggest several proposals:

- To get better age control, more accurate age-depth models are necessary (if possible). In addition, in accordance with the resulting sedimentation rates, it is strongly recommended to design the sampling resolution strategy.

-In order to get a multiproxy approach, future palaeoecological studies should be based on, but not limited to pollen, spores, algal remains, charcoal particles, physico-chemical proxies, sedimentology, local independent proxies for temperature and hydrological balance, and diversity measurements.

- Charcoal analysis should be improved by comparative analysis between paleo-charcoal morphotypes and charcoal produced by burning modern plant material, in order to recognise the type of vegetation burnt (e.g., herbs-savanna fires, woody taxa-forest fires). It has been proved by experiments that different taxa produce recognisable charcoal types that are preserved in sediments (Jensen et al., 2007).

- Finally, it is recommendable to make more detailed survey of modern-day vegetation and its posterior palynological collection.

5. REFERENCES

Accatino, F., De Michele, C., 2013. Humid savanna–forest dynamics: A matrix model with vegetation–fire interactions and seasonality. *Ecol. Model*. 265, 170–179.

Bilbao, B.A., Leal, A.V., Méndez, C.L., 2010. Indigenous Use of Fire and Forest Loss in Canaima National Park, Venezuela. Assessment of and Tools for Alternative Strategies of Fire Management in Pemón Indigenous Lands. *Hum. Ecol*. 38, 663–673.

Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. *New Phytologist*. 165, 525-538.

Buhay, W.M., Wolfe, B.B., Schwalb, A., 2012. Lakewater paleothermometry from Deep Lake, Minnesota during the deglacial Holocene transition from combined $\delta^{18}O$ analyses of authigenic carbonate and aquatic cellulose. *Quaternary International*. 260, 76-82.

Cole, H., 2009. Vegetation responses to early Holocene warming as an analog for current and future changes. *Conservation Biology*. 15, 601-612.

Dezzeo, N., Chacón, N., Sanoja, E., Picón, G., 2004. Changes in soil properties and vegetation characteristics along a forest-savanna gradient in southern Venezuela. *For. Ecol. Manag.* 200, 183–193.

Fölster, H., Dezzeo, N., Priess, J., 2001. Soil-vegetation relationship in base-deficient premontane moist forest-savanna mosaics of the Venezuelan Guayana. *Geoderma*. 104, 95-113.

Gillson, L., 2004. Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity*. 1, 281–298.

Gillson, L., Ekblom, A., 2009. Resilience and Thresholds in savannas: Nitrogen and Fire as drivers and responders of vegetation transition. *Ecosystems.* 12, 1189-1203.

Haugh, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward Migration of the Intertropical Convergence Zone Through the Holocene. *Science*. 293, 1304-1308.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett*. 15, 759–768.

Lea, D.W., Pak, D.K., Peterson, L.C., Hughen, K.A., 2003. Synchroneity of tropical and high-latitude Atlantic temperatures over the last Glacial Termination. *Science*. 301, 1361-1364.

Leal, A., Bilbao, B., Berrío, J.C., 2013. A Contribution to Pollen Rain Characterization in Forest-Savanna Mosaics of the Venezuelan Guayana and Its Use in Vegetation Reconstructions from Sedimentary Records. *American Journal of Plant Sciences.* 4, 33–52.

Magrin, G.O., J.A. Marengo, J.-P. Boulanger, M.S. Buckeridge, E. Castellanos, G. Poveda, F.R. Scarano, and S. Vicuña, 2014: Central and South America. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1499-1566.

Montoya, E., Rull, V., 2011. Gran Sabana fires (SE Venezuela): a paleoecological perspective. *Quat. Sci. Rev*. 30, 3430–3444.

Montoya, E., Rull, V., Nogué, S., Díaz, W.A., 2009. Paleoecología del Holoceno en la Gran Sabana, SE Venezuela: Análisis preliminar de polen y microcarbones en la Laguna Encantada. *Collectanea Botanica,* 28, 65–79.

Montoya, E., Rull, V., Nogué, S.,2011a. Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE Venezuela): Palynological evidence from El Paují record. *Palaeogeogr. Palaeoclimatol. Palaeoecol*. 310, 413–426.

Montoya, E., Rull, V., Stansell, N.D., Abbott, M.B., Nogué, S., Bird, B.W., Díaz, W.A., 2011b. Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quat. Res*. 76, 335–344.

Montoya, E., Rull, V., Stansell, N.D., Bird, B.W., Nogué, S., Vegas-Vilarrúbia, T., Abbott, M.B., Díaz, W.A., 2011c. Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas chron. *J. Quat. Sci.* DOI: 10.1002/jqs.1445

Murphy, B.P., Bowman, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna? *Ecol. Lett.* 15, 748–758.

Rull, V., 1992. Successional Patterns of the Gran Sabana (Southeastern Venezuela) Vegetation During the Last 5000 Years, and its Responses to Climatic Fluctuations and Fire. *J Biogeogr.* 19, 329-338.

Rull, V., 1999. A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela. *J. Quat. Sci*. 14, 137–152.

Rull, V., 2007. Holocene global warming and the origin of the Neotropical Gran sabana in the Venezuelan Guayana. *J. Biogeogr*. 34, 279–288.

Rull, V., 2009. New paleoecological evidence for the potential role of fire in the Gran Sabana, Venezuelan Guayana, and implications for early human occupation. Vegetation History and Archaeobotany 18, 219-224.

Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T., Safont, E., 2013. Ecological palaeoecology in the neotropucal Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. *Perspectives in Plant Ecology, Evolution and Systematics.* 15, 338–359.

Rull, V., Montoya, E., Vegas- Vilarrúbia, T., Ballesteros, T., 2015a. New insights on palaeofires and savannisation in northern South America. *Quaternary Science Reviews.* 122,158-165.

Rull, V., Vegas-Vilarrúbia, T., Montoya, E., 2015b. Neotropical vegetation responses to Younger Dryas climates as analogs for future climate change scenarios and lessons for conservation. *Quaternary Science Reviews.* 115, 28-38.

Sandgren, P., Snowball, I., 2001. Aplication of mineral magnetic techniques to Paleolimnology. In: Last, W., Smol, J.P (eds.) Tracking Environmental Changes Using Lake Sediment. Volumen 2. Springer Netherlands. pp 217-237.

Schubert, C., Briceño, H.O., Fritz, P., 1986. Paleoenvironmental aspects of the Caroní-Paragua river basin (southeastern Venezuela). *Interciencia.* 11, 278-289.

Sletto, B., 2008. The Knowledge that counts: Institutional identities, policy science, and the conflict over fire management in the Gran Sabana, Venezuela. *World Development*. 36(1), 1938-1955.

Sletto, B., Rodríguez, I., 2013. Burning, fire prevention and landscape productions among the Pemon, Gran Sabana, Venezuela: towards and intercultural approach to widland fire management in Neotropical savannas. *Journal of Environmental Management.* 115, 155-166.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E., 2011. Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. *Quaternary Science Reviews*. 30, 2361-2388.

Wolfe, B.B., Falcone, M.D., Clogg-Wright, K.P., et al., 2007. Progress in isotope paleohydrology using lake sediment cellulose. *Journal of Paleolimnology*. 37, 221-231.

CONCLUSIONS

General conclusions

-Savannisation has not occurred continuously from the Late Glacial to the present. Instead, two savannisation processes have been recorded that correspond to different periods: the Late Glacial (13,000-10,000 cal yr BP) and the last ~5400 years, the latter has resulted in the present-day treeless savanna. Fire (natural or anthropogenic, or both) has been an influential driver of both processes, which have been associated with decrease in diversity, loss of resilience and erosion. The positive feedback between fire and herbs has accentuated both savannisation processes. Similar trends in savannisation have occurred in the other savanna localitites of the GS.

- Vegetation changes from forest areas to savanna appear to have been irreversible on the timescales studied.

-Fire alone has not driven the vegetation dynamics in the two locations studied. Instead, vegetation changes (either decreased or increased tree cover) have resulted from the interplay between fire and different sets of environmental factors (biotic and abiotic).

-Woody communities dominated during the Late Glacial. The synergitic effect of a number of environmental factors caused the origin of grassland vegetation during this period.

Specific conclusions

The specific conclusions are based on the specific objectives of the thesis, which are sorted out by chapters.

Chapter 1 (An 8700-year record of the interplay of environmental and human drivers in the development of the southern Gran Sabana landscape, SE Venezuela):

Objective 1: To evaluate the interplay and synergies between vegetation, climate (hydrological balance), fire and soil erosion, and the associated feedback processes, since the early Holocene.

-The predominance of savanna during early-middle Holocene (~8700-6700 cal yr BP) was probably the result of the positive feedback between dry conditions, fires, and grassy vegetation. Fire regime may have been unaffected by humans during this interval.

-The synergistic action between reduced fires and wetter climate appears to have been determinant in the development of rainforests (forest-savanna mosaic) around 6400 cal yr BP. However, even though wet climate occurred from ~5400 cal yr BP, vegetation in the basin changed to open savanna with forest patches. Forest burning could have contributed greatly to the vegetation shift, potentially driven by human-land use practices.

- Modern treeless savanna with *morichales* surrounding the lake established around 1700 cal yr BP. This vegetation change was possibly related to a change to savanna-like culture with extensive use of fire in open landscape. Positive feedback between drier conditions, fires and herbs could have maintained the treeless savanna vegetation for the ~last two millennia.

- Soil instability (erosion) was likely promoted by increased fire occurrence. Thus, the synergy between fire and erosion could have contributed greatly to destabilise the forest patches since the middle Holocene, enabling the aforementioned savanna expansions.

Objective 2: To test the hypotheses about the long-term presence savanna vegetation.

-The current vegetation of Lake Encantada's basin is the result of the complex interplay between climate, fire, erosion, and vegetation.

Chapter 2 (Vegetation changes during the Late Glacial in the uplands of the Gran Sabana (SE Venezuela): insights of the origin of grassland):

Objective 1: To analyse the vegetation responses to the abrupt climate changes during the Late Glacial.

- Very low pollen counts between ~12,725 and 12,385 cal yr BP prevented us from evaluating the vegetation responses to the abrupt YD's cooling. Therefore, based on the available evidence to date, it was not possible to discern vegetation responses to the YD's abrupt cooling in flat areas of the GS nor determine whether vegetation shifts occurred during the Bølling-Allerød/YD transition

-Vegetation responses were driven by the interplay between climate (hydrological balance, temperature), fire occurrence and availability of fuel loads between ~12,385 and 9520 cal yr BP (upper half of the Younger Dryas and early Holocene).

Objective 2: To evaluate the alternative hypotheses about the origin of southern GS savannas.

-The most likely cause of origin of treeless savanna in Fidencio was the synergy between warming, drier climate than the present, fire occurrence (natural, anthropogenic, or both), and availability of fuel loads. This multifactorial synergism appears to have been strong enough to destabilise the Late Glacial forests, leading the change towards treeless savanna.

- The available evidence suggests that the synergy of factors which may have occurred in Fidencio could have also operated in Mapaurí and Chonita at the origin of open vegetation.

Objective 3: To assess whether vegetation shift at the Younger Dryas-Holocene transition could be considered a past analogue of the the global warming.

-The forests replacement by grassland at the YD-Holocene transition could be considered as a potential past analogue of the current and future environmental setting for the GS region. This suggests that grassland vegetation might expand similarly to that observed historically.

Chapter 3 (Long-term evaluation of vegetation resilience and regime shifts in a savanna region (the Gran Sabana, SE Venezuela):

Objective 1: To assess resilience and regime shifts for the last ~13,000 cal yr BP, based on the palaeoecological information provided by the two sequences studied in the previous chapters.

-Forest patches in the basin of Lake Encantada were resilient to fire disturbance during specific intervals, on a centennial timescale. It is proposed that the interplay between particular abiotic (medium to high levels of available moisture, selective burning) and biotic (medium-high degree of taxa equitability, high Rates of Recovery-RRs) factors could have contributed to resilience of past forests communities in the basin.

-The interplay between lower fire occurrence, increase in diversity and high RRs was associated with the regime shifts characterised by expansion of tree cover within savanna.

- The interplay of a number of factors such as repetitive fires, drier climate, decrease in diversity and low RRs, probably contributed to loss of resilience in Encantada's basin.

-Concerning Fidencio's area, the evidence indicates that the Late Glacial forests were not resilient to a number of disturbances. The vegetation change towards grassland (regime shift) was characterised by a remarkable decreasing trend of diversity.

- Loss of resilience in both locations studied could be considered as a phenomenon highly associated with expansion and domination of grasses.

APPENDIX

List of Appendices

Chapter 1

Chapter 2

A1. Main plant communities and their dominant taxa in the GS

Plant formation	**Dominant taxa**
Forest –montane type (800-1500 a.s.l)	*Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignonaceae), *Anaxagorea* (Annonaceae), *Alexa* (Fabaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Simarouba* (Simaroubaceae), *Porouma* (Cecropiaceae), *Byrsonima* (Malpighiaceae), etc.
Morichales (also considered as savanna with palms)	Large stands of the palm *Mauritia flexuosa* (Arecaceae) accompanied by the following plant formations: Grasses-*Hypogynium, Andropogon*, *Panicum* (Poaceae); Sedges-*Rhynchospora* and *Bulbostlylis* (Cyperaceae). Shrubs-*Miconia* (Melastomataceae), *Mahurea* (Calophyllaceae), *Piper* (Piperaceae).
Shrubland-sclerophyllous type	*Euphronia* (Euphroniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Byrsonima* (Malpighiaceae), etc.
Savanna	C_4 grasses-*Axonopus* and *Trachypogon* (Poaceae) Sedges-*Bulbostylis*, *Rhynchospora*, *Hypolytrum* and *Scleria* (Cyperaceae).

A2.1. Percentage diagram of pollen modern sample

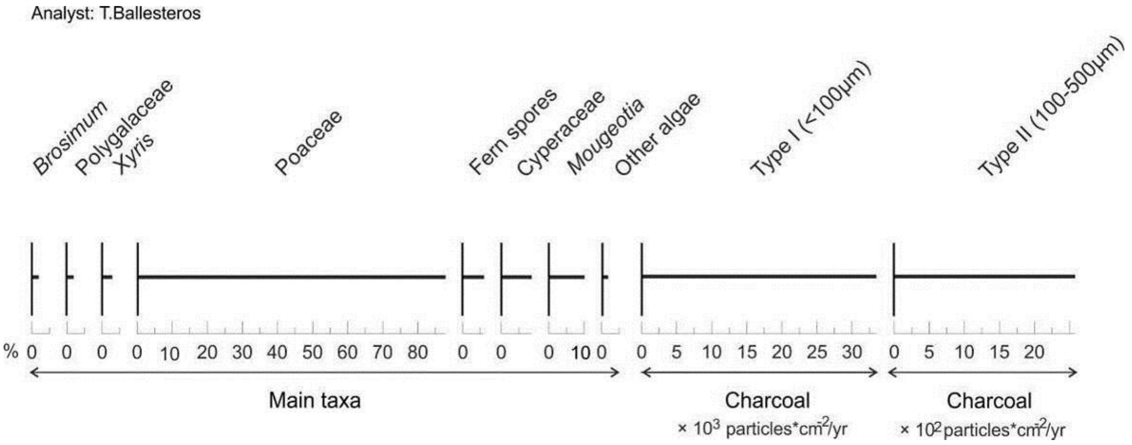


Figure A2.1. Diagram of the modern sample, showing the abundances of pollen, fern-spores, aquatic plants and algal remains expressed in percentages.

A2.2. Percentage diagram of fossilpollen

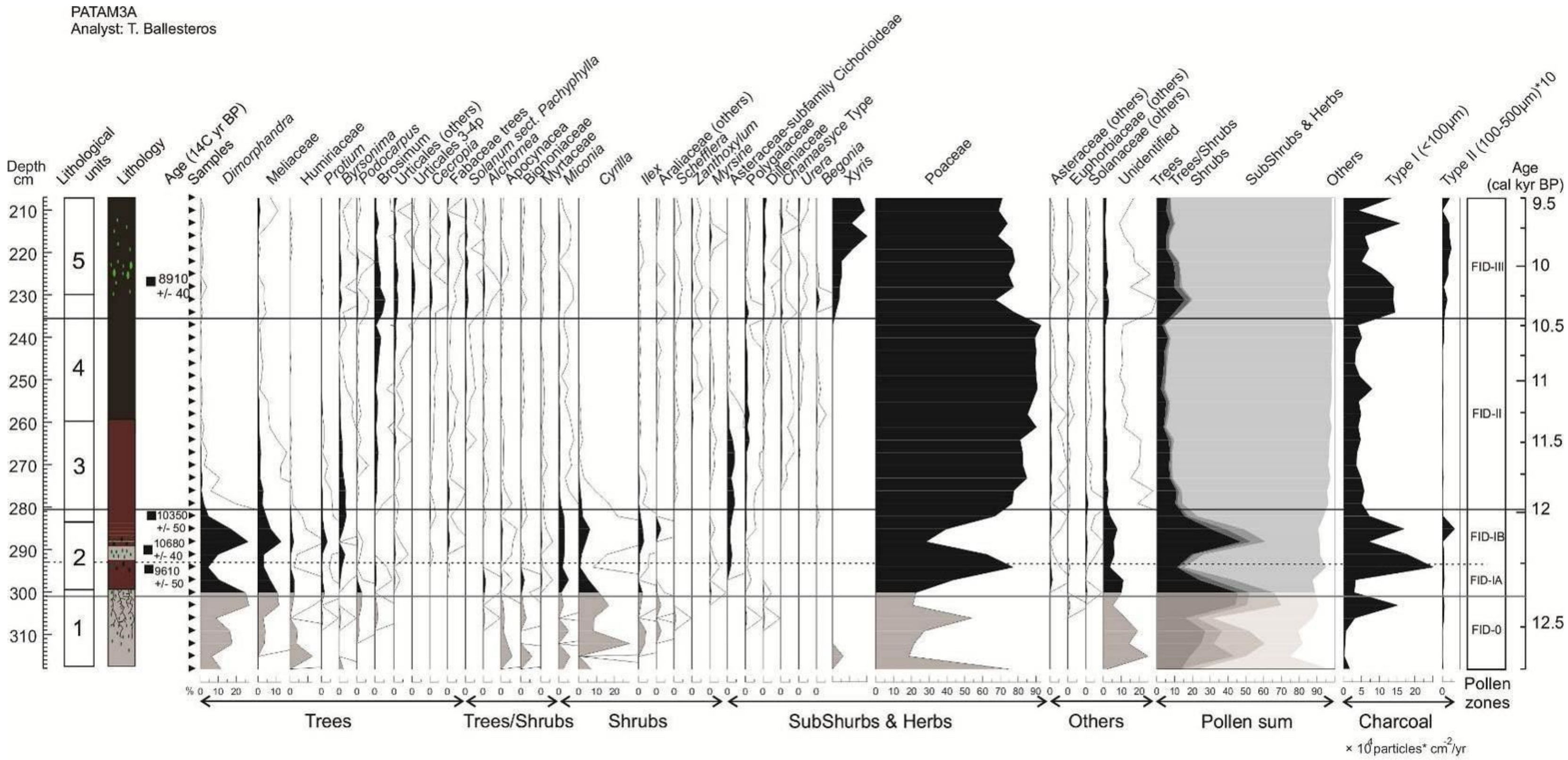


Figure A.2.2. Diagram showing pollen taxa and charcoal particles expressed in percentages and influx values, respectively. Solid lines represent ×10 exaggeration. The pollen counts of FID-0 are below 150 grains, so percentages similar to other zones might be a methodological artefact. Therefore, FID-0 was considered as an independent zone and was not included in the zonation analysis.

A2.3. Percentage diagram showing the elements outside de pollen sum of fossil pollen

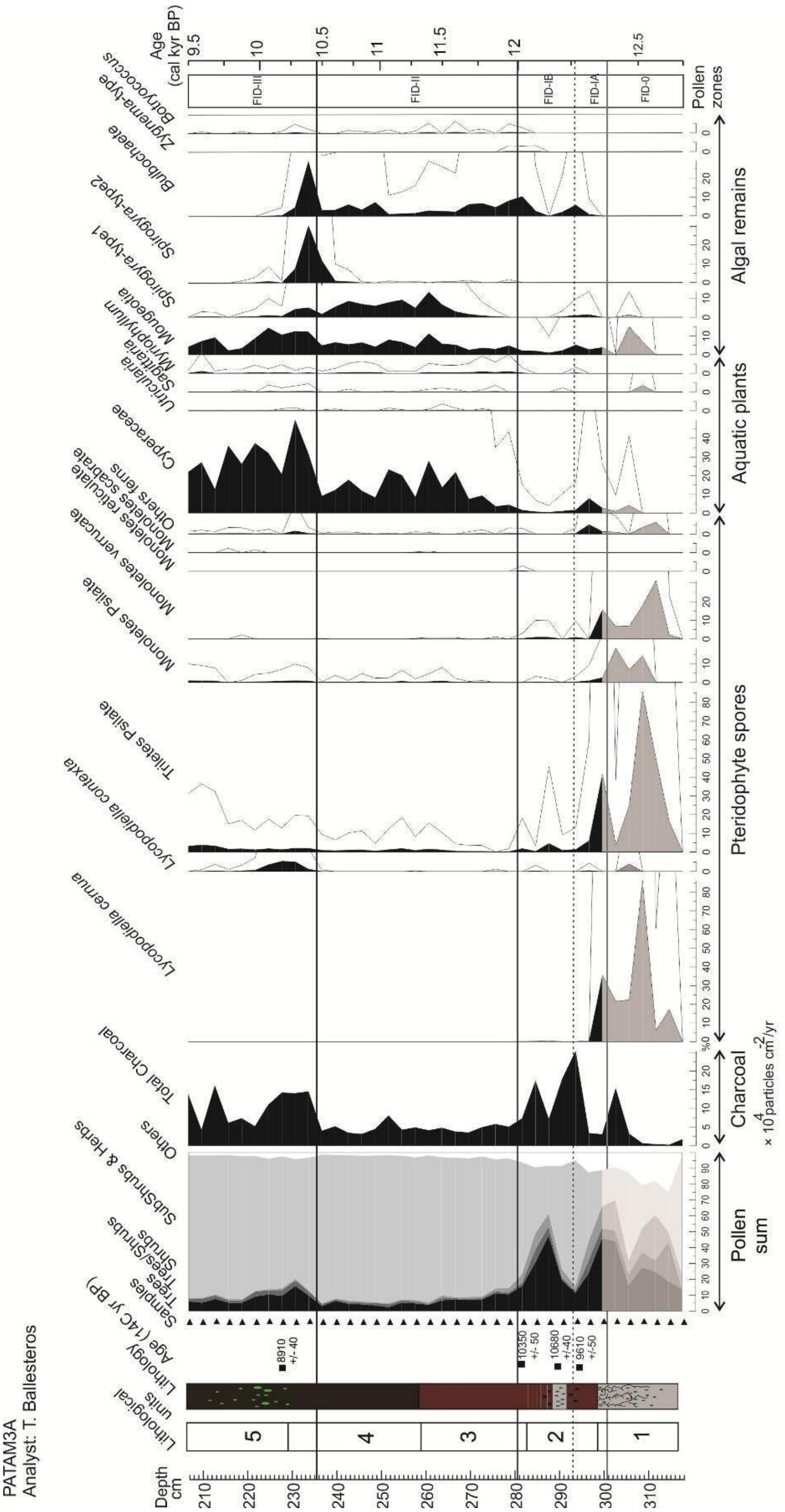


Figure A.2.3. Diagram showing the elements outside the pollen sum, such as theaquatic and semi-aquatic plants, pteridophyte spores and algal remains. The abundances are expressed in percentages with respect to the pollen sum. Solid lines represent x10 exaggeration. Plot of zone FID-0 follows the same structure as figure A1.