Paleoecology of the southern Gran Sabana (SE Venezuela) since the Late Glacial to the present.

Departament de Biologia Animal,
Biologia Vegetal i Ecologia,
Universitat Autònoma de
Barcelona.

Laboratori de Palinologia i
Paleoecologia, Institut Botànic
de Barcelona (IBB-CSIC-ICUB)

Encarnación Montoya Romo
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Memòria de tesi presentada per:
Encarnación Montoya Romo
Per optar al títol de Doctor en Biologia de la Universitat Autònoma de Barcelona.

Amb el vist-i-plau de:

Valentí Rull del Castillo
Laboratori de Palinologia i Paleoecologia
Institut Botànic de Barcelona (IBB-CSIC-ICUB)
Director de tesi.

Iñigo G. de la Cerda
Unitat de Botànica
Departament de Biologia Animal, Biologia Vegetal i Ecologia
Universitat Autònoma de Barcelona
Tutor de tesi.

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Dejé de contar los días, ya no tengo dedos suficientes,
para contar las penas y alegrías me hacen falta tus manos, vente!
El bicho; La azotea.

A Jose, por todo,

por siempre.

Señores y señoras, por fin estamos aquí. Parece que la tesis se resume en la publicación de un número X de artículos y la redacción y defensa de un manuscrito, pero desde mi punto de vista, supone mucho, muchísimo más. En este caso, han sido cuatro años de dedicación a la tesis y cinco años y medio desde mi llegada a Barcelona, en los cuales he pasado mucho (casi siempre bueno tengo que decir), y por supuesto siempre acompañada por personas que han hecho que este camino sea mucho más fácil y agradable. Pero además de esta época *culé*, mis intenciones doctorales comenzaron tiempo atrás. Al ser esta una tesis sobre paleoecología, con una marcada escala temporal, no se me ocurre una mejor manera que intentar resumir lo agradecida que estoy a la gente que ha vivido conmigo este periodo del mismo modo que se hacen las reconstrucciones temporales, es decir, mirando desde el pasado hacia el presente, y relatar este viaje como mi propia secuencia polínica, la secuencia EMR.

En toda secuencia hay una datación radiocarbónica clave, que además de intervenir en el modelo de edad, te ayuda a establecer la antigüedad de dicha secuencia. Es lo que yo llamo la edad-base del testigo. Sin duda, esa información tan importante en mi secuencia ha sido mi director Valentí Rull. El poder agradecerte Valentí todo lo que has hecho por mí me resulta casi imposible: la confianza depositada en mí (incluso antes de conocerme), el apoyo continuo tanto en lo profesional como en lo personal, los debates sobre las secuencias de la Gran Sabana, las charlas científicas en nuestros "ratos libres", inculcarme seguridad siempre en lo que hago, hacer que defienda aquello en lo que creo, poder empaparme un poco de tu conocimiento y de tu soberana paciencia (muchas veces frustrada conmigo), etc. En fin, por todo lo que has hecho y todo lo que has sido para mí durante este tiempo, sólo puedo decir GRACIAS.

Como ya he dicho, mis afanes *doctoriles* comenzaron bastante antes de obtener una beca predoctoral. Durante esos momentos de ilusión, miedos, y por qué vamos a negarlo, ignorancia, siempre ha habido alguien a mi lado para que no decayeran mis ánimos. Los principales, mi familia. Lo increíble de las familias no es que bajo un mismo techo vivan personas tan dispares como es nuestro caso, sino que estemos siempre próximos, apoyando y consolando cada vez que haga falta, sin importar las diferencias, ideales o ambiciones de cada uno; y lo más importante, sintiéndonos cercanos aunque haya de por medio un país. La primera parada es para mis padres: apoyar a una hija en su empeño por meterse en fangos hasta el cuello sin entender el por qué, es muestra de que el amor hacia las personas no se escoge. A mis hermanos les debo, entre otras muchas cosas, la capacidad de analizar al milímetro el mundo que me rodea. Mi familia es muy, pero que muy extensa, no sólo por la abundancia de primos, tíos, etc., sino porque la familia es algo más que compartir un apellido. Este es el caso de mi "hermana postiza" Fuen y su nueva familia; mis sobrinos mayores y sus padres, mi gemelo Diego y mi chancha Lidia; mi cuñadísima Isa; Tere y su *Zarissa*; la gente de Barriomar; etc. Todas las personas que son nombradas (y las que se me olvidan) son personas importantes en mi vida, pero si una de estas personas merece un apartado especial aquí, es mi héroe. Todas las personas tienen un héroe en su vida, y yo tengo a mi yaya. Muchas gracias Yaya por enseñarnos a todos lo que significa el esfuerzo, la entrega total a la familia, el orgullo, la lucha diaria por vivir, el amor incondicional, y la bondad (y en mi caso, decir verdades como puños). Son tantas las cosas que me has enseñado, que un doctorado no es suficiente para poder explicarlo. Esto va por ti chiquiliquichiquichurri.

Aún hay más gente en esta primera zona polínica o EMR-I, y como yo digo, atemporal en mi vida: aquí aparecen la gente del barrio (sois muchos y no nombraré a todos, pero no puedo pasar por alto a Willy y David, mis pellejeros incombustibles), que por muchas vueltas que dé la vida siempre nos vuelve a reunir, les agradezco personalmente que sean algo que no cambia en mi vida; y mis niñas (Leonor, Raquel, Lourdes, Llanos, María y Laura; y la incorporada María Ilino!), esas mujeres maravillosas (y sus respectivos por supuesto) que me aceptan y quieren aún cuando no conseguimos entendernos la mayoría de las veces.

La zona polínica EMR-II corresponde a mi paso por la UMU. Me licencié en la Universidad de Murcia y agradezco la formación recibida, enseñarme a mirar desde diferentes puntos de vista, y darme la posibilidad de encontrarme con algunos "morfotipos" muy importantes para mí. Sin Pepe Carrión es más que probable que yo hoy no estuviera aquí. No sólo por introducirme en la paleoecología y presentarme al que ha resultado ser mi mentor y director de tesis, sino por permanecer siempre cercano y dispuesto a ayudar, y por hacerme sentir una más de su camada (es bueno volver al útero de vez en cuando). El resto de morfotipos son mis compañeros de carrera, muchos y muy variados: Ilu y sus calzadas; la familia (Jos, Antuan, Barbini, Doctor y Barbas Jul, y mis compañeros de viento Maximum y Minimum); Franki (el no biólogo) y las tardes de biblioteca; y el grupo de la comisión y sus posteriores extensiones: Adrián (aaiiiiiiii mi Adri!!), Andrés, Bea, Carmen, Cristina, Damián, Estefanía, Helena, Lorena, Mar, Myriam (esa personita mágica), Nati, Rocío, Rubén, Tere…(si se me olvida alguien ha sido sin querer, sin rencor ok?).

El paso de la zona EMR-II a la EMR-III es lo que se denomina un "abrupt shift", que en mi caso fue el traslado a Barcelona. EMR-III estuvo marcada en la zona basal por unas condiciones ambientales algo desfavorables. La llegada a un sitio nuevo, donde no conoces a nadie, sin trabajo y sin dinero, no parecen ser las condiciones más idóneas para el esplendor de una comunidad vegetal (en este caso yo). Pero las apariencias engañan. Mi llegada estuvo marcada por una acogida sobrenatural. La primera subzona de este periodo se caracterizó por las oportunidades laborales que me ofrecieron y las personas que en ellas conocí: Jordi y Eli de ING; CIMITEC y el grupo de becarios: Fito, Fran, Gerard, Guillem, Hender, Javi, Joan, Jordi, Marta, Núria, Paredes, etc. La parte superior de esta zona está marcada por mis comienzos en el mundo de la investigación, los cursos de doctorado. Gracias a Anna, Roger, Miquel (nuestro electrón), Albert, Salva, Miriam, el viaje a Granada (gracias a Paco Lloret por esa intensa y a veces lingüísticamente accidentada experiencia), Martin, Trevor, Benja, Viçent, Lasse, etc., por haber compartido risas y frustraciones al unísono. Para que una comunidad tenga éxito, las condiciones edáficas son esenciales; en este caso, mis nutrientes particulares, que han estado siempre de colchón (y a veces de suelo puro y duro), y han sido los responsables de que tomara esta ciudad como la mía propia, son mi familia de Barcelona: Miguelón (mi estrella, ¿cómo podría dejarte por orden alfabético? Es lo que tiene que seas de los poquitos que me hacen recapacitar); Lawrika; Martuki; Danielo; Julito; Luiiih -Phelps el negro-, Franker y Thor (vivan los solapes y el colonialismo murciano!); Javivi; Esti; Jorge; Leonor; Victor; el jans (Jordi -ese cover designer!!-, Toni, Jacky); la farinera o farinosa y sus jam sessions; kolomba; chakataga; la big band banana reunion; heces fálicas…para mí, una persona es en gran parte producto de su entorno, y yo no hubiera sido nadie sin vosotros, muchísimas gracias de corazón por todo lo vivido y compartido.

El siguiente paso de esta carrera de fondo, fue la entrada en botánica. Allí tuve la oportunidad de empezar a investigar en primera persona, y de practicar la docencia universitaria por primera vez. Gracias al profesorado de la Unitat de Botànica de la UAB por sus consejos y el recibimiento ofrecido, en especial quiero agradecer a los novatos, que como yo, empezamos sin un rumbo muy fijo: Ainhoa, Alex, y Pep, ya que entre todos conseguimos dominar la materia, y a los alumnos!. Esta zona tiene una formación que aunque no es dominante, ha sido sumamente imprescindible en mi secuencia: el secretariado del BABVE. Quiero hacer un agradecimiento especial a Flora (ayy, qué vamos a hacer sin el caos), Pilar y Oscar, sin los cuales directamente me habría vuelto loca en más de una ocasión; definitivamente, lidiar con la burocracia no es apto para todos los públicos. Otra formación muy especial es el lugar donde desarrollé el primer año de beca: la segunda planta. Muchas gracias a Alba, Conchi, David, Gorka, Elena, Jordina, Rebeca (niña-cerveza catalano-turolense y 1/3 del núcleo), Ruth y Silvia, por el cariño demostrado en todo momento, y por los buenos momentos de los desayunos.

Si alguien de ese departamento merece una atención especial, es Iñigo de la Cerda: sin él, directamente, me habría quedado en la calle antes casi de empezar. Muchísimas gracias Iñigo por todo el apoyo ofrecido de manera altruista; apareciste, como en las películas, en el momento en el que la chica está realmente en apuros, y la salvaste.
No puedo acabar la descripción de la zona EMR-IV sin nombrar el nicho propiamente: el grupo PATAM y sus micro-nenas. Con Sandra, Núria (niña-cerveza catalana y otro 1/3 del núcleo), Arantza, Lucía, Laia, Marta, Cons, Eli, Olga, Tania y Teresa (ay! y Paolo, hemos tenido a un chico aunque sea fugazmente!), he pasado grandísimos momentos, tanto científicos como más profanos. Con las “cofundadoras” además he tenido la suerte de compartir vida dentro y fuera del trabajo, muchas gracias niñas por estar ahí siempre y aguantar mis subidas de azúcar chocolateras y mi jerga murciana (y nuestro fabuloso diccionario catañol, o más bien, panochán: os haré cinco céntimos; no me viene de gusto; es que estoy muy acelga; noia, sembla que tinguis azogue; te escañaría; pero tú eres de senglar vell?; fa frescor...), espero que sigamos así por mucho tiempo, ya sabéis: I’ll missss youuuu!

La zona EMR-V estuvo marcada por la consecución de la beca pre-doctoral (uehhhh!!). Una vez que entré oficialmente en el desarrollo de la tesis, en mi caso la credencial de becaria vino con un pasaporte debajo del brazo: Venezuela, EEUU, Eslovenia, Alemania, Holanda, Francia, México, Hungría…fueron muchas las ciudades visitadas (y no sólo una vez), y la gente conocida allí. La experiencia vivida en el trabajo de campo de la Gran Sabana fue indescriptible, mi sueño hecho realidad. Durante este trabajo fueron muchas las manos que ayudaron: Ana Mª Pérez con los permisos, Wilmer Díaz y Otto Huber en la inmersión de la vegetación sabanera, Johny y Jesús de Turi Express con el transporte de material, y Fidencio Montáñez, los hermanos Aquiles y José Luis Fernández, y la comunidad indígena de El Paují por su colaboración en el muestreo de sus tierras. El primer choque cultural que destacó en las cartas de viaje tituladas *Las aventuras de una murciana en…* fue con el grupo yanqui. El grupo de investigación de Mark Abbott (en especial Mark, Nathan y Broxton) me ayudó a incorporar la visión geológica necesaria para este trabajo, además de la ayuda imprescindible durante el trabajo de campo. La beca otorgada por la ESF para asistir a un curso intensivo sobre cronología y datación me dio la oportunidad de conocer a unos, hasta el día de hoy, magníficos colegas tanto en lo profesional como en el plano personal. No puedo dejar de nombrar a Maarten Blaauw, quien me introdujo en el mundo del age-depth modeling y me ha apoyado durante todos estos años siempre que lo he necesitado; a Frederike, Daniel y Zaire, con los que compartí la paleo-euforia diaria y nocturna. Mis estancias en la Universiteit van Amsterdam bajo la tutela del gran maestro de los NPP Bas van Geel fueron claves para el desarrollo de gran parte de este trabajo. Allí además, fui adoptada por la gran colonia latina y sus extensiones, comandados por Zaire (mi mamita loca) y formada por Anita, Anna, Caro, Casper, Cleve, Erik, Geert, Giovanni, Jenny, Jesús, María, Marian, Meritxell, Paola, Thomas, Ximena, y nuestros lugares de encuentro como el polder, the windmill, etc.; chicos, por fin llegó el día de la macarena y…siento que muero! mil besos y sólo yogurt!

Y llegamos a la última zona del diagrama EMR, que ha sido el “sprint” final de la tesis, desarrollada en el Institut Botànic de Barcelona, en Montjuïc (que no Barcelona). La acogida en el centro no ha podido ser mejor, gracias por el apoyo continuo tanto a los investigadores del CSIC (Alfonso, Ángel, Nùria, Roser, Teresa); como a los becarios/técnicos (Andreas, Dani, Gemma, Isma, Jaume, Javi, Jordi, Juancho, Kostya, Laia, María, Mercé, Noemí, Piotr, Sara, Sergi, Sónia); y al personal de administración, servicios e investigación del jardín (Álvaro, Anna, Carmen, Diana, Isi, Jordi, Jose, Josep Mª, Karina, Lola, Mari, Miquel, Miriam, Montserrat, Neus I., Neus N., Nicolás, Nishan, Ramón, Rosa, Samuel, Santi, Tamara). Será raro no cerrar el instituto por las noches!!!

Para terminar, que ya sé que tengo mucho rollo, vuelvo a nombrar a algunas personas que tienen un rincón muy especial en mí y se merecen una dedicatoria aparte. Son, como una vez me definió a mí una de ellas, *princesas sin tacones, de pelo revuelto y sabor a sal*; mujeres imprescindibles en mí día a día. Núriii, Sorfe, Mima, mil gracias de corazón por dejarme formar parte de vuestras vidas.

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PD: Muchas gracias a todos los que habéis mostrado un gran interés en las fantásticas montañas tabulares conocidas como tepuis que hay en la zona de estudio donde he desarrollado esta tesis, pero antes de que comencéis con la lectura he de decir…que yo trabajo en las sabanas de abajo!!! ;)

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a: years
AD: *Anno Domini* (calendar years)
BC: before Christ
ca.: *circa*
cal yr BP: calibrated years before present (being present AD 1950)
EHW: Early Holocene Warming
GS: Gran Sabana
IPCC: Intergovernmental Panel on Climatic Change
ITCZ: Inter-Tropical Convergence Zone
kyr: kiloyears
LG/EH: Late Glacial/Early Holocene
NPP: non-pollen palynomorphs
OD/BA: Oldest Dryas-Bølling/Allerød
P/E: precipitation/evaporation ratio; water (or hydrological) balance
YD: Younger Dryas
yr: years

ABSTRACT:

This thesis is aimed to study the paleoecology of the southern Gran Sabana region (GS; SE Venezuela) since the Late Glacial to the present. This region is characterized nowadays by the occurrence of large extent of savannas in a climate suitable for rainforests. For this purpose, three sequences (two from peat bogs and one from lake sediments) have been analyzed for pollen and spores, non-pollen palynomorphs (NPP), and microscopic charcoal particles. Among the sequences analyzed, two of them are located currently within treeless savannas (Lakes Chonita and Encantada); whereas the third one is placed in the boundary between GS savannas and Amazon forests (El Paují). The Late Glacial interval of Lake Chonita was characterized by a shrubland that was replaced by a treeless savanna at the end of Younger Dryas (YD) and the onset of the Holocene, linked to the occurrence of regional fires since *ca.* 12.4 cal kyr BP. The beginning of local fires was dated synchronous with the vegetation replacement, *ca*. 11.7 cal kyr BP. A similar shrubland, though not identical, is located nowadays around 200 m elevation above the lake, so the replacement by surrounding savannas was interpreted as a probably upward displacement of the former vegetation and an increase in average temperatures of approximately 0.7 - 1.5ºC. This section represents the oldest interval analyzed for GS so far, and the presence of fires during the Late Pleistocene is among the oldest fire records documented for northern South America. The peat bog records of Lake Encantada and El Paují showed the main vegetation trends of the last 8 cal kyr BP, which were characterized by the continuous occurrence of regional fires. In Lake Encantada, the presence of treeless savannas was reported during the whole interval analyzed as the dominant vegetation type, despite variations in forest abundance and composition taxa of the community also occurred. The vegetation changes in this record were interpreted as mainly due to climatic shifts until the Late Holocene. At El Paují, the occurrence of forests and savanna/forest mosaics was reported during the same interval, and fire was postulated to have been the major driver of the vegetation shifts. In this sequence, a treeless savanna was not recorded as the dominant vegetation of the landscape until the last millennia, and the presence of two different indigenous cultures was postulated as responsible of the shifts in fire regime registered, with an interval of human land abandonment between them. This interval was characterized by the cessation of fires, and the establishment of a secondary dry forest. The Late Holocene was characterized, in the three sequences studied, by a sudden increase of fires, which likely favored the expansion of savannas and the establishment of the present GS landscape. The join interpretation of the records presented in this thesis, together with previous analyses in the region, highlighted some key aspects for understanding the main trends of GS landscape and vegetation, e.g., the appearance and establishment of *morichales* (*Mauritia* palm stands typical of current southern GS landscapes) has been restricted to the last two millennia, synchronous with the increase in fire incidence. Moreover, it has been possible to gather empirical evidence for testing some previous hypothesis regarding GS. For example, the proposal of an extended aridity prior the Holocene has been rejected, whereas the hypothesis about the post-glacial expansion of *morichales* has been supported. In this sense, with all the available information to date, some suggestions have been proposed: (i) Climate and fire have been the major forcing factors operating in the GS; (ii) During the Late Glacial and the beginning of the Early Holocene, the landscape of southern GS was likely formed by a mosaic of forests, shrubs, and savannas, without the current supremacy of the last vegetation type, which only established during the last 2 cal kyr BP onwards; (iii) Some general climatic trends have been inferred for the study area, as for example an increase in average temperatures around the Late Glacial/Early Holocene transition, a dry interval from 8 to 5 cal kyr BP, and a wetter phase during the Mid-Holocene centered around 4 cal kyr BP; (iv) The establishment of *Mauritia* in the region has been likely driven by a synergism between biogeographical, climatic and anthropogenic factors, as well as the likely pyrophilous nature of this palm given its synchronous appearance with the increase of fires; (v) The settlement of the modern indigenous culture (Pemón) occurred at least since around *ca.* 2000 cal yr BP onwards, 1500 yr earlier than previously thought, but previous human presence in the region has been also documented; and (vi) The fire activity observed in the long-term has caused a huge impact on GS landscape.

RESUMEN:

El presente trabajo está centrado en la paleoecología de la región sur de la Gran Sabana (GS; SE Venezuela) desde el Tardiglacial hasta el presente. Esta región se caracteriza hoy en día por la presencia de sabanas en un clima propicio para el desarrollo de bosques. Para ello, se llevó a cabo el análisis de 3 secuencias (dos de turberas y una de sedimentos lacustres), basado principalmente en la identificación de polen y palinomorfos no polínicos (NPP), y en el análisis de microcarbones. Dos de las secuencias analizadas (Chonita y Encantada) se encuentran actualmente emplazadas en sabanas, mientras que la tercera (El Paují) pertenece a una localidad fronteriza entre sabanas de GS y bosques amazónicos. El intervalo Tardiglacial de la secuencia del Lago Chonita se caracterizó por la presencia de una comunidad arbustiva, que fue reemplazada por una sabana de manera sincrónica con el final del Younger Dryas (YD) y el comienzo del Holoceno. Se documentó la presencia de fuegos regionales desde *ca.* 12.4 cal kyr BP, mientras que el comienzo de los fuegos locales ocurrió sincrónico con el reemplazamiento de la vegetación, *ca*. 11.7 cal kyr BP. En la actualidad, un arbustal similar está presente a unos 200 m del lago, por lo que el cambio de vegetación se interpretó como resultado de un desplazamiento altitudinal, proponiéndose un aumento de las temperaturas medias alrededor de 0.7 - 1.5ºC. Esta secuencia es la más antigua hasta la fecha para GS, y la presencia de fuegos supone uno de los registros de incendios más antiguos para el norte de Sudamérica. Las secuencias de la Laguna Encantada y El Paují mostraron las principales variaciones de la vegetación desde los últimos 8 cal kyr BP hasta el presente, que estuvieron caracterizadas por la presencia de fuegos regionales desde el principio. En la Laguna Encantada se observó la presencia continua de sabanas como vegetación dominante, a pesar de que también se registraran variaciones en la abundancia de taxones forestales. Las variaciones de la vegetación parecieron responder principalmente a las condiciones climáticas hasta el Holoceno Tardío. En El Paují, se observó la presencia de bosques y mosaicos bosque/sabana, siendo el fuego el agente que ejerció una mayor influencia en los cambios de vegetación registrados. En esta secuencia la presencia de sabana como vegetación dominante no se observó hasta los últimos milenios, y se propuso la existencia de dos culturas indígenas diferentes con un lapso de abandono intermedio, como responsables del régimen de incendios. Este intervalo de abandono se caracterizó por un cese de incendios y la aparición de un bosque seco secundario. El Holoceno Tardío estuvo caracterizado en las tres secuencias por un aumento drástico del régimen de fuegos, lo que favoreció la expansión de sabanas y el establecimiento del paisaje actual. La interpretación conjunta de estas secuencias y otras analizadas previamente ha puesto de manifiesto varios aspectos claves para el entendimiento de las tendencias de la vegetación de la región, como por ejemplo, que la aparición y establecimiento de los *morichales* (comunidades casi monoespecíficas de *Mauritia*) se haya producido durante los últimos dos milenios, y de manera sincrónica con el aumento de fuegos. A su vez, ha servido para evaluar algunas hipótesis existentes sobre el origen y evolución del paisaje de GS. Por ejemplo, la existencia de climas áridos antes del Holoceno ha sido cuestionada, mientras que la hipótesis acerca de una expansión post-glacial de los *morichales* parece reforzarse. De este modo, con la información obtenida hasta el momento se han sugerido varias hipótesis: (i) Los principales agentes causantes de las variaciones de la vegetación en GS han sido el clima y el fuego; (ii) El paisaje del sur de GS estuvo probablemente formado durante el Tardiglaciar y el principio del Holoceno por un mosaico entre bosques, arbustales y sabanas, sin la predominancia actual de este último tipo de vegetación, estableciéndose el paisaje actual hace alrededor de 2000 años; (iii) Se han inferido algunas tendencias climáticas regionales, como un posible aumento de las temperaturas medias al comienzo del Holoceno, un intervalo seco entre 8 y 5 cal kyr BP, y una fase más húmeda durante el Holoceno Medio centrada *ca.* 4 cal kyr BP; (iv) El establecimiento de *Mauritia* en la región es posiblemente el resultado de la interacción entre factores biogeográficos, climáticos y antrópicos, y se ha propuesto la probable naturaleza pirófila de esta palmera debido a su aparición sincrónica con el aumento del régimen de incendios; (v) El asentamiento del actual grupo indígena que puebla la zona (los Pemón) se debió producir, como mínimo, hace unos 2000 años, unos 1500 años antes de lo propuesto hasta ahora, aunque han sido documentadas presencias antrópicas anteriores; y (vi) La incidencia de fuegos a largo plazo observada ha provocado un gran impacto en el paisaje de GS.

CHAPTER 0:

Thesis Structure.

Todo tiempo pasado…fue anterior.
Les Luthiers.

This thesis is composed of an introduction, six chapters, a general discussion and main conclusions. The work focuses mainly on the paleoecology of southern Gran Sabana (GS; SE Venezuela). All chapters have been written in English (except Chapter 4 that consists of an article, published in a Spanish journal, which is written in Spanish). Chapters 2 to 7 also correspond to articles that have been published in or submitted for international distribution in peer-reviewed scientific journals (all journals are cited in JCR, except the Spanish journal in which Chapter 4 was published). Depending on the journals' requirements, chapters have been written in American or British English and specific acronyms have been used (see Acronym list). At the beginning of each chapter, the current status of the related paper is indicated.

CHAPTER 1. **Introduction.** The present work comprises a compilation of publications, so a general overview of the main issues related to the purposes of each study is given in the introduction and study area paragraphs of Chapters 2 to 7. Here, brief explanations are provided about relevant aspects of general knowledge and specific remarks on the study area or about the focus of the thesis, along with the main objectives of the thesis.

CHAPTER 2. **Methodology.** Due to the scarce knowledge that exists about the study area, the first steps in defining the scope of this thesis were to target the improvement of existing techniques and proxies currently used in paleoecology to achieve the most accurate reconstructions possible. These enhancements were performed in different neotropical sediments, in addition to those obtained from the Gran Sabana (e.g., Andean sediments). This chapter contains two sections: 2.1) variations of the standard laboratory procedure for tropical lacustrine and peat sequences, taking into account the chemical features of the sediments and optimizing their further microscopic analysis; and 2.2) increasing the numbers of proxies analyzed. Among different proxies, the study of non-pollen palynomorphs (NPP) deserves special attention due to their uncommon use in neotropical studies, despite the broad range of inferred information that can be obtained through them (e.g., water body features and levels; aquatic plant presence; landscape processes, such as erosion; and human activities, such as herding, grazing or tree plantations). A special case addressed in this work is the investigation of fire incidence, which is of great importance in the study area. In producing this thesis, it has been possible to approach these dynamics through three independent proxies: fungal spore identification (included in this Chapter in section 2.2 and in Chapters 5, 6 and 7) and pteridophyte spore identification and microcharcoal analysis (included in Chapters 3 to 7).

CHAPTER 3. **Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas Chron.** Paleoecological analysis of the oldest time interval found to date in Gran Sabana. This chapter is focused on the Late Glacial/Early Holocene interval at Lake Chonita, the regional vegetation dynamics and the forcing factors involved in such dynamics. The reconstruction is based on radiocarbon dates, palynomorph identification (pollen and pteridophyte spores), and microcharcoal analysis. Additionally, international collaborations (in the form of article coauthorship) provided physical parameters and diatom analyses that were added for joint interpretation of all results.

CHAPTER 4. **Paleoecología del Holoceno en la Gran Sabana, SE Venezuela: Análisis preliminar de polen y microcarbones en la Laguna Encantada.** (Written in Spanish). This study concerns the general trends of Lake Encantada regional vegetation over the last 7500 years and the relationship of the lake with nearby zones. It is based on radiocarbon dates, palynomoph and algae identification and microcharcoal analysis.

CHAPTER 5. **Forest-savanna-*morichal* dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia.** A higher resolution study of the last millennia performed at Lake Chonita (the same sequence of Chapter 3). This chapter is focused on establishment of the present vegetation and the possible forcing factors (climatic or anthropogenic) that have played a role in its establishment. Hypotheses about the modern-day *Mauritia* (Arecaceae) distribution pattern (See Chapter 1 for palm community definition) and early human occupation in Gran Sabana have also been suggested. The reconstruction is based on radiocarbon dates, palynomorph and non-pollen palynomorph identification, and microcharcoal analysis. Additionally, international collaborations (in the form of article coauthorship) have yielded physical parameters that were added for joint interpretation of all results.

CHAPTER 6. **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.** Paleoecological analysis of a peat bog located at the southern boundary of the Gran Sabana, close to northern Amazonia and currently surrounded by a different landscape than in previous analyses. This chapter is aimed at reconstruction of the vegetation dynamics of a major ecotone between the Amazon forests and the GS savannas, as well as the major drivers of community variations over time, including the climate and possibly humans. For this purpose, radiocarbon dates, palynomorph and non-pollen palynomorph identification, and microcharcoal analysis were used.

CHAPTER 7. **Fire in the Gran Sabana (SE Venezuela): a paleoecological perspective.** Long-term study of fire dynamics in southern Gran Sabana. This study is addressed at understanding the origin and establishment of the present fire regime in southern Gran Sabana and its effects on vegetation, based on the available paleoecological sequences obtained to date. The potential implications of these results for other disciplines, such as archaeology and landscape management and conservation, are also discussed. This study employed the paleoecological fire proxies studied in this thesis (charcoal, pteridophyte and fungal spores, and vegetation assemblages observed in pollen diagrams), and it was supported by other southern Gran Sabana sequences with related information.

CHAPTER 8. **Discussion.** In this section, the main results presented in the preceding chapters are discussed together in a regional context and compared to other paleoecological studies from nearby locations. The contribution of the present work to understanding the paleoenvironmental history of southern Gran Sabana since the Late Glacial period are discussed, as are possible directions for future work.

CHAPTER 9. **Conclusions.** A list of the main conclusions of the thesis based on the conclusions from each chapter and grouped according to the main objectives described in Chapter 1.

CHAPTER 1:

Introduction.

Sabio no es aquel que dice todo lo que piensa,
si no el que siempre piensa todo lo que dice.
Adaptada de Aristóteles.

1.1. General Background

Paleoecology is broadly defined as the ecology of the past, as it is an ecological discipline focused on the study of past ecosystems (Birks and Birks, 1980). This discipline is based in the principle of uniformitarianism (Simpson, 1970), broadly defined as "the laws of nature are invariant with time", using present-day information to make inferences about the past (Birks and Birks, 1980). Although this premise is frequently forgotten, paleoecology should consider time as a continuum, rather than as discrete events, without disconnecting the past from the present or future (Rull, 2010).

To develop these studies of past environments, paleoecology utilizes several independent but complementary proxies, with palynology being among the most used. In addition to pollen and pteridophyte spores (palynomorphs), other remains of biological origin present on microscopic slides can also be analyzed (e.g., fungal spores, animal and/or algal remains, plant fibers), where these are referred to as non-pollen palynomorphs (NPP) (see van Geel, 2001). Another useful tool that has been continuously improving during the last decades is charcoal analysis, which is used to reconstruct long-term variations in fire occurrence or regimes (Whitlock and Larsen, 2001). Thus, in some cases, pollen and charcoal data from the same sediments are used to examine the linkages among climate, vegetation, and fire, as well as anthropogenic activities (Whitlock and Larsen, 2001).

The study of paleoecology is currently directed not only at making inferences about past ecosystems, but also in relation to several applied disciplines. For instance, the last Intergovernmental Panel on Climate Change (IPCC) report highlighted the need for paleoecological studies to document past biotic responses to climatic shifts and their use as possible past analogs given the ongoing and future climatic change scenario (Solomon *et al.,* 2007). An important remark of the IPCC report is the need to incorporate these results for management and/or conservation purposes (e.g., Willis *et al.,* 2007). In this sense, a globally important impact highlighted by the IPCC is the effect of fire on ecosystems. At present, studies about fire dynamics are frequently constrainted by the availability of only short-term data (several years or decades; short-term studies). This restriction is a handicap to obtaining an accurate view of the real fire regime, given the long time intervals required for recurrence of the dynamics of many ecosystems. These kinds of data are only provided by paleoecology (long-term studies), although this frequently is not taken into account in developing management or conservation strategies (Whitlock *et al.,* 2010).

Another key question about biological processes addressed by paleoecology lies in understanding the origin, distribution and present extent of biomes (e.g., Mayle, 2006). An important and extensively studied biome is the savanna, which comprises C_4 plant-dominated grasslands (Beerling and Osborne, 2006), due to factors such as its extent and geographical range (approximately three million square kilometers in the American tropics alone [Huber, 1987]). Although its origin appears to be closely related to a decline in the atmospheric CO_2 concentration (Edwards *et al.,* 2010), its present distribution and extent are likely driven by different mechanisms related to fire (Keeley and Rundel, 2005). Savanna fires are currently considered the largest source of natural pyrogenic emissions, showing the highest fire activity of all major land cover types (Pereira, 2003), with these fires being mostly of anthropogenic origin (Shlisky *et al.,* 2009). An extreme case of fire-prone savannas are those occurring in the tropical region, where, often, environmental conditions (mainly climate and soil properties) are suitable for the development of forests (Bond *et al.,* 2005). Indeed, Bond *et al.* (2005) have postulated that forests would double their global coverage from 27% to 56% of vegetated landscapes in the total absence of fires, mostly at the expense of savannas.

Within the neotropical region, variations in the coverage of these vegetation types (savannas and forests) over time have been the subject of numerous studies (e.g., Behling and Hooghiemstra, 2001). The paleoecological and paleoclimatological research developed in the Neotropics has been continuously improving (e.g., Mayle *et al.,* 2000; Berrío *et al.,* 2002; Bush *et al.,* 2007b; Rull *et al.,* 2010) since pioneer studies began several decades ago (e.g., Wymstra and van der Hammen, 1966). However, due to the vast extent covered and the different ecosystems present in this region (Colinvaux *et al.,* 2000), many areas remain poorly studied, and, in some cases, this prevents obtaining a regional perspective about, for example, vegetation-climate-human interactions over time. Contrary to what was previously assumed, the Neotropics have been sensitive to climatic changes and variations over time (Ashton, 1969; Bush, 1994). Neotropical plant communities have suffered changes in their composition according to the requirements of each taxon and have not responded homogenously to these climatic conditions (Colinvaux *et al.,* 2000; and literature therein). Several records have documented that not only climate, but also human influences have been the main forcing factors on the landscape, generally acting in synergy (Bush *et al.,* 2007a). Moreover, in some cases, the current landscapes have been shown to correspond to heavy human management and modeling from ancient practices, rather than to be the result of climatic condition variations alone (Bush and Silman, 2007). Therefore, the role of humans in shaping the environment must be also considered in ecosystem dynamics studies. Thus, paleoecological research has proved to be a key component within the field of archaeology (e.g., Piperno, 2008), providing clear evidence of ancient human impacts on the landscape, even in the absence of plant cultivation signs in pollen records (Bush *et al.,* 2007a).

Regarding neotropical savannas, paleoecology has demonstrated their existence during the Holocene and earlier, especially in lowlands (e.g., Wymstra and van der Hammen, 1966; Behling and Hooghiemstra, 2001). These studies have highlighted the importance of the last millennia for shaping the current extent of savannas, which has often been related to intervals of high human pressure and impacts upon the landscape (Rull, 1992; Berrío *et al.,* 2002).

The present study was carried out in a midland region under high fire stress that is among the largest savanna areas of northern South America (Figure 1.1). The area is known as the Gran Sabana (GS), and is located in the SE of Venezuela (see Section 1.3 and the Study Area of Chapters 3 to 7 for further definition).

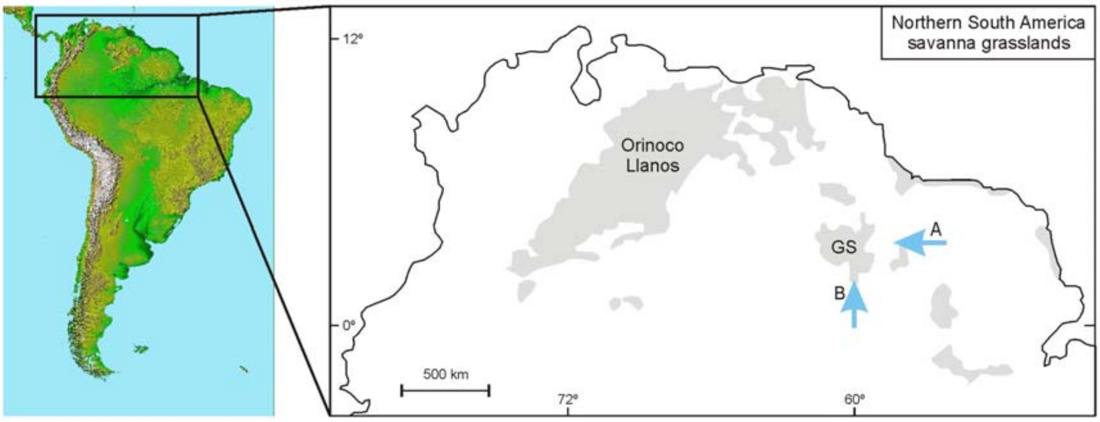

Figure 1.1. Major savanna areas in northern South America. Blue arrows show the potential migration routes of Pemón: A) from Rupununi savannas of Guyana; and B) from Rio Branco (Boa Vista, Brazil). Redrawn from Behling and Hooghiemstra (2001) and Eva et al. (2004). Radar image courtesy of NASA/JPL-Caltech; GS: Gran Sabana.

1.2. Study Area

The GS is an area of approximately 18,000 km^2 located in the south Venezuelan Bolívar State between the Orinoco and Amazon Basins (4.6089 - 6.6331 N and 61.0679 - 74.0478 W; Figure 1.2), within the Venezuelan Guayana. This region is characterized by elevations ranging from 750 to 1450 m in a north-south downward gradient. The Gran Sabana is placed mainly on the geologic formation of Roraima Group sandstones/quartzites that has been eroded since the Precambrian, and in a minor extent, younger diabase intrusive rocks (Huber, 1995a). For the Venezuelan Guayana, three physiographic units have been described:

- Lowlands: from 0 to 500 m altitude.
- Uplands: from 500 to 1500 m altitude; also referred to as midlands.
- Highlands: from 1500 to 3000 m altitude.

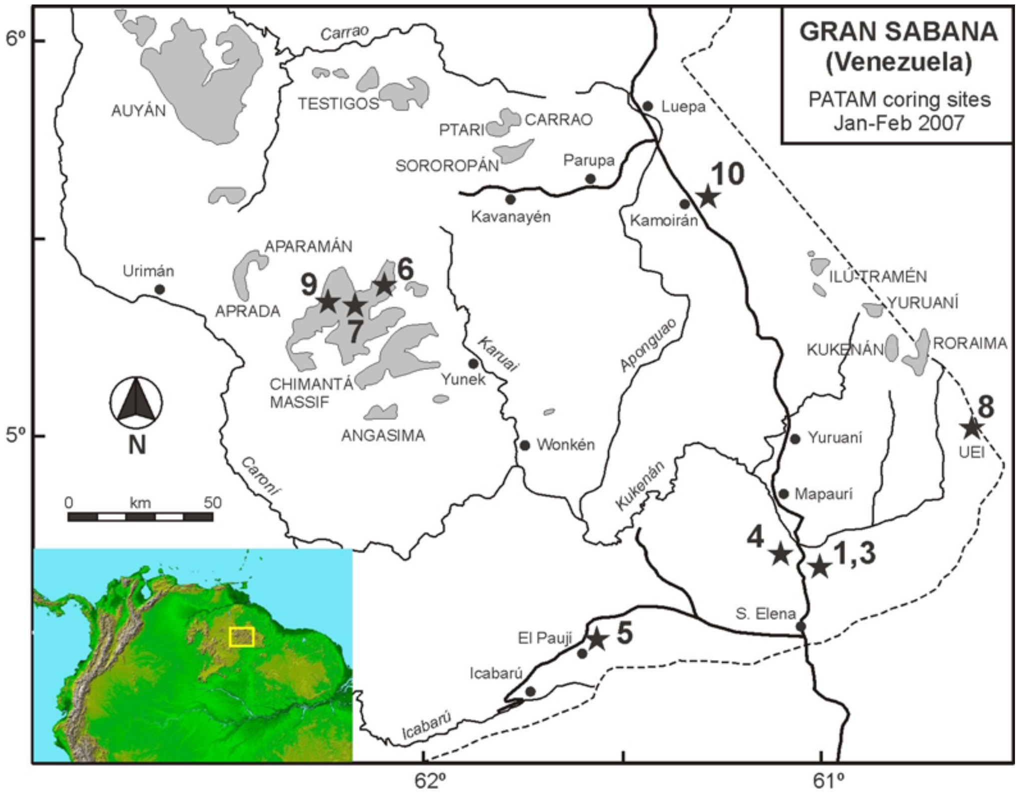

Figure 1.2. Location of the study area in the context of northern South America. The localities visited by the 2007 PATAM expedition are marked by stars. Among these, the Gran Sabana localities where different cores were obtained are 1, 3, 4, 5, and 10. (Radar image courtesy of NASA/JPL-Caltech).

Two of these physiographic units are present in GS: uplands, where the present study is located, which are included geomorphologically within the Wonkén planation surface proposed by Briceño and Schubert (1990); and highlands. The GS landscape is marked by a major contrast between flat, slightly undulating valleys characteristic of uplands and the abrupt tabular mountains known as *tepuis* that form the highlands (Figure 1.3).

Figure 1.3. Typical Gran Sabana landscape. (Photo: V. Rull, 2007).

The climate in the region has been defined as submesothermic, with average temperatures between 18ºC and 20ºC, presenting slightly higher temperatures in the southern part of the region (the site of this work). The precipitation regime is considered ombrophilous, with values ranging between 2000 to 3000 mm/yr, but the region presents marked local variations that determine a north-south gradient. The southeastern part of the region is characterized by a drop in precipitation values (2000 - 1600 m/yr), which is not only remarkable regarding annual average precipitation values, but also with respect to seasonality. Thus, a dry period, from December to March, and a wet period, from June to September, can be distinguished (Huber, 1995a). Seasonality in this region is strongly influenced by the annual migration of the Intertropical Convergence Zone (ITCZ; Figure 1.4) (Huber, 1995a). The ITCZ is a low-pressure tropical belt of maximum cloudiness and rainfall, and its position is determined by insolation and the convergence of the NE and SE tropical easterlies (McGregor and Nieuwolt, 1998). Huber and Febres (2000) have proposed that the presence of tepuis in the southeastern region could be responsible for these differences between north and south Gran Sabana precipitation values, likely preventing rainy discharge in the southern zone.

Concerning vegetation, GS is a vast island of savannas within the forested landscape of the Venezuelan Guayana (Fig. 1.1). These large extensions of treeless savannas are intermingled with forest and shrub associations in some cases and form sparse forest/savanna mosaics, which are relegated to watercourses in most cases (Fig. 1.3). Forests of this region are normally defined as lower montane forests due to their intermediate position between lowland and highland forests (Hernández, 1999), although their composition varies with altitude (Huber, 1995b). Common genera include *Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignoniaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Clathrotropis* (Fabaceae), *Aspidosperma* (Apocynaceae), *Caraipa* (Clusiaceae), *Dimorphandra* (Caesalpiniaceae), and *Byrsonima* (Malpighiaceae), among others.

GS shrublands are usually located between 800 and 1500 m elevation, being more frequent in the northern than in the southern region (Huber, 1994). These vegetation types generally occur on rocky sandstone substrates, but in some instances, they also occur on deep white sands of alluvial origin (Huber, 1995b). Common genera are *Euphronia* (Euphroniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Ochthocosmus* and *Cyrillopsis* (Ixonanthaceae), *Thibaudia, Notopora* and *Befaria* (Ericaceae), *Spathelia* (Rutaceae), and *Byrsonima* (Malpighiaceae), among others (Huber, 1995b). The most extensive biome in the region, as indicated by the place name, is savanna, comprising the typical GS landscape of treeless savannas. These savannas are species-poor communities dominated by C_4 grasses of the genera *Axonopus* and *Trachypogon*, along with sedges, such as *Bulbostylis* and *Rhynchospora*. Woody elements are scarce and rarely emerge above the herb layer (Huber, 1995b). Three different savanna landscapes can be distinguished, according the non-herbaceous taxa that may appear as minor elements: (i) open, treeless savanna, which is the most widespread type of GS grassland, growing on poor oxisols; (ii) savanna with *morichales*, which is a unique neotropical vegetation type characterized by the presence of large stands of *moriche* palm (*Mauritia flexuosa*, Arecaceae). This community is strongly linked to poorly drained, seasonally flooded soils at altitudes below approximately 1000 m and is restricted in GS to the southern region due to the N-S altitudinal gradient; and (iii) savanna with shrubs, which grows on extremely nutrient-poor, acidic soils, normally occurring on rocky hills and slopes, marked by the dominance of sedges instead grasses (Huber, 1995b). The reason for the dominance of savanna vegetation in this region, where the climate is apparently more suitable for the development of extensive rain forests, is controversial (Huber, 1995a,b), and this has led to several hypotheses:

- The savannas are favored by poor edaphic (hydrology, nutritional status) conditions (Fölster, 1986; Fölster *et al.,* 2001).
- They are relics of larger savanna extensions that originated in colder and drier epochs (e.g., the Last Glacial Maximum, LGM) (Eden, 1974).
- The savannas are the consequence of deforestation due to frequent and extensive fires (Dezzeo *et al.,* 2004a).
- The present savannas are derived from former smaller, scattered savanna patches, the expansion of which has been favored by both climate change and fire (Rull, 2007; Huber, 2006).

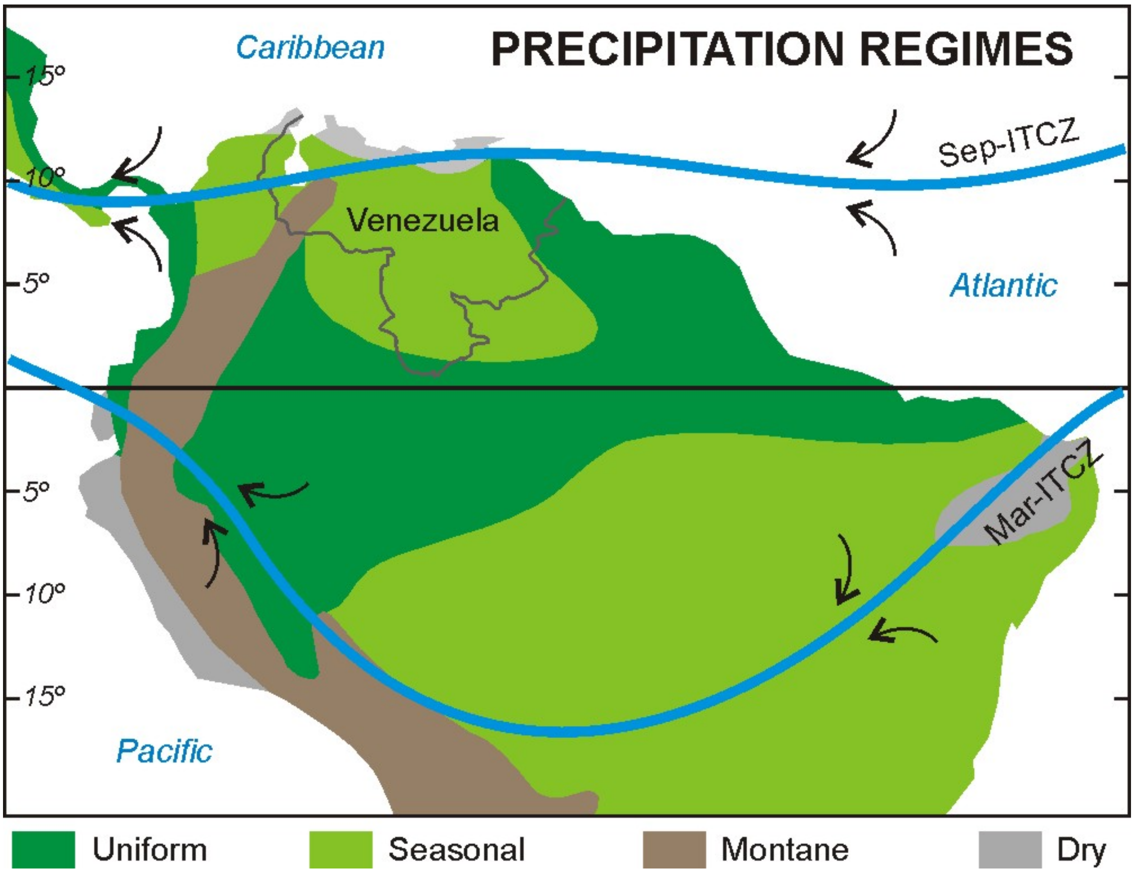

Figure 1.4. Seasonal migration of the Intertropical Convergence Zone (ITCZ) over northern South America. The main regional precipitation regimes are indicated. Extracted from Rull et al. (2010).

GS is the homeland of the Pemón indigenous group from the Carib-speaking family. Today they are sedentary, living in small villages, usually in open savannas. Although the population density in this area is currently low, the indigenous settlements have experienced an expansion since the arrival of modern-day European missions (in the early 20th century), and more than 17,000 people live in GS today (Medina *et al.,* 2004). The arrival timing of the Pemón people to GS is still unknown. It has been postulated that this culture became established approximately 300 years ago and came from the East (from the Rupununi savannas of Guyana; Thomas, 1982; Colson, 1985; Kingsbury, 1999), or around 500-600 years ago, migrating from Río Branco in northern Brazil (Huber, 1995a), although an earlier occupation cannot be dismissed (see Fig. 1.1 for potential migration routes). There is some archaeological evidence, consisting of pre-Hispanic remains (spearheads and bifacially worked knives), similar in style to others from approximately 9000 years ago found at other Venezuelan localities (Gassón, 2002). Therefore, a definitive assessment is not yet possible.

Fire is a key component of the Pemón culture, as they use it every day to burn wide extensions of savannas and occasionally forests (Kingsbury, 2001). The reasons for the extent and frequency of these fires are related to activities such as cooking, hunting, fire prevention, communication, magic, etc (Rodríguez, 2004; 2007). Surprisingly, land use practices, such as extensive agriculture or cattle raising, which are typical of other cultures strongly linked to fire, are not characteristic of the Pemón culture (Rodríguez, 2004).

The many fires currently occurring in GS (between 5000 and 10,000 fires per year [Gómez *et al.,* 2000]) are generally of human origin, which has resulted in a debate related to the sustainability of the present landscape and the possible factors that have caused it (Rodríguez, 2004; Dezzeo *et al.,* 2004b; Rull, 2009a).

Regarding conservation issues, GS is located within Venezuelan Protective Zone and Canaima National Park, which is a UNESCO Biosphere Reserve and World Heritage Site (Huber, 1995c; http://whc.unesco.org/en/list/701). Given the background described above, it seems logical to postulate that fire is a key factor to consider in the region, due to the intensive and extensive fires that are currently occurring there. For this purpose, since 1981, the government of the region (through the regional hydroelectric company, EDELCA) has developed several actions focused mainly on fire suppression (EDELCA, 2004). However, the low effectiveness of these measures, with approximately 13% of fires being controlled and extinguished, has brought into question the utility of such expensive measures (Sletto, 2008; Bilbao *et al.,* 2010). This low success percentage is mainly due to (i) the large extent of the area susceptible to fires; (ii) the high number of daily fires; and (iii) the anthropogenic character of the fires, which make any kind of prevention measures unpredictable (Rodríguez, 2007; Bilbao *et al.,* 2010).

In 2007, an international, multidisciplinary expedition formed by geologists, botanists, and paleoecologists from the PATAM research group (with participants from: University of Pittsburgh: Nathan Stansell and Broxton Bird; Botanical Garden of Orinoco: Wilmer Díaz; Botanical Garden of Merano: Otto Huber; University of Barcelona: Teresa Vegas-Vilarrúbia; and Autonomous University of Barlceona/Botanical Garden of Barcelona: Valentí Rull, Sandra Nogué, and Encarni Montoya), travelled to GS with the aim of obtaining different sedimentary sequences for paleoclimatical and paleoecological purposes. During that field trip, several records were collected in both uplands and highlands (Fig. 1.2) with a modified Livingstone piston corer (Wright *et al.,* 1984) and a Russian corer (Jowsey, 1966) for lake sediments and peat bogs, respectively (Figure 1.5). A total of ten localities were visited, and fifteen sequences were collected. A number of the sequences obtained (from upland localities) were analyzed for the present work:

- Lake Chonita (Location 1, core PATAM1 B07; 4.6501 N - 61.0157 W). Lake sequence obtained from the deepest part of the lake, 4.67 m in length (Figure 1.6).
- Lake Encantada peat bog (Location 4, core PATAM4 D07; 4.7110 N - 61.0821 W). Peat bog sequence extracted from the lakeshore, 3.93 m in length (Figure 1.7).
- El Paují (Location 5, core PATAM5 A07; 4.4746 N - 61.5883 W). Peat bog sequence 2.19 m in length (Figure 1.8).

Two of these cores were obtained in locations currently located within the typical south GS landscape (treeless savannas with *morichales*; Lake Chonita and Lake Encantada), whereas the third sequence was collected from a major ecotone site between GS savannas and Amazon rainforests (El Paují).

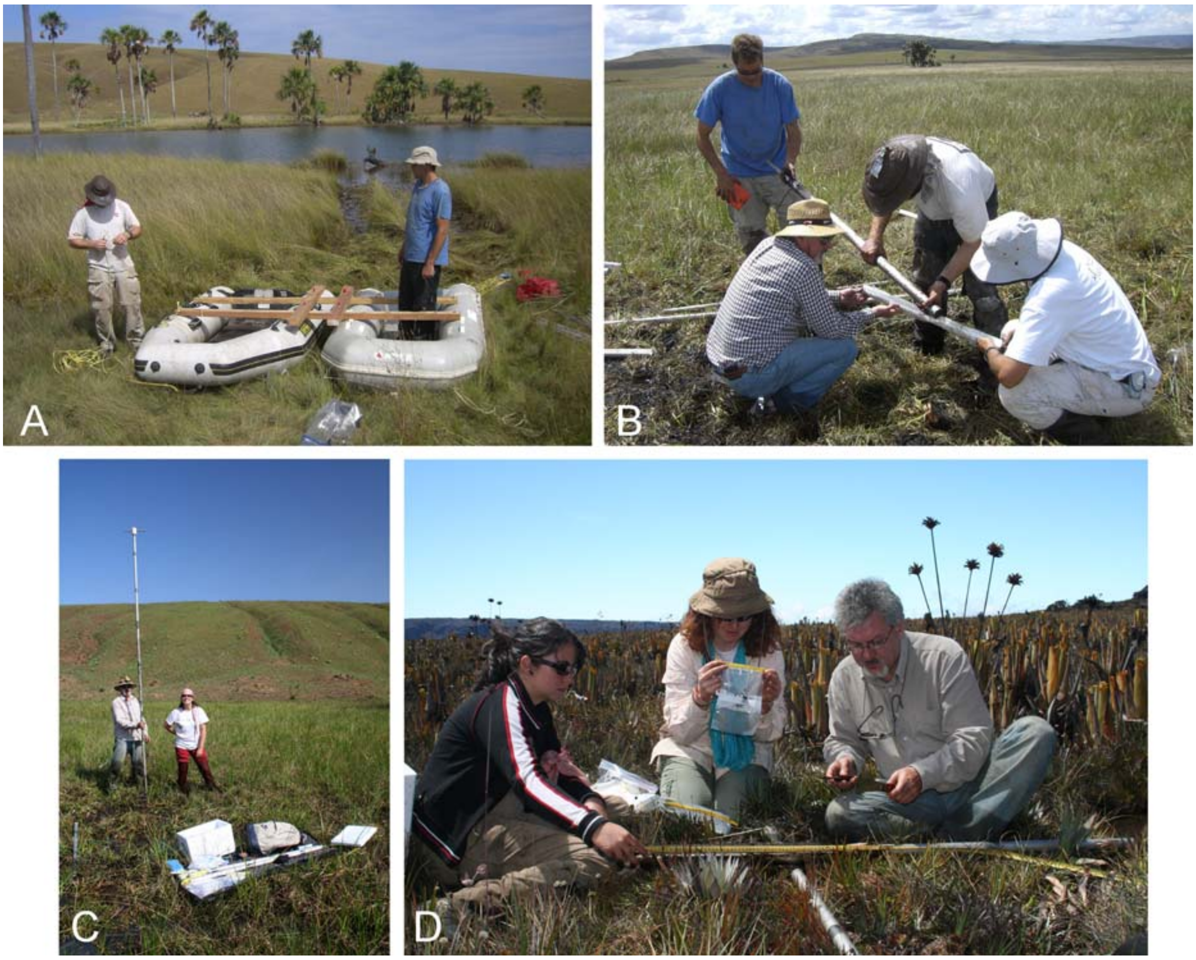

Figure 1.5. Core sampling during PATAM 2007 field trip. A-B: Lake sampling with modified Livingstone piston corer (Photos: E. Montoya, 2007); C-D: Peat bog sampling with Russian corer. (Photos: S. Nogué, 2007).

Figure 1.6. Lake Chonita sequence analyzed in the present work. Drives obtained for core PATAM1 B07. (Photos: E. Montoya, 2007).

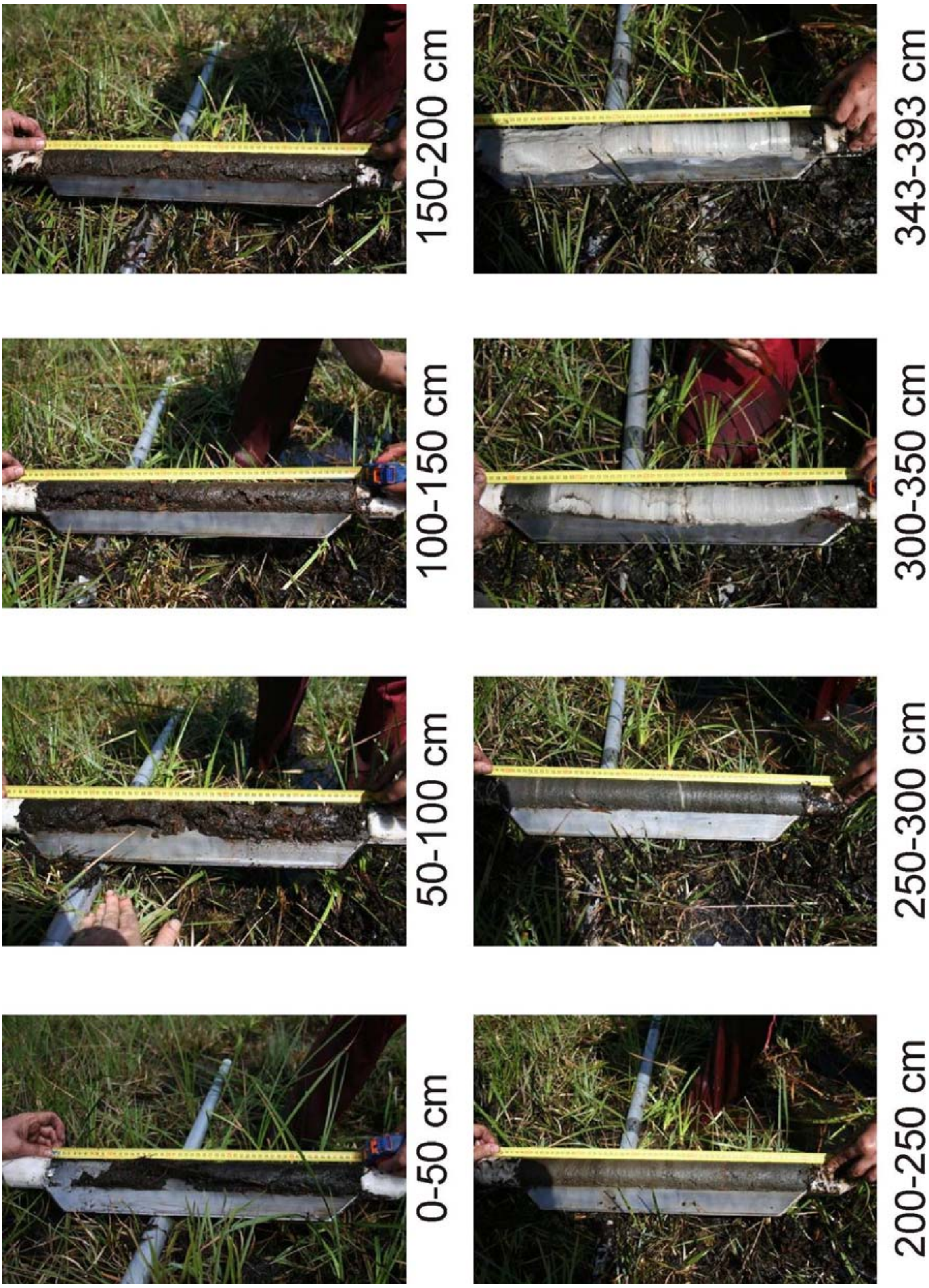

Figure 1.7. Lake Encantada sequence analyzed in the present work. Drives obtained for core PATAM4 D07. (Photos: S. Nogué, 2007).

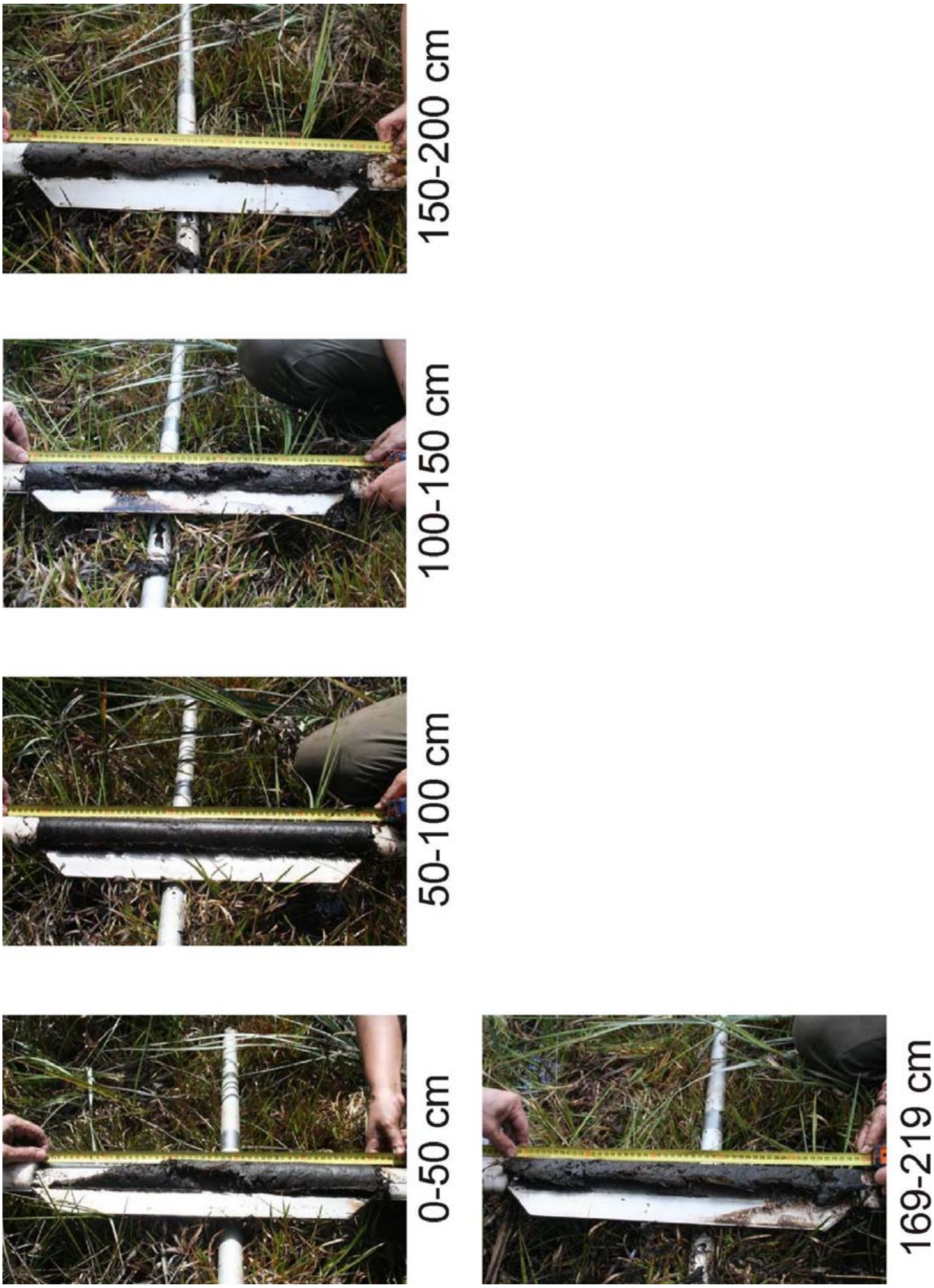

Figure 1.8. El Paují sequence analyzed in the present work. Drives obtained for core PATAM5 A07. (Photos: S. Nogué, 2007).

1.3. Paleoecology of the Gran Sabana: state of the art

The GS region remained an almost unknown area from a paleoecological point of view before the last two decades (Rull *et al.,* 2010). From the early nineties to the present, several paleoecological investigations have been carried out in the region, mainly in the southern part of GS (Rull, 1992). Although some specific remarks about these studies have been made in the relevant chapters and they will be considered in detail, together with the findings of the present work, in Chapter 8 (Discussion), a general overview of all of the GS sequence studies carried out to date is provided here. Recently, five GS records (two from northern, two from central, and one from southern GS) were analyzed by Leal (2010) in her PhD dissertation, but these have not yet been published.

Most of the GS records studied thus far correspond to the Holocene and were obtained from peat bogs. Pioneering geological works documented the apparent absence of Pleistocene sediments in this region, which were associated with a hypothetical period of extended aridity in Guayana before the Holocene (Schubert and Fritz, 1985, Schubert *et al.,* 1986). However, further GS sequences contradict this hypothesis (see Chapter 3).

The paleoecological studies developed in GS have revealed that several climatic and vegetation changes have occurred since the Early Holocene. The oldest section of the Mapaurí sequence (Rinaldi *et al.,* 1990) has been re-studied and re-interpreted by Rull (2007, 2009b) due to the improvement of the related botanical and pollen morphology literature (Steyermark *et al*., 1995-2005; Rull, 2003). In this record, the Early Holocene was characterized by an abrupt vegetation replacement from *Catostemma*-dominated cloud forests to treeless savannas *ca.* 10 cal kyr BP (Rull, 2007). These forests are currently situated on tepuian slopes (see Section 1.2) at higher altitudes, so it was proposed that upward displacement of these forests had occurred, likely due to an increase in average temperatures of approximately 2°C to 3°C during the Pleistocene-Holocene transition. The nature of this vegetation shift was therefore interpreted mainly in climatic terms, as well as being manifested in a decrease of available moisture (Rull, 2007). The record also documented the occurrence of surrounding savannas, which likely replaced forests, and regional fires. The same author postulated that these fires were probably addressed to the savanna vegetation due to the positive correlation between savannas and fire proxies, and linked them with possible evidence of an early human presence in the area (Rull, 2009b).

The remaining GS sequences are of the Mid-Holocene age and are mostly marked by the presence of treeless savannas with variations in the composition of taxa. In the Divina Pastora and Santa Teresa records, the landscape was dominated by treeless savannas during the last five kyr (Rull, 1992). However, forests were located close to these sites and/or expanded their range between 5.4 and 4.0 cal kyr BP, and subsequently the extent of the forest decreased, which was interpreted as a shift to drier climate (Rull, 1992). Wetter conditions returned by 2.7 cal kyr BP, resulting in the establishment of modern *morichales* (*Mauritia flexuosa* palm swamps, see Section 1.2) from approximately 1.6 cal kyr BP onwards, rather than expansion of the former forests. In the Urué record (Rull, 1999), environmental trends for the last two millennia were analyzed at a high resolution. In this sequence, after recurrent forest fires dated *ca.* 1.7 cal kyr BP, a secondary succession was documented. This succession, determined by fire effects, was characterized by an expansion of savannas, a decrease of the forest extent, and the appearance and establishment of *morichales*.

Hence, the overall picture suggests that climate and fire have had similar effects upon GS vegetation, i.e., the expansion of treeless savannas, the decline of forests, and the appearance and establishment of *morichales*. According to Rull (1998), the *morichales* would have been expanding their range since the Last Glacial Maximum, favored by both climate and fire. The decrease or disappearance of forests in all sequences studied reveals that these are probably not favored by present-day conditions (climatic and fire incidence). Indeed, this evidence, which mainly comes from the Urué record, also highlights the importance of fire in shaping the current GS landscape. The landscape shift recorded at Urué also agrees with a potential impoverishment of GS soils after fire disturbance, which could influence plant succession processes (Fölster *et al.,* 2001; Dezzeo *et al.,* 2004a; Dezzeo and Chacón, 2005).

1.4. Main objectives

The general objective of this study was to achieve an understanding the Gran Sabana landscape dynamics from the Late Glacial period to the present, as well as the origin and main drivers of modern GS landscapes. The data obtained will hopefully provide insights regarding the resilience of the Gran Sabana ecosystems to perturbations. To this end, multi-proxy palynological analyses of three sequences were carried out based mainly on pollen, NPP and pteridophyte spore identification, and charcoal analysis.

The specific objectives of the present work are summarized as follows:

- To enhance the number of proxies that can be useful for paleoecological research in the Neotropics, as well as to adjust the laboratory protocol for neotropical sediments.
- To reconstruct past plant communities and their changes since the Late Glacial period at a sub-millennial scale. Within this objective, emphasis will be placed on attempting to infer the major drivers involved, as well as possible synergies between these and dating the origin of the present GS ecosystems.
- To compile an overview of the paleoecological research that has been carried out to date in the Gran Sabana aimed at (i) clarifying whether the different sequences studied are subject to local or regional forcing factors; (ii) making comparisons with other sub-continental records (from northern South American low- and midlands); and (iii) attempting to establish regional trends.
- To study the real fire regime in GS, including its origin in the study area, its relationships with past and modern indigenous practices, and its effects upon vegetation. A derived aspect of this topic is a focus on improving our knowledge about the time of arrival human settlements in the region through paleoecological data.

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CHAPTER 2:

2.1. Laboratory procedure and adjustment for neotropical sediments.

2.2. Non-pollen palynomorphs from surface sediments along an altitudinal transect of the Venezuelan Andes.

I've been long, a long way from here.
Put on a poncho, played for mosquitos, and drank til I was thirsty again.
We went searching through (thrift store) jungles: found Geronimo's rifle, Marilyn's shampoo
and Benny Goodman's corset and pen

Well, o.k. I made this up, I promised you I'd never give up
Sheryl Crow; If it’s make you happy.

The contents of this chapter have been published at:
2.1. Rull, V., Stansell, N.D., Montoya, E., Bezada, M. & Abbott, M.B. 2010. *Palynological signal of the Younger Dryas in the tropical Venezuelan Andes*. Quaternary Science Reviews 29, 3045-3056. doi:10.1016/j.quascirev.2010.07.012. (In the form of supplementary information).
2.2. Montoya, E., Rull, V. & van Geel, B. 2010. *Non-pollen palynomorphs from surface sediments along an altitudinal transect of the Venezuelan Andes.* Palaeogeography, Palaeoclimatology, Palaeoecology 297, 169-183. doi:10.1016/j.palaeo.2010.07.026.

2.1. Laboratory procedure and adjustment for neotropical sediments.

Laboratory processing of palynological samples (by E. Montoya).

- Transfer the samples into 50 ml test tubes (glass)
- Spike with *Lycopodium* tablets
- Add 15 ml of potassium hyodroxide solution (10%), stir and heat in a water bath for 20 min
- Add distilled water up to 50 ml, stir, centrifuge and decant
- Rinse with water until the pH of distilled water is attained (minimum two times)
- Sieve trough a 200 µm mesh
- Add 15 ml of hydrocloric acid (37%), stir and heat in a water bath for 10 min
- Add distilled water up to 50 ml, stir, centrifuge and decant
- Rinse with water until the pH of distilled water is attained (minimum two times)
- Rinse with glacial acetic acid (two times)
- Add 15 ml of acetolysis mixture*, stir and heat in a water bath for 4 min
- Add glacial acetic acid up to 50 ml, stir, centrifugue and decant (two times)
- Rinse with water until the pH of distilled water is attained (minimum two times)
- Transfer the suspension to teflon test tubes, centrifuge and decant
- Add 15 ml of hydrofluoric acid (70%), stir and heat in a water bath for 20 min, centrifuge and decant
- Add 15 ml of HF, stir and left overnight (~12 hours)
- Add distilled water up to 50 ml, stir, centrifuge and decant
- Add a mixture (1:1) of ethanol (96%) and distilled water up to 50 ml, stir centrifugue and decant
- Add pure ethanol (96%) up to 50 ml, stir centrifugue and decant
- Add a mixture (1:1) of ethanol (96%) and tertiary butyl alcohol (TBA, 99%) up to 50 ml, stir centrifugue and decant
- Add pure TBA up to 50 ml, centrifugue and decant
- Transfer the suspension to small glass vials with screw cap
- Add 4-5 drops of silicon oil (12,500 *cs*) and homogenize
- After the complete evaporation of the TBA, the silicone suspension is ready for mounting

* 9 parts of acetic anhydride (%) and 1 part f sulfuric acid (%)

2.2. Non-pollen palynomorphs from surface sediments along an altitudinal transect of the Venezuelan Andes.

ABSTRACT

Palynological studies including records of non-pollen palynomorphs (NPP) are uncommon in the Neotropics, in spite of their demonstrated usefulness in other regions. Modern analog studies to improve palaeoecological interpretations of NPP are even more scarce. Here, we report the NPP assemblages recorded in modern surface samples from an altitudinal transect of the Venezuelan Andes, ranging from about 2300 and 4600 m. We compared the assemblages with the results of previous pollen analyses of the same samples. The variables considered to explain NPP patterns along the transect are altitude and the local habitat of the sampling site (“sample type”). A total of 65 NPP taxa – classified into algal and zoological remains, and fungal spores – have been found. Unidentified taxa (23) have been named with a code, depicted and described for further reference. Fungal spores are well represented along the whole transect, whereas algal and zoological remains are absent or very scarce in the lower and the uppermost ranges. The altitudinal zonation of fungal spores matches with that of pollen and the corresponding vegetation belts, suggesting a close relationship. The known environmental requirements of some of the fungi identified allowed inferences on particular ecological features, in agreement with previous palynological interpretations. Both elevation and sample type are needed to explain the observed differences in the assemblages of the three groups, the elevation being more decisive for fungal spores and the local habitat of the sampling site for algal and zoological remains. The sample type effect is minimised when the NPP studied are considered altogether, thus increasing their usefulness as palaeoecological proxies. This study reinforces the utility of modern analog surveys of NPP with palaeoecological purposes and encourages further research, particularly in poorly known areas, as for example tropical regions.

Keywords: Altitudinal transect; Andes; Modern analogs; Non-pollen palynomorphs; Sample type; Venezuela.

2.2.1. Introduction

The study of microfossils other than pollen and pteridophyte spores present in pollen slides, also called “non-pollen palynomorphs” (NPP), proved to be useful in palaeoecological interpretations (van Geel, 1986, 2001). NPP are of diverse origin, including fungal spores, algal remains, as well as plant and animal fragments of different nature. A common handicap in these studies is that the taxonomic identity of many NPP is not yet known, thus the indicator-species approach (Birks and Birks, 1990) is difficult to apply. This has lead to a classification system of NPP in morphological types using codes to name them, developed at the University of Amsterdam (Hooghiemstra and van Geel, 1998 and references therein). In this way, when a NPP type is identified, information from previous studies can be used for the environmental interpretation. This procedure has been applied successfully in many palaeoecological, palaeoenvironmental and palaeoanthropological studies (e.g. van Geel, 1976, 1978, 2001; van Geel *et al*., 1981, 1983, 1989, 1994, 1996). The study of modern analogs is another useful approach for palaeoecological reconstructions. It is of increasing significance during the last few decades (Jackson and Williams, 2004). The idea is to associate the palynomorph content of surface samples to present-day environmental and biotic features, in order to infer past conditions from fossil assemblages, using the principle of uniformism. Despite some promising attempts (Grabandt, 1990; Rull and Vegas-Vilarrúbia, 2001), this approach has not yet been adequately tested in NPP studies. Another general handicap in both modern analog and palaeocological studies is the choice of the best local habitat for sampling (sample type), in order to obtain accurate proxy representation (Medeanic, 2006; Rull, 2006).

In the Neotropical region, NPP studies are scarce, though several surveys have been conducted in Mexico (Almeida-Lenero *et al*., 2005), Brasil (Medeanic *et al*., 2003; Ledru *et al*., 2006; Medeanic, 2006), Colombia (van Geel and van der Hammen, 1978; Hooghiemstra, 1984; Kuhry, 1988; Grabandt, 1990), and Venezuela (Rull and Vegas-Vilarrúbia, 1997, 1999, 2001; Lovera and Cuenca, 2007; Rull *et al*., 2008). Besides identification issues, the lack of taxonomical and autoecological studies on potentially involved organisms is an added problem in this region. For example, Rull *et al*. (2008), working on the Venezuelan Andes, found a NPP indicator of the Younger Dryas chron (an event that has not been clearly recorded in the region, so far), that could not be related to any known organism and, hence, its palaeoenvironmental significance remains unknown. Another potential problem is that a number of studies assign some neotropical NPP types to the same taxa as recorded in temperate zones, which can be considered as doubtful (Ledru *et al*., 2006; Rull *et al*., 2008).

The aim of the present paper is to test the potential palaeoecological indicator value of modern NPP analogs in the Venezuelan Andes. The study uses the same altitudinal sampling transect from a previous modern analog survey on pollen and pteridophyte spores (Rull, 2006). In this way, besides the information that NPP may provide by themselves, the NPP record can be compared with pollen and altitudinal vegetation patterns, thus enhancing their interpretative usefulness.

2.2.2. Study Area and Methods

The sampling area is described in detail by Rull (2006); here a summary will be provided. The transect is in the Sierra de Santo Domingo, in the northernmost part of the Andes (Fig. 2.2.1). In this area, the montane Cloud Forest extends up to 3000 m, with 100–200 m local variation due to human activities. The Páramo ranges from this altitude to the snowline (4700 m), and its physiognomy is determined by the presence of the typical stem rosettes of *Espeletia* (Asteraceae).

The transition between Cloud Forest and Páramo is not sudden but transitional, determining a narrow ecotone of one or a few hundred meters dominated by shrubs (Subpáramo or Páramo Shrubland). Similarly, the contact with the snowline shows a gradient from the densely vegetated Páramo to barren rocky environments, called Superpáramo or Desert Páramo, which extends between around 4000 and 4700 m altitude. Climatically, the upper and lower Páramo boundaries are characterised by respectively the 0 °C and 10 °C isotherms of annual average temperature (Monasterio and Reyes, 1980), and there is a fairly constant decrease of 0.6 °C/100 m altitude (Salgado-Labouriau, 1979). Total annual precipitation is not related to altitude, ranging from about 700 to 900 mm (Monasterio, 1980). Peat bogs are common in the whole range of the Venezuelan Páramos, while glacial lakes are especially abundant above 3500 m.

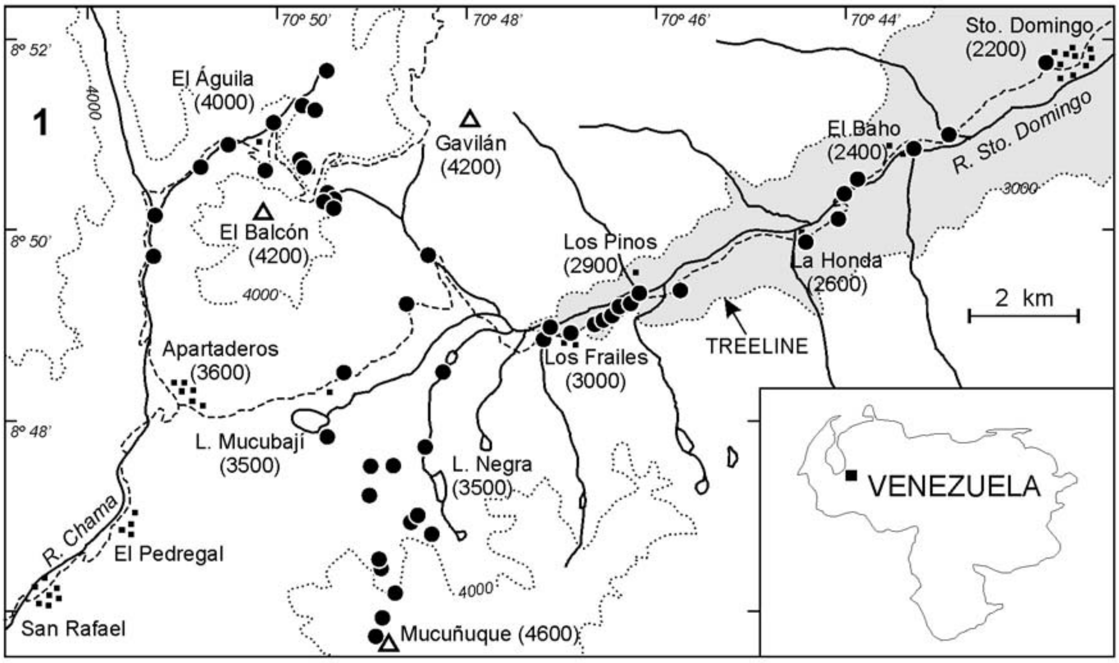

Figure 2.2.1. Sketch map showing the sampling sites (black dots). The grey area corresponds to montane forests and the white area to Páramos s.l. (after Rull, 2006). Number 1 indicates the location of Laguna Verde Alta record (Rull *et al*., 2008), mentioned in the text. Altitudes are given in meters (m).

A total of 57 surface samples were taken from wet soils, moss polsters, lake shores and peat bog surface sediments, ranging from about 2300 to 4600 m altitude. Samples below ~3100 m are mostly from soils, bogs and mosses due to the scarcity of lakes at these elevations (Table 2.2.1). In the Páramo zone, most samples are from peat bogs, up to around 4100 m. In the Superpáramo, sample types are more varied, but mainly from mosses and bogs. This transect includes most of the sites cored in previous palaeoecological studies (Rull, 2006).

The samples were processed according to standard palynological procedures including KOH, HCl and HF digestions, and acetolysis (Faegri and Iversen, 1989). Slides were mounted with glycerine jelly. NPP abundance was expressed as percentage with respect to the pollen sum, which includes all pollen taxa apart from aquatic plants (Rull, 2006). NPP identification was made according to Bell (2005), Charman *et al*. (2000), Grabandt (1990), Hooghiemstra and van Geel (1998) and references therein, Jankovská (1990, 1991), Jankovská and Komárek (2000), Kuhry (1997), Rull and Vegas-Vilarrúbia (2001) and Vánky (1994). Diagrams were plotted with psimpoll 4.10 and the different zonations were performed by “optimal splitting by information content” (OSIC), using the broken stick method to determine the significant number of zones (Bennett, 1996). Correspondence analyses (CA) and cluster analysis were performed with MVSP 3.13, after root-square transformation of percentages. Rare taxa were not downweighted. In the cluster analysis, the NPP were classified using the squared Euclidean distance and the minimum variance agglomerative method.

Table 2.2.1. Sample types according to the altitudinal arrangement of vegetation.

	Soil	**Moss**	**Bog**	**Lake**	**TOTAL**
Superpáramo	1	4	7	3	15
Páramo	4	2	22	2	30
Subpáramo	1	2	0	0	3
Cloud Forest	5	0	4	0	9
TOTAL	11	8	33	5	57

2.2.3. Results

A total of 65 NPP morphological types were recorded, including 38 forms of fungal spores, 10 forms of algal remains, and 17 forms corresponding to protozoans and diverse other zoological remains (Appendix A). Some of them have been identified to some extent. Among the unidentified forms, some could be assigned to previously described types of the Amsterdam classification and referred to the corresponding literature, while others have been described for the first time and named using a code with the prefix IBB — (Institut Botànic de Barcelona) and a sequential number.

The altitudinal distribution of the three NPP groups has been illustrated in Fig. 2.2.2. Fungal spores are present throughout the whole transect, showing their maximum values in the uppermost Cloud Forest and the Subpáramo (~2600–3000 m). The lower fungal spore values are around the middle of the Páramo zone (~3500–3800 m), and from these altitudes to the Superpáramo (up to 4600 m), percentages are intermediate. Algal and zoological remains show a different altitudinal pattern. These two types of NPP remains are very scarce or absent below ~3800 m, but show a pronounced increase above this altitude. Algae show their maximum values between 3900 and 4000 m (Páramo–Superpáramo transition), while zoological remains peak around 3900 m, decrease at the Páramo–Superpáramo transition, and increase again at the top of the transect. Concerning sample type, there is some differentiation regarding the different NPP abundances (Table 2.2.2): i) Algae are frequent and abundant in bog and lake samples, and scarce in moss polsters; ii) Zoological remains are also more frequent in bogs but interestingly absent in lake samples (except for the occurrence of *Neorhabdocoela* in one single sample, Fig. 2.2.4); and iii) Fungal spores are important in all sample types except for lake samples. All sample types have been productive for most of the NPP found, bogs being the sample type containing frequent and abundant representatives of all NPP groups, whereas moss samples are scarce in algal and zoological remains, and soil samples contain few zoological remains.

Table 2.2.2. Dominance of the studied NPP categories depending on: A) sample type; and B) vegetation arrangement (numbers represent the samples where the NPP group was the dominant). SSP = Superpáramo; P = Páramo; SBP = Subpáramo; CF = Cloud Forest.

A

	Soil	Moss	Bog	Lake
Algae	2	1	3	2
Animals & others	0	1	11	0
Fungi	8	6	14	2

B

	SSP	P	SBP	CF
Algae	5	3	0	0
Animals & others	6	4	0	2
Fungi	5	15	3	7

Algae are restricted between ~3300 and ~4100 m (Fig. 2.2.3). *Concentricystis* (which is also known in the literature as *Pseudoschizaea*) is included here because it is likely of algal origin (Milanesi *et al*., 2006), although the phylogenetic relationship has not yet been confirmed, thus supporting other opinions and nomenclature (Scott, 1992). *Concentricystis* has a low abundance in the sequence; it is only present in four samples from the Páramo zone and in three samples from the lower Subpáramo and Cloud Forest zones (between 3800 and 2800 m). From 3760 m upwards, several Chlorophyte taxa show a short sequence until 4150 m, beginning with *Zygnema*-type and ending with *Spirogyra* (morphotype 1, see Appendix A), with *Pediastrum* and *Botryococcus* (two of the more frequent algae in palaeoecological studies) in an intermediate position between 3900 and 4000 m. Among the more abundant types, it is worth mentioning that *Botryococcus* and *Zygnema*-type are also present – though in very low values – at lower altitudes, whereas *Pediastrum* is absent. It is also noteworthy that algal types are common in lake samples and also occur in bog samples, but algae are absent or very scarce in soil and moss samples.

The altitudinal distribution of zoological remains is similar to the distribution of algae, except for the occurrence of *Assulina*, *Neorhabdocoela* and *Acari* in soil samples from the upper Cloud Forest zone (Fig. 2.2.4). Most zoological types are absent in the lower Páramo zone, appearing around 3500 m and extending to the top (4600 m), except for some types (*Centropyxis aculeata*-type, *Conochilus natans*-type and *Centropyxis cassis*-type), which occur until around 3900 m, and thus not reaching the Superpáramo. They are abundant in bog samples (Table 2.2.2), but they are also present in several moss samples.

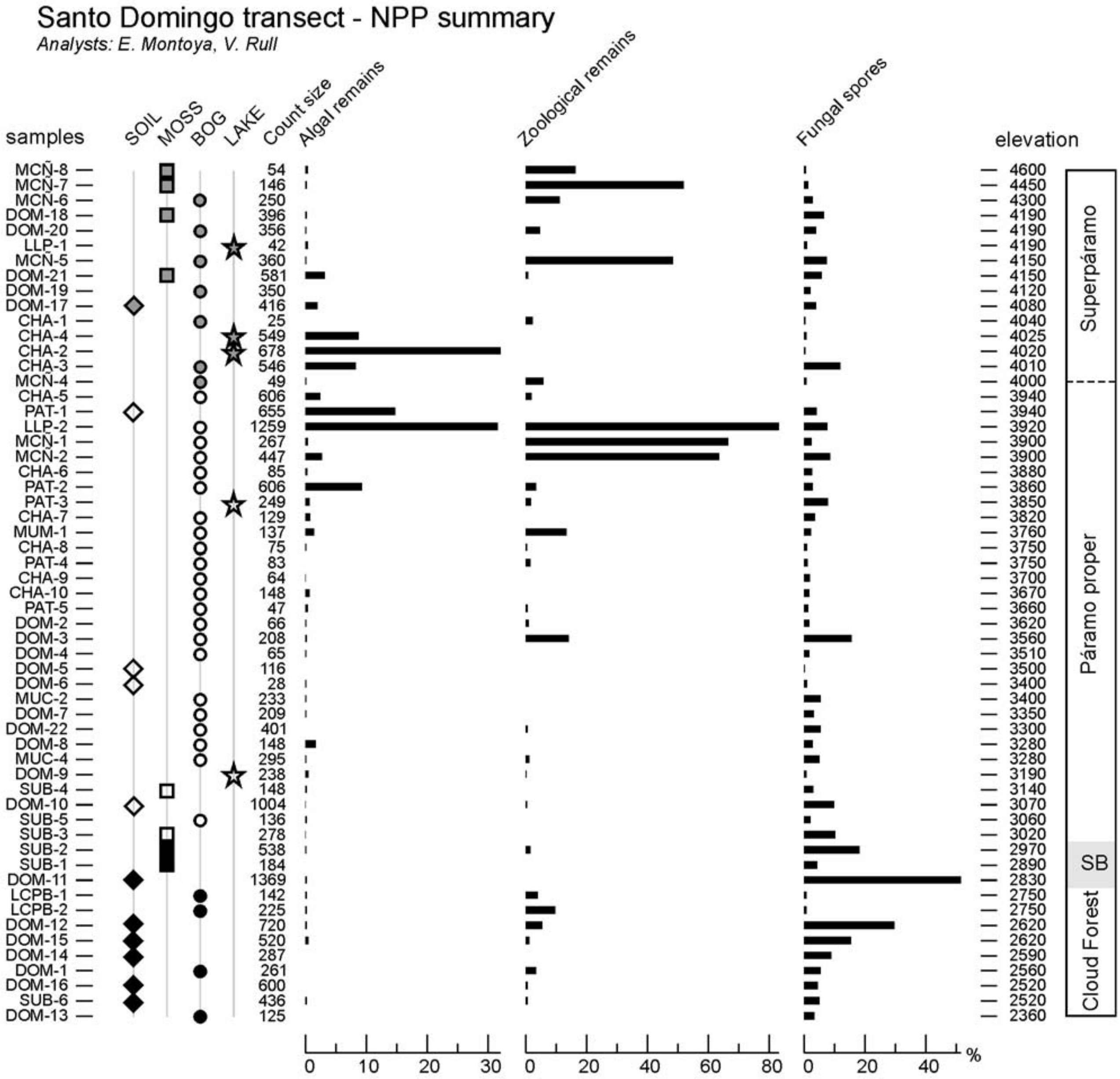

Figure 2.2.2. NPP summary diagram. Percentages are based on pollen sum (see methods). The sample type (bog, lake, moss, and soil) is indicated at the left side of the diagram (black = Cloud Forest/Subpáramo, white= Páramo, grey = Superpáramo). The altitudinal vegetation patterns (Cloud Forest, Páramo, etc.) are indicated at the right column. SB = Subpáramo or Shrub Páramo.

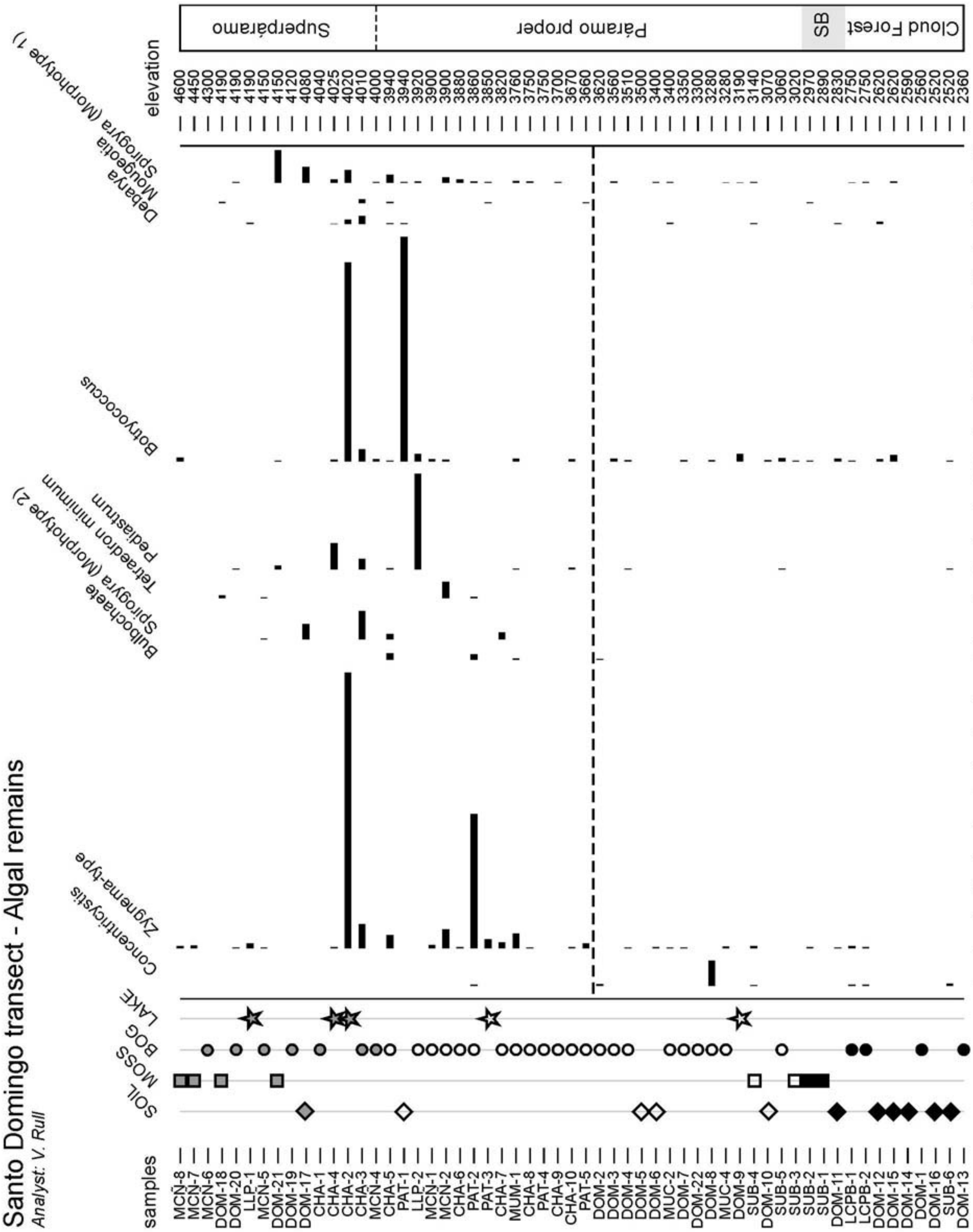

Figure 2.2.3. Percentage diagram of algal remains, following the same representation patterns as in Fig. 2.2.2. The broken line indicates the zone boundaries using the OSIC zonation method (see Methods for details).

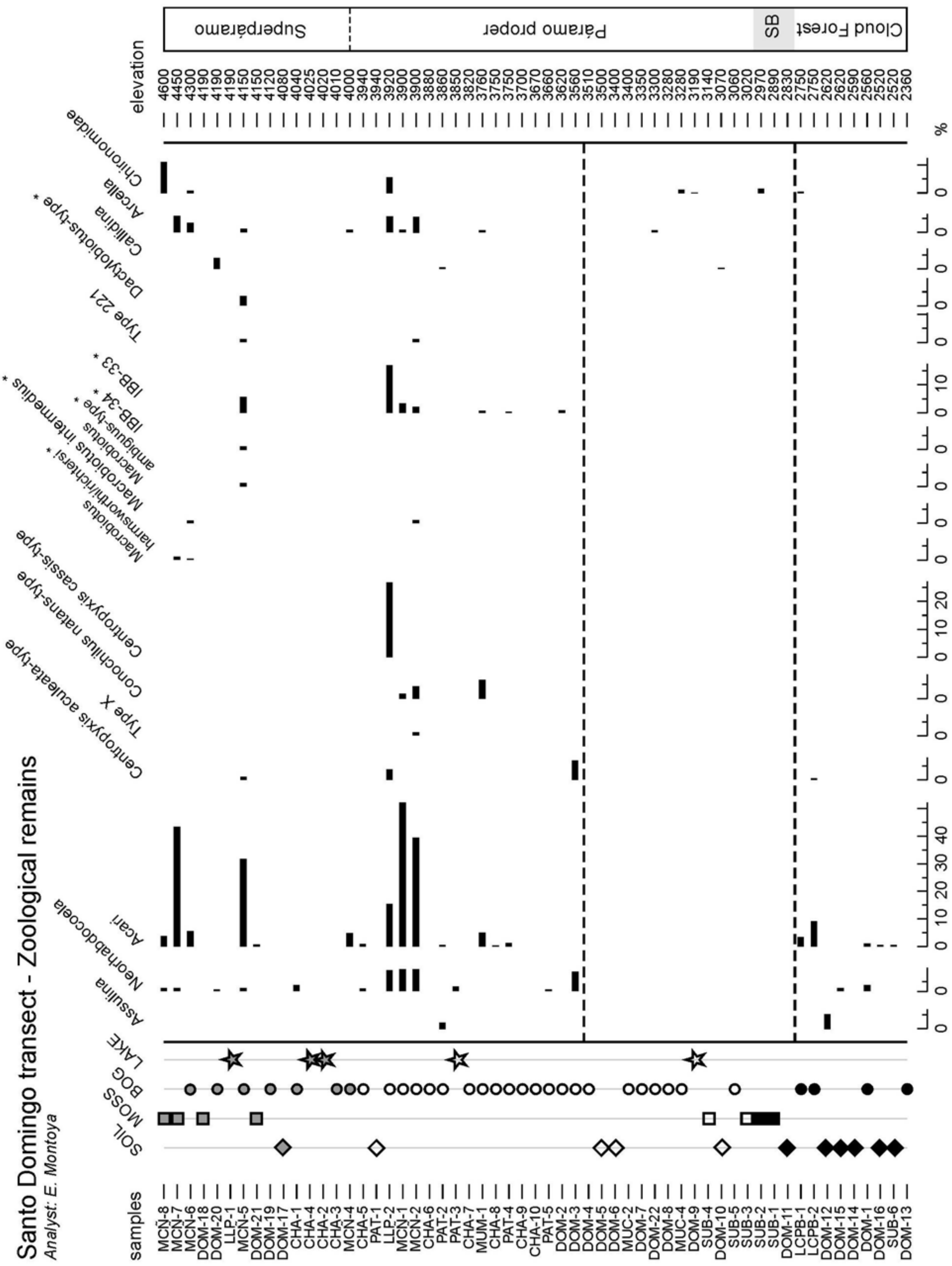

Figure 2.2.4. Percentage diagram of zoological NPP, following the same representation patterns as in Fig. 2.2.2. The broken lines indicate the zone boundaries using the OSIC zonation method (see Methods for details). (*=Tardigrada egg morphotypes).

Fungal spores are more diverse than algal and zoological remains, and show a more extended and continuous elevational distribution (Fig. 2.2.5). The zone boundaries obtained in this case almost coincide with the vegetation boundaries. In the Cloud Forest zone, the assemblage is dominated by *Coniochaeta* cf. *ligniaria* and IBB-31, with a significant contribution from *Cercophora*-type, Sordariales, IBB32 and IBB-29. Other morphotypes such as Types 495, IBB-22, IBB-24 and IBB-6 occur in low frequencies. In the Páramo, these types decrease or disappear and are replaced by others, such as *Sporormiella*-type and Type 201, among the more abundant. *Sordaria*-type is present throughout the transect but in this part of the transect it reaches the maximum values. The Superpáramo is characterised by a diversity decline due to the scarcity or absence of most of forest and Páramo types, except for *Sporormiella*-type and Type 201 which decrease compared to the Páramo zone, and IBB-15, which slightly increases. *Coniochaeta* cf. *ligniaria* also appears again at the top of the transect, but in a lower frequency than in the Cloud Forest zone.

The cluster analysis defined three main NPP groups with some subgroups (Fig. 2.2.6):

Group 1 includes 45 of the 65 identified NPP. All the zoological remains are present within this assemblage. Three well defined subgroups could be distinguished (excluding *Acari* from these subgroups):
- Subgroup 1A represents NPP from the three established categories and is mainly formed by types present in few samples at low frequencies. Most of these types occur from ~3800 m upwards (Fig. 2.2.6.B).
- Subgroup 1B mainly includes fungal spores, but *Concentricystis* is also included. The maximum values of these types are found along intermediate elevations (2800–3300 m), though they are present until the lowest part of the transect (Fig. 2.2.6.B).
- Subgroup 1C includes a high number of zoological remains, although the three NPP categories are represented. Their maximum values are from ~3700 m upwards (Fig. 2.2.6.B).

Group 2 is entirely formed by fungal spores; two subgroups could be distinguished:
- Subgroup 2A includes 11 fungal spore types, the more abundant are *Cercophora*-type, Sordariales, IBB-31 and *Glomus*. These taxa are present in the lower part of the transect, being more abundant from 3000 m downwards.
- Subgroup 2B includes only two fungal spore types wich are practically absent at intermediate elevations (between 3000 and 4000 m), and show their maximum values from 2800 m downwards (Fig. 2.2.6.B).

Group 3 is the group less well defined; two subgroups could be differentiated (excluding *Pediastrum* from the subgroups):
- Subgroup 3A only includes three fungal spore types, which are present along the whole transect, but with maximum values at the intermediate elevations (from around 3000 to 4000 m, Fig. 2.2.6.B).
- Subgroup 3B only includes two different algal types. Their maximum values are represented between 3800 and 4000 m (Fig. 2.2.6.B).

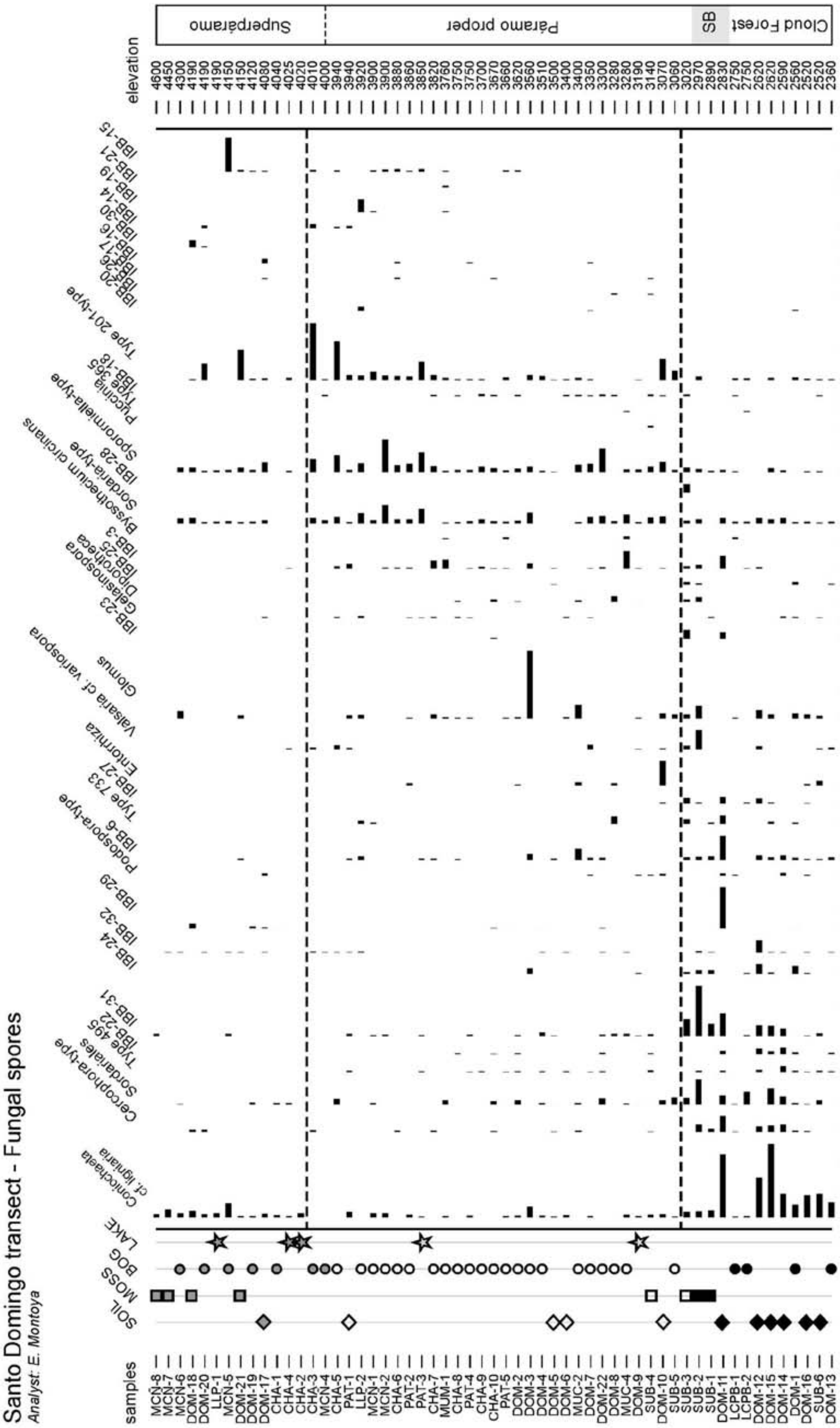

Figure 2.2.5. Percentage diagram of fungal spores, following the same representation patterns as in Fig. 2.2.2. The broken lines indicate the zone boundaries using the OSIC zonation method (see Methods for details).

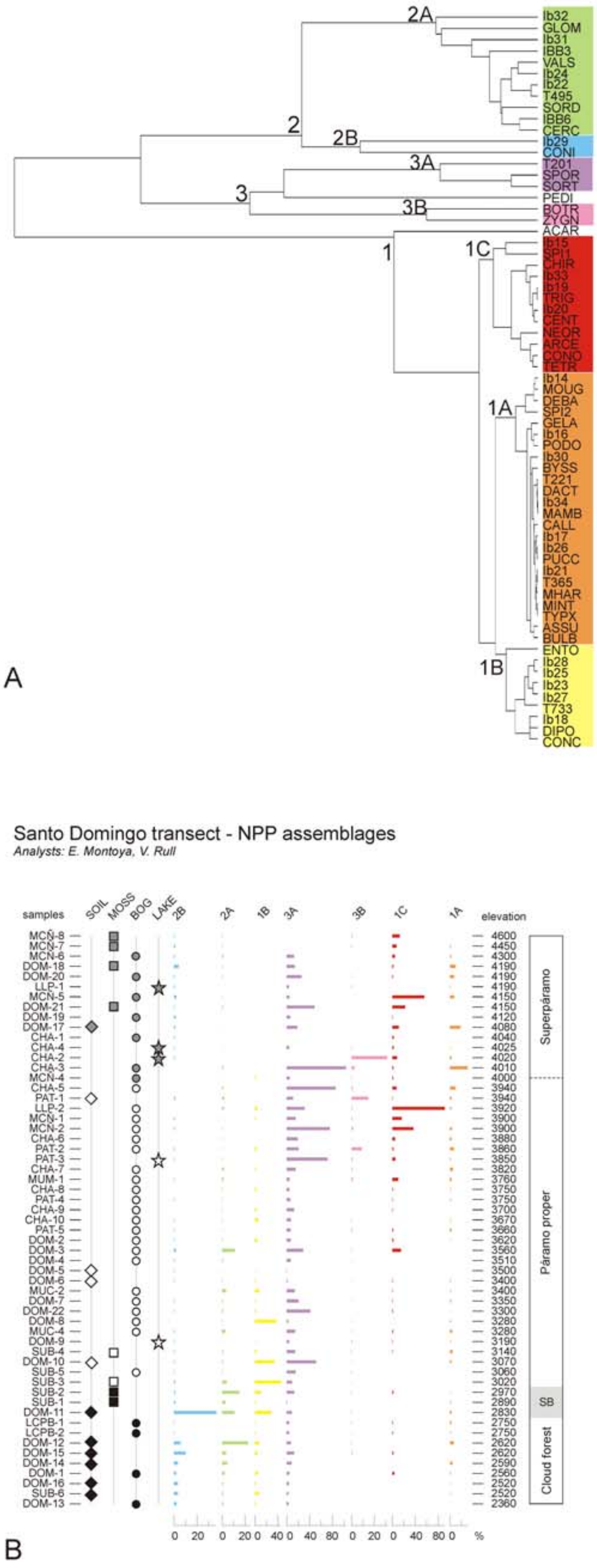

Figure 2.2.6. NPP assemblages. A. Scatter plot using the cluster analysis results, based on minimum variance and squared euclidean distances. See acronyms in Appendix A. B. Percentage diagram of the assemblages obtained in cluster analysis, following the same representation patterns as in Fig. 2.2.2.

Fig. 2.2.7.A shows the arrangement of sampling sites in the space of the first two axes of the CA analysis, which account for 18% of the total variance. Axis 1 likely represents an altitudinal gradient with Cloud Forest/Subpáramo samples at the left side, Superpáramo samples at the right, and Páramo proper samples in between. However, six samples deviate from this pattern. This is the case in one Páramo sample (LLP-2) that lies in the Superpáramo region (Fig. 2.2.7.A). This sample, however, is from a bog at 3920 m elevation, which is very close to the Páramo–Superpáramo boundary. Also, two Cloud Forest/ subpáramo bog samples (LPCB-1 and LPCB-2) are within the Superpáramo and Páramo regions, respectively. Despite their elevation (2750 m) below the regional upper Cloud Forest limit, these bogs are in an area where human activities have significantly lowered the treeline. The vegetation now consists of open Páramo vegetation. Finally, two bog samples (CHA-1 and DOM-19) and one moss (DOM18) Superpáramo sample fall within the Cloud Forest domain. In this case, there are no apparent environmental features that distinguish these samples from others taken at Superpáramo elevations. The Pearson product-moment correlation coefficient between axis 1 and altitude is $r = 0.417$, which is significant at $p < 0.001$. Axis 2 could be related to sample type, possibly linked to water content, as all lake samples are within the negative side, while most soil and moss samples are at the positive side. The dispersion along axis 2 increases with altitude, indicating that the effect of sample type is larger at higher than at lower altitudes.

Fig. 2.2.7.B shows the arrangement of the NPP types in the space of the first two axes of the CA analysis. Although some of them deviated from the general rule, they form three clear groups according to their taxonomic origin. Fungal spores are widespread along axis 1, but they occur mostly at medium to lower elevations. Algal and zoological remains lie mostly at intermediate to high values, respectively. With respect to axis 2, fungal spores show little dispersion as compared to other NPP types. This axis clearly segregates algal (mostly negative) from zoological remains (mostly positive) at the right side of the plot.

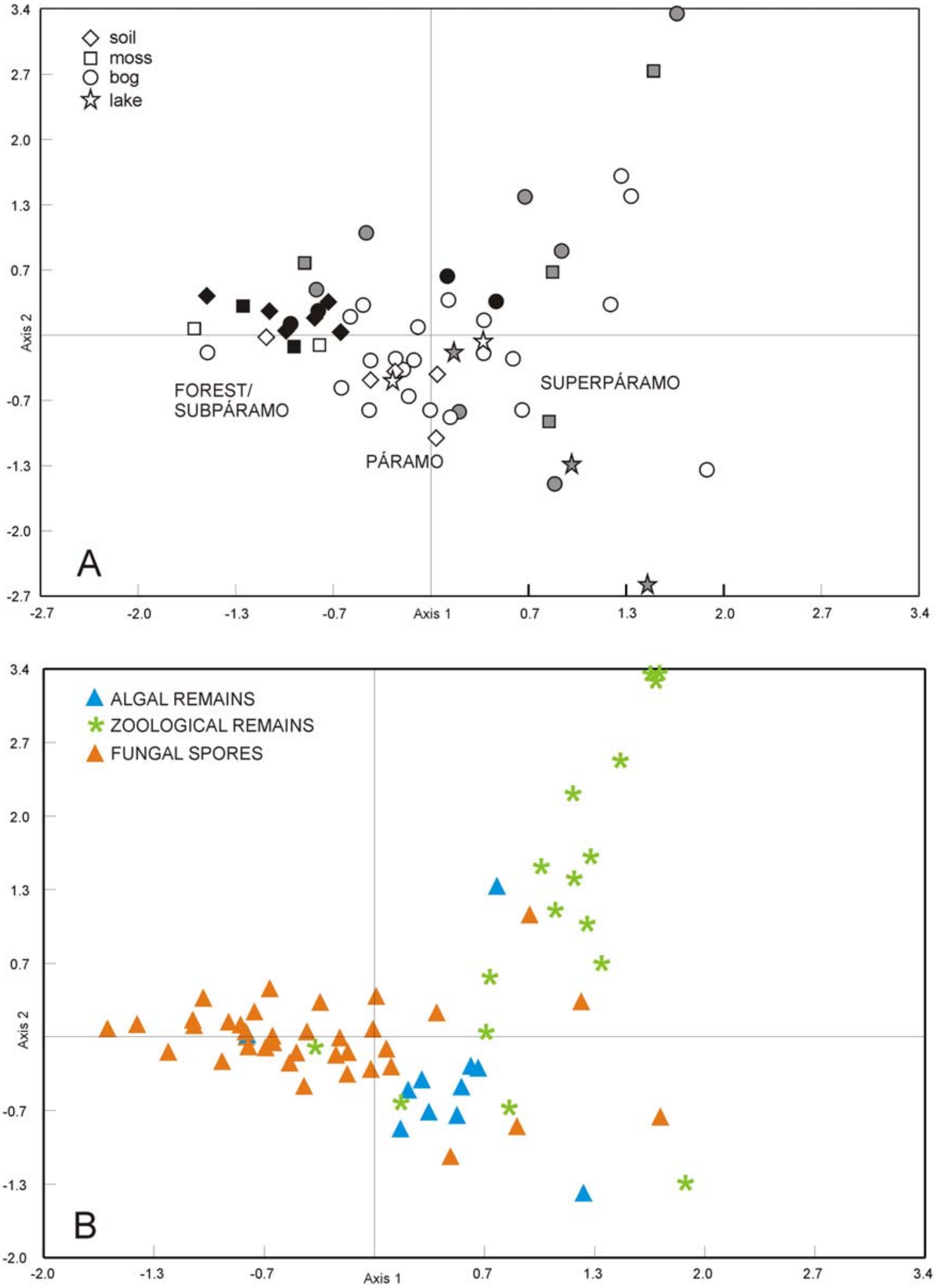

Figure 2.2.7. Ordination analyses. A. Sample ordination analysis. Scatter plot using the first two CA axes. Samples are differentiated according to two criteria: sample type (see legend) and vegetation type (black = Cloud Forest/Subpáramo, white = Páramo, grey = Superpáramo). B. NPP ordination analysis. Scatter plot using the first two CA axes. NPP are differentiated according to their taxonomic origin.

2.2.4. Discussion

The main environmental variables tested in this study are altitude and sample type. In a previous study, altitude was found to be the main environmental feature needed to interpret pollen and pteridophyte spore presence and abundance along the same transect (Rull, 2006). The record of pollen and pteridophyte spores was linked with the distribution of pollen and spore producing plants but in the case of NPP, the situation is somewhat different, as is discussed below. The discussion is organised according to the different NPP groups found.

2.2.4.1. Algal remains

The maximum abundance of this group, as a whole, occurs around the transition between Páramo and Superpáramo vegetation belts in different sample types (wet soils, bogs and lake sediments; Fig. 2.2.2), suggesting a major influence of elevation. However, the abundance of each NPP type differs according to both altitude and sample type (Fig. 2.2.3), which points towards an influence of this factor at individual NPP level (Fig. 2.2.7.B). For example, the influence of altitude is especially significant in *Spirogyra* morphotype 1, which is almost restricted to the Superpáramo and increases with elevation until about 4200 m (Fig. 2.2.3). Contrastingly, *Spirogyra* morphotype 2 occurs in bog and soil samples but not in lake sediments (Fig. 2.2.3). *Botryococcus* is abundant in lakes and soils but not in bogs, whereas *Pediastrum* and *Zygnema*-type have their maxima in bogs and lakes. Previous palaeoecological studies in the northern Andes have documented the same or similar algal remains and have interpreted them in palaeoenvironmental terms. In the Venezuelan Andes, Salgado-Labouriau and Schubert (1977) used *Botryococcus* and zygospores of Zygnemataceae as indications of warmer climates, while Rull and Vegas-Vilarrúbia (1993) emphasised that habitat preference (i.e. littoral vs. pelagic conditions) would be more determinant. In a neighbouring area (Fig. 2.2.1), Rull *et al*. (2008) suggested that the *Pediastrum*–*Botryococcus* alternation would be the reflection of colder–warmer climates in the Superpáramo belt. The results of the present work do not support evident climatic (i.e. altitudinal) differences for these NPP, as habitat peculiarities (i.e. sample type) seem to play a role. In the Colombian Andes, van Geel and van der Hammen (1978) linked *Debarya* with cool climates and *Mougeotia*, *Spirogyra* and *Zygnema*-type with Páramo conditions, and that conclusion is supported by the results of our Venezuelan transect study.

2.2.4.2. Zoological remains

The maximum abundance of these NPP as a group occurs in the uppermost Páramo and Superpáramo samples (Fig. 2.2.2), and therefore elevation is a factor to be taken into account. However, maximum abundances occur almost always in bog samples and never in lakes (Table 2.2.2), indicating that sample type should also be considered (Fig. 2.2.7.B). Individually, some interesting relationships can be established. For example, the maximum around 3900 m is mainly due to *Acari* remains and coincides with a maximum of *Isoëtes* (Rull, 2006), an aquatic fern living on flooded bogs and shallow waterbodies. The association of Oribatid mites and aquatic macrophytes is well known elsewhere (Erikson, 1988), and has also been documented in the Venezuelan Páramos (Rull and Vegas-Vilarrúbia, 1997). Testate amoebae show very different patterns as *Assulina* is scarce and present in the Cloud Forest and Páramo belts, while *Arcella* was recorded almost only in Páramo and Superpáramo belts, reaching the uppermost levels (Fig. 2.2.4). Grabandt (1990) found a similar distribution for *Arcella* in the Colombian Andes. Other important types are *Neorhabdocoela* and the different Tardigrada egg morphotypes (Fig. 2.2.4). In this study, *Neorhabdocoela* peaks around the Páramo–Superpáramo transition in bog samples.

Rull *et al*. (2008) suggested that increases in *Neorhabdocoela* oocites could be related to higher lake levels but this is not supported here; a more detailed study of the different lacustrine sub-environments would be necessary to test this hypothesis. In general, Tardigrada eggs have been found at high latitudes and at low-latitude high altitudes, usually under cold climates, in shallow permanent oligotrophic and acidic water bodies (Jankovská, 1990, 1991; Kaczmarek *et al*., 2008). According to Cromer *et al*. (2008), this is because these environments provide better preservation conditions, but a bias in sampling efforts should also be considered. For example, in the present study, most of the six classes of these eggs were found in bog samples and none of them was recorded in lake sediments (Fig. 2.2.4).

2.2.4.3. Fungal spores

The evident and continuous gradient of these spores along the transect, independent from sample type (Fig. 2.2.5), suggests that altitude is the main environmental feature that controls their distribution (Fig. 2.2.7.B). Furthermore, the corresponding fungal spore zonation and pollen zonation suggest a close relationship, probably because flowering plants create the habitats for various saprophytic and parasitic fungi. This is manifest, for example, in the lower zone, corresponding to the Cloud Forest and Subpáramo belts, dominated by ligneous plants, where *Coniochaeta* cf. *ligniaria* and *Cercophora*-type – two taxa typical of environments with abundant decaying wood; van Geel *et al*., 2003; van Geel and Aptroot, 2006 – are dominant. Likewise, the frequent occurrence of *Glomus*, though in low frequencies, is also noteworthy as this is a mycorrhizal fungus commonly associated to the roots of trees and shrubs (van Geel *et al*., 1989). The highest abundance of *Glomus*, however, occurs in one single sample (DOM-3) within the Páramo belt. This sample was taken in a bog near a *Pinus* plantation, which could explain the high abundance of this mycorrhizal fungus. In the Páramo belt, *Sporormiella*-type and *Sordaria*-type are almost continuously present. Both genera have been described as coprophilous (van Geel and Aptroot, 2006), and often related with the presence of large herbivores (van Geel *et al*., 2003; Raper and Bush, 2009). In our transect *Sporormiella*-type and *Sordaria*-type are linked with the abundance of herbaceous vegetation and both fungal spore types are probably associated with grazing (Almeida-Lenero *et al*., 2005). Most fungal spore types found in the Superpáramo belt were unknown morphotypes, so environmental information could not yet be obtained. However, their record at higher elevations might be useful for future palaeoecological interpretations.

In this study, both altitude and sample type are linked to NPP assemblages. This is manifested in the low correlation of CA axis 1 with sample elevation and the high dispersion of the different sample types along CA axis 2 (Fig. 2.2.7.A). Some interaction exists between these two variables, as they are not totally independent. For example, soil and moss samples predominate below *ca.* 3200 m, whereas lake sediment samples extend from around 3800 m upwards. Bog samples are more or less widespread, but they are more frequent between 3000 and 4000 m. At higher elevations, moss surface samples are more frequent again, while no soil samples were collected. These patterns are determined by the availability of the different habitats at different altitudes, which is mainly due to climatic, geomorphological and vegetation features. In this sense, due to the relationship observed between algal and zoological remains and sample type, it can be suggested that local conditions of sample locations (such as pH, dissolved oxygen, macrophyte presence, etc.) probably influence the NPP distribution. On the other hand, although the human impact at these locations is practically absent, the distribution of lower vegetation belts could be disturbed by human activities, as is the case of *Pinus* plantation named above. Therefore, when using the results of the present study for palaeoenvironmental interpretations, all these factors should be considered.

In spite of this apparently similar influence of altitude and sample type on NPP groups, the NPP assemblages found by cluster analysis show a genuine elevational pattern (Fig. 2.2.6). Assemblages 2A and 2B only include fungal spores, and are clearly related to the Cloud Forest–Subpáramo belt; assemblage 1B characterises the Cloud Forest– Páramo transition; assemblage 3A is widespread along the whole transect but peaks around the Páramo proper–Superpáramo transition; assemblage 3B (*Botryococcus* and *Zygnema*-type) is also characteristic of this transition; and assemblages 1C and 1A are typical of the higher elevations, within the Superpáramo belt. The combination of the fungal spores gradient with a clear altitudinal pattern (Fig. 2.2.5) with the higher abundance of algal and zoological remains — more affected individually by local conditions (Fig. 2.2.7.B) – at upper levels (Figs. 2.2.3 and 2.2.4) – minimises the influence of sample type. Thus, the representation of the NPP assemblages (Fig. 2.2.6.B) is mainly linked to the altitudinal gradient and, therefore, useful to interpret past records in terms of altitudinal (and indirectly, climate) shifts.

2.2.5. Conclusions

Sixty-five different NPP types – classified as algal and zoological remains, and fungal spores – have been identified in an altitudinal transect in the Venezuelan Andes mountains. Among the environmental variables considered, altitude was found to be important for the observed differences in the NPP assemblages, whereas sample type and probably water body characteristics also influence algal and zoological remains distribution. In the case of fungal spores, the relationship with altitude is clearly linked to the altitudinal vegetation patterns, in agreement with the previously studied pollen record. The sample type effect is minimised when the NPP studied are considered altogether, and grouped into 7 assemblages by cluster analysis. In this way, their usefulness as palaeoecological proxies is maximised. This study reinforces the utility of modern analog studies for NPP as a complement of traditional pollen surveys. Besides the altitudinal patterns, which can provide general palaeoenvironmental information, the influence of sample type on NPP assemblages can be useful to derive inferences on *in situ* ecological characteristics. Further studies based on NPP distribution considering local habitat features will surely improve the accuracy of the present results. The study of modern sedimentation of these microremains with palaeoecological purposes is thus encouraged, particularly in poorly known areas, as tropical regions.

2.2.6. Acknowledgements

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APPENDIX A

Name, acronym used for the ordination analyses and brief description of the non-pollen palynomorphs (NPP) types recorded in the present study. Illustrations of non-identified NPP (IBB types) and Tardigrada eggs are attached.

Algal remains

Concentricystis: CONC. Classified by Christopher (1976), also known as Pseudoschizaea (Scott, 1992). They have been related to freshwater marshes (Rossignol, 1962; Milanesi *et al*., 2006).

Zygnema-type (HdV.213 and HdV.314): ZYGN. Classified by van Geel *et al*. (1981, 1989), Bakker and van Smeerdijk (1982) and Kuhry (1997). Heterogeneous group of hyaline, spheroidal and flattened spores from different species. The occurrence suggests stagnant, shallow, mesotrophic to eutrophic, open water.

Bulbochaete: BULB. Classified by van Geel and van der Hammen (1978).

Spirogyra morphotype 2 (HdV.132): SPI2. Classified by Pals *et al*. (1980) and van der Wiel (1983). Reticulate Spirogyra spores.

Tetraedron minimum (HdV.371): TETR. Classified by Bakker and van Smeerdijk (1982). Indicative for eu-to mesotrophic conditions of open freshwater.

Pediastrum: PEDI. See, e.g., Jankovská and Komárek (2000) and Komárek and Jankovska (2001). *Pediastrum* species seem to be indicative of a wide range of environmental responses, such as change in erosion at the catchment, turbidity, water chemistry, nutrient status and pH (Batten, 1996). The range of responses may be due to the fact that in palynological records often different *Pediastrum* species are lumped together (van Geel, 2001).

Botryococcus: BOTR. See, e.g., Jankovská and Komárek (2000). Modern *Botryococcus* occurs in temperate and tropical regions, and is known to tolerate seasonally cold climates. It generally lives in freshwater fens, temporary pools, ponds and lakes, where it may form a thick surface scum, but considerable abundances in variable salinity habitats are also known (Batten and Grenfell, 1996).

Debarya (HdV.214): DEBA. Classified by van Geel *et al*. (1989) and observed in the initial phase of sandy pools (Ellis-Adam and van Geel, 1978), but also in Colombian Andes lake deposits (van Geel and van der Hammen, 1978).

Mougeotia (HdV.133): MOUG. Classified by Pals *et al*. (1980). Van Geel and Grenfell (1996) showed an example of a short successional phase in which *Mougeotia* zygospores played a pioneer role after a local rise of the water table in a Holocene northwest European raised bog.

Spirogyra morphotype 1 (HdV.130): SPI1. Classified by Pals *et al*. (1980), van der Wiel (1983) and van Geel *et al*. (1983). Psilate *Spirogyra* spores. Species of *Spirogyra* are common in stagnant, shallow water.

Zoological remains

Assulina (HdV.32): ASSU. Identified and illustrated by van Geel (1978). The occurrence of this oligotraphentous thecamoeba has been related to a low-nutrient situation and, although they are probably the most common genus in all studies, they appear more abundant in intermediate to relatively dry locations (Charman *et al*., 2000).

Neorhabdocoela (HdV.353): NEOR. Classified by van Geel *et al*. (1981). Its morphology suggests a cocoon of the non-parasitic flatworm order Rhabdocoela (Class Turbellaria). The cocoons usually appear broken.

Acari (HdV.36): ACAR. Classified by van Geel (1976) as various types of animal remains that may be part of mites.

Centropyxis aculeata-type: CENT. Illustrated by Charman *et al*. (2000). Mostly associated with aquatic habitats (De Graaf, 1956) or very wet conditions (Warner, 1987).

Type-X: TYPX. Recorded by Grabandt (1990). It has been found in Colombian Andes sediments and tentatively related to *Hyalosphenia* sp. (Testate Amoebae). Both in Venezuelan (the present study) and Colombian Andes it was found in very low frequencies.

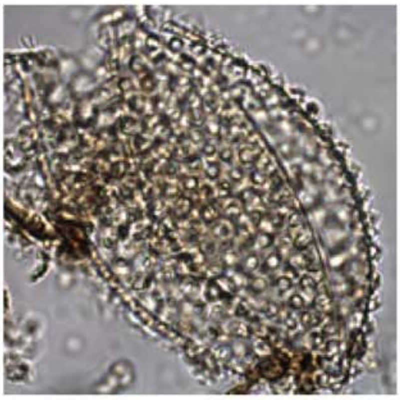
Conochilus natans-type: CONO. Illustrated by van Geel (2001). Resting eggs of rotifers are of regular occurrence in lake deposits.

Centropyxis cassis-type: TRIG. Illustrated by Charman *et al*. (2000). According to De Graaf (1956) this taxon is typical of hygrophilous, submerged and wet mosses.

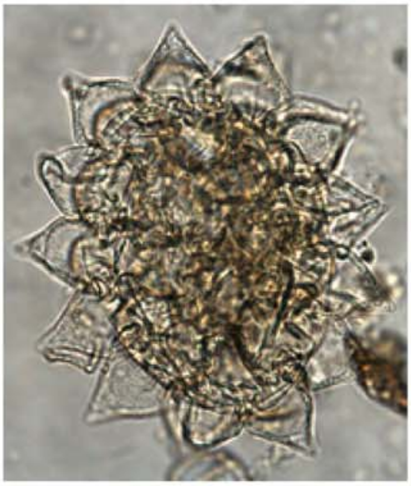
Macrobiotus harmsworti/richtersi (Plate I): MHAR. Classified by Jankovská (1991).

Macrobiotus intermedius (Plate I): MINT. Classified by Jankovská (1991).

Macrobiotus ambiguus-type (Plate I): MAMB. Unidentified microfossil remains which could proceed from Tardigrada egg remains. It has been tentatively related in this study with *Macrobiotus ambiguus* egg remains (Jankovská, 1991).

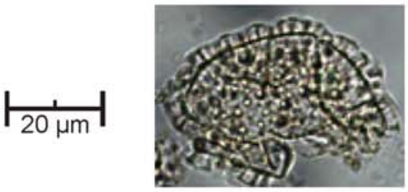


Dactylobiotus-type



Macrobiotus harmsworti/richtersi

Macrobiotus ambiguus-type



Macrobiotus intermedius

IBB-33

IBB-34

Plate I. Illustrations of the different Tardigrada egg morphotypes found. Non-identified types are now described and named with IBB prefix.

Tardigrada IV (IBB-34; Plate I): Ib34. Unidentified microfossil remains which could proceed from Tardigrada egg remains.

Tardigrada II (IBB-33; Plate I): Ib33. Unidentified microfossil remains which could proceed from Tardigrada egg remains. It has been tentatively related in this study with *Macrobiotus* sp. Type 3 egg remains from Jankovská (1990).

Type 221: T221. Classified by van Geel *et al*. (1989). Hyaline microfossils probably of invertebrate origin, that are of regular occurrence in samples from sandy pool deposits.

Dactylobiotus-type (Plate I): DACT. Unidentified microfossil remains which could proceed from Tardigrada egg remains. It has been tentatively related in this study with *Dactylobiotus* sp. egg remains (Kaczmarek *et al*., 2008); also of similar morphology to *Macrobiotus* sp. Type 2 egg remains from Jankovská (1990). *Dactylobiotus luci* was identified by Kaczmarek *et al*. (2008) and related to permanent marsh pools with acid pH from high altitudes of tropical African mountains.

Callidina (HdV.37): CALL. Classified by van Geel (1978), van Geel *et al*. (1981) and Kuhry (1985). This rotifer occurs in pools and peat bogs. *Callidina* is a terrestrial form that sometimes remains dormant for the greater part of the year in a desiccated condition, but becomes active, immediately when moistened by rain water.

Arcella (HdV.352): ARCE. Classified by van Geel *et al*. (1981) and Kuhry (1997). Taxa from the genus *Arcella* often appear at the wetter end of sampled gradients (Charman *et al*., 2000).

Chironomidae: CHIR. Heterogeneous group which represent several types of animal remains (mainly mandibles) that may be part of Chironomidae.

Fungal spores

Most ecological remarks are based on northwest European records.

Gelasinospora (HdV.1): GELA. Classified by van Geel (1978) and Garneau (1993). *Gelasinospora* species are mainly fimicolous, but also carbonicolous and lignicolous. Previous studies of Holocene peats have revealed that maxima in the frequency of *Gelasinospora* sp. occur in highly decomposed peat formed under relatively dry, oligotrophic conditions.

Coniochaeta cf. *ligniaria* (HdV.172): CONI. Classified by van Geel *et al*. (1983). This type is common on dung and wood but is also of regular occurrence in soil surface samples from a Roman Period settlement site with strong evidence for a high population density of domesticated animals (van Geel *et al*., 2003).

Cercophora-type (HdV.112): CERC. Classified by van Geel *et al*. (1981, 1983) and van der Wiel (1983). *Cercophora* species are coprophilous or occur on decaying wood, on clumps and on other herbaceous stems and leaves and can be used as indicators for (extra) animal dung in the surroundings of the sample site (van Geel and Aptroot, 2006). There are different morphotypes within this taxon.

Sordariales: SORD. See Bell (2005). Included several morphotypes within this order but without genus identification.

Type 495 (HdV.495): T495. Classified by van Smeerdijk (1989). Globose fungal spores with evenly distributed spines.

Podospora-type (HdV.368): PODO. Classified by van Geel *et al*. (1981). Van Geel and Aptroot (2006) suggest a relationship between increased occurrence and the presence of man or domesticated animals (providing dung as a substrate).

Type 733 (HdV.733): T733. Classified by Bakker and van Smeerdijk (1982). Globose microfossils which occur in mesotrophic conditions.

Entorrhiza (HdV.527): ENTO. Classified by van Geel *et al*. (1983). *Entorrhiza* species occur as parasites on a variety of plants (Vánky, 1994).

Valsaria cf. *variospora* (HdV.140): VALS. Classified by van Geel *et al*. (1983) and van der Wiel (1983). Ascospores of this type were recorded in peat deposits formed under wet eutrophic conditions.

Glomus (HdV.207): GLOM. Classified by van Geel *et al*. (1989). *Glomus* species with their globose chlamydospores have a vesicular–arbuscular endomycorrhizal relationship with flowering plants and occur on the roots of local vegetation. In lake deposits the occurrence of chlamydospores points so soil erosion in the catchment area (Anderson *et al*., 1984).

Diporotheca (HdV.143): classified by van Geel *et al*. (1986, 1989) and van der Wiel (1983). Spores were regularly recorded in Holocene deposits formed in eutrophic to mesotrophic conditions. Representatives of Diporothecaceae often have specific parasite–host relationships (van Geel and Aptroot, 2006).

Byssothecium circinans (HdV.16): BYSS. Recorded by van Geel (1978) and identified by van Geel and Aptroot (2006). The species is a saprobe or weak parasite on woody substrates.

Sordaria-type (HdV.55): SORT. Classified by van Geel (1976) and van Geel *et al*. (1983). Most *Sordaria* species are coprophilous (van Geel and Aptroot, 2006).

Sporormiella-type (HdV.113): SPOR. Classified by Ahmed and Cain (1972) and van Geel *et al*. (2003). *Sporormiella* species are mainly coprophilous. Separate spore cells of *Sporormiella*-type were distinguished by Davis *et al*. (1977) and by van Geel *et al*. (2003) who concluded that the spores are a reliable proxy for faunal biomass.

Puccinia (HdV.529): PUCC. Classified by van Geel *et al*. (1983). Many of the species in this genus are plant pathogens.

Type 365 (HdV.365): T365. Classified by van Geel *et al*. (1981). Fungal spores with rounded protuberances.

Type 201-type (HdV.201): T201. Classified by van Geel *et al*. (1989) and Kuhry (1997). Type 201 was described as fungal spores (conidia?) 7–10 septate, often broken off at one or both ends. For the present study there are different morphotypes included in Type 201 (HdV.201).

IBB-3 (Plate II): IBB3. Ascospores fusiform, 9.9–13.3 × 6.4–8.6 µm, with an apical pore.

IBB-6 (Plate II): IBB6. Fungal spores ellipsoidal to cylindrical, 10.6 – 14.7 × 5.2 – 6.5 µm, with a soft longitudinal germ slit.

IBB-14 (Plate III). Ib14. Ascospores one-septate 34.3 – 47 × 13.3 – 25.4 µm, constricted at the septum. Usually one cell larger than the other one. An outer, light-coloured wall showing an irregular pattern of longitudinal furrows and ridges up to *ca.* 2.7 µm high.

IBB-15 (Plate III): Ib15. Ascospores lemon-shaped, 37–49 × 23–30 µm, with two different protruding pores, in apical and subapical positions, *ca.* 2 and 4.8 µm in diameter. Wall thickened around the pores.

IBB-16 (Plate II): Ib16. Ascospores one-septate, 37.7 – 52.3 × 14.3 – 22.3 µm, constricted at the septum. Originally the spores may have been 3-septate, with hyaline, thin-walled (not-preserved) end cells.

IBB-17 (Plate II): Ib17. Ascospores fusiform, 20.1 – 24.1 × 9.9 – 12.6 µm, with two apical pores and a reticulate surface. IBB-17 spores are present in many samples along the transect, but always in low frequency.

IBB-18 (Plate II): Ib18. Fungal spores kidney-shaped, 19.3– 23.1 × 9.6–16.8 µm, with apical pores. Present in several samples in very low frequency.

IBB-19 (Plate III): Ib19. Ascospores one-septate fusiform, 66 – 73.3 × 7.9 – 10.6 µm, slightly constricted at the septum. One cell somewhat shorter than the other. Wall showing a regular pattern of longitudinal narrow ridges and furrows.

IBB-20 (Plate II): Ib20. Fungal spores formed by a circular dark cell, *ca.* 11.2 – 15 µm in diameter, with (normally five) hyaline additional cells, up to 8.7 µm in diameter.

IBB-21 (Plate III): Ib21. Globose microfossils of unknown origin, 54.5 – 98.3 µm in diameter; wall showing dark appendages, 2.1 – 3.3 µm in diameter, some of those connected by black lines. IBB-21 type often appears broken and is present only in sample MUM-1. The presence of IBB-21 within the animal assemblage is noteworthy (Fig. 2.2.7.B). Although its morphology did not reveal its nature, the position in the CA analysis could suggest an animal origin.

IBB-22 (Plate II): Ib22. Ascospores one-septate, 26.7 – 31 × 10.9 – 11.9 µm, constricted at the septum. Each cell showing an S-shaped furrow. It has been tentatively related in this study with *Delitschia* genus spores.

IBB-23 (Plate II): Ib23. Spores globose, 13.9 – 20.2 µm in diameter, showing a thicker internal wall and a slightly undulating outer wall.

IBB-24 (Plate II): Ib24. Ascospores one-septate, fusiform, 28.3 – 38.3 × 9.7 – 9.5 µm, constricted at the septum, with a variable number of longitudinal furrows.

IBB-25 (Plate II): Ib25. Ascospores one-septate, 28.2 – 38.9 µm, with many longitudinal light-coloured furrows. Present at low frequencies in several samples. It was found in Colombian Andes sediments and tentatively identified as *Neurospora* sp. (Hooghiemstra, 1984).

IBB-26 (Plate II): Ib26. Ascospores one-septate, slightly fusiform, 31.7 – 32 × 15.4 –15.5 µm, strongly constricted at the septum, probably originally 4-celled. With (8–) 10 longitudinal dark furrows. Present in several samples in very low frequency.

Plate II. Illustrations of some non-identified NPP, now described and named with IBB prefix.

IBB-27 (Plate II): Ib27. Ascospores ellipsoidal, 16.6 – 20.3 × 9.3 – 11.8 µm, with (6–) 8 oblique light furrows. Hooghiemstra (1984) found this morphotype also in Colombian Andes sediments and tentatively identified it as *Spirotremesporites ecuatorialis*.

IBB-28 (Plate III): Ib28. Fungal remains (conidia or chlamydospores?) 3-septate, 51.6 –70.5 × 9.4 – 11.2 µm, each dark cell *ca.* 13.4–24.6 µm long. End cell rounded. Basal cell paler (thinner-walled) and narrow.

BB-29 (Plate II): Ib29. Fungal spores globose, 22 – 29.3 µmin diameter, with a protruding pore 2.3 – 6 µm wide.

IBB-30 (Plate II): Ib30. Fungal spores pyriform, 21.4 – 30.4 × 10.9 – 18.6 µm, truncate at one end.

IBB-31 (Plate II): Ib31. Ascospores fusiform (17.9) 20–29.4 × 6 – 9 µm, one side flattened and bearing a longitudinal or sometimes S-shaped slit. Wall paler around the apices. It has been tentatively related in this study with *Rosellinia* genus spores.

IBB-32 (Plate II): Ib32. Ascospores fusiform, dark brown, 27.4 – 37.2 × 8 – 9.9 µm, one side flattened and bearing a longitudinal slit.

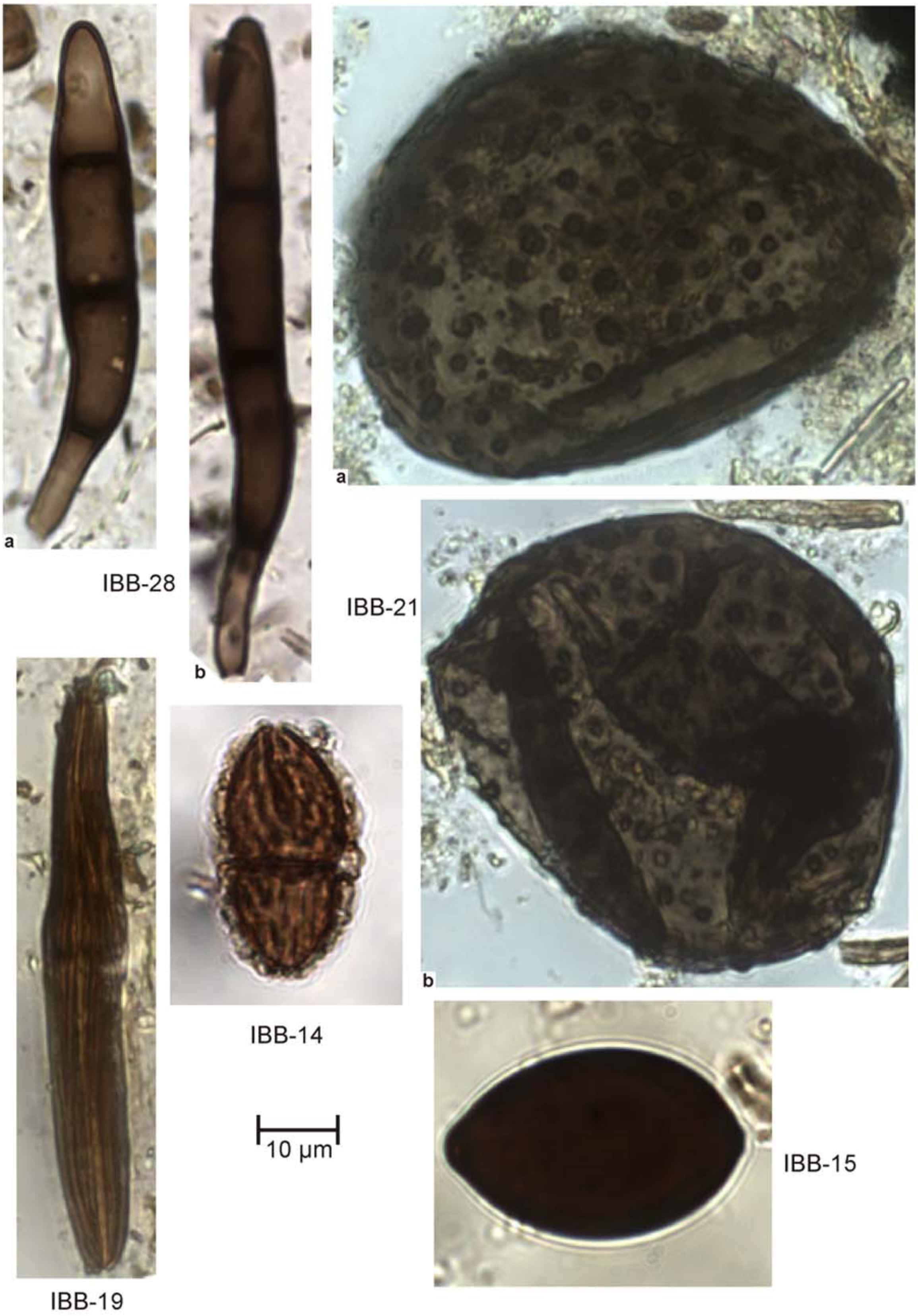


Plate III. Illustrations of some non-identified NPP, now described and named with IBB prefix.

CHAPTER 3:

Vegetation changes in the Neotropical Gran Sabana (Venezuela) around the Younger Dryas Chron.

La mayoría de las historias erróneas son las
que creemos que mejor conocemos y, por tanto,
nunca examinamos o preguntamos.
Stephen Jay Gould.

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ABSTRACT

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

Keywords: Fire; Late Glacial; Neotropics; Vegetation change; Younger Dryas.

3.1. Introduction

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

There is a general lack of sufficient age control between 14 and 10 k cal a BP in most palaeoecological records within the Neotropical region to allow for clear identification of YD events (van't Veer *et al.*, 2000). In Central America, there are two records from Guatemala and Costa Rica which show a clear relationship with the onset of the YD, but the transition to the Holocene remains poorly dated (van't Veer *et al.*, 2000). For example, in a well-dated record from northern Guatemala, Hodell *et al.* (2008) observed a gypsum deposit was formed at 12.8 k cal a BP, indicating the onset of dry conditions. In Costa Rica, a cold reversal termed the La Chonta stadial was recorded, characterized by a downward migration of mountain forest by 300–400 m, which equates to a decrease of 2–3 ºC (Islebe *et al.*, 1995). In South America, most YD evidence has been restricted to the Andes. However, reconstructions at different Andean sites have led to conflicting results (Rodbell *et al.*, 2009). For instance, Thompson *et al.* (1998) documented a cold and wet reversal during the YD from Bolivian ice cores. Others have used glacial deposits to identify the YD as a period of increased aridity in the Peruvian Andes associated with glacial retreat (Rodbell and Seltzer, 2000; Seltzer *et al.*, 2000). North of the equator, one of the more convincing Andean YD equivalents is the El Abra stadial, recorded in Colombia since 11.2 k ^{14}C a BP (13.1 k cal a BP), for which a temperature decrease of 1–3 ºC below present has been estimated (van der Hammen and Hooghiemstra, 1995; van't Veer *et al.*, 2000). In the Venezuelan Andes, the Mucubají Cold Humid phase, between 11.7 and 9.4 k ^{14}C a BP (13.5–10.6 k cal a BP), was characterized by a temperature decrease of 2–3 ºC below present (Salgado-Labouriau, 1989), although dating lacks the required precision. Other studies in nearby locations show decreases in pollen forest around 12.6 k cal a BP, but clear evidence of vegetation and climate change has not been found (Rull *et al.*, 2005, 2008). Mahaney *et al.* (2008) provided evidence of several peat layers and wood fragments within postglacial moraines and sediments dated between 18.8 and 12.4 k cal a BP, some of which might correspond to potential YD glacial advances. Recently, Stansell *et al.* (2010) documented a decrease in average temperatures of 2.2–2.9 ºC between 12.85 and 11.75 k cal a BP, with a downward vegetation displacement of 400–500 m (Rull *et al.*, 2010b). Other evidence has been found in marine cores from the Cariaco Basin (Fig. 3.1), where the YD appears as a cold and dry event, attributed to the combined action of changes in both the Atlantic Ocean circulation and the position of the Intertropical Convergence Zone (ITCZ) (Peterson *et al.*, 2000; Werne *et al.*, 2000; Haug *et al.*, 2001; Lea *et al.*, 2003; Hughen *et al.*, 2004).

Therefore, the bulk of the evidence for the potential occurrence of the YD in the northern South America Neotropics comes from high mountain and marine records, and there is a manifest lack of information at low and mid altitudes (Heine, 2000; van't Veer *et al.*, 2000).

Here we present a palaeoecological study of a lake core from the Gran Sabana (a mid-altitude plateau situated between the Orinoco and the Amazon basins, Fig. 3.1), based on pollen and spore analysis, and supported by charcoal, diatoms, magnetic susceptibility (MS), bulk density (BD) and organic matter analyses. The aim is to reconstruct the Late Glacial vegetation dynamics from 15.3 to 10.6 k cal a BP, as well as to derive potential palaeoclimatic and palaeoecological inferences. The study is focused on the potential changes that occurred around the YD chron, and was prompted by the lack of Late Glacial palaeoecological studies in the region and the unknown responses of its unique ecosystems to potential environmental changes.

3.2. Study Area

The Gran Sabana (GS) is a vast region of about 18,000 km^2 located in south-east Venezuela (4.6089–6.6331 ºN, 61.0679– 74.0478 ºW, Fig. 3.1). It is part of an undulating erosion surface developed on the Precambrian Roraima quartzites and sandstones, and forms an *altiplano* slightly inclined to the south, ranging from about 750 to 1450m elevation (Briceño and Schubert, 1990; Huber, 1995a). The climate has been described as submesothermic ombrophilous, with annual average temperatures of around 18–22 ºC and precipitation of 1600–2000 mm a^1, with a dry season (<60 mm month^1) from December to March (Huber and Febres, 2000). The GS is a huge island of savanna within the normally forested Guayanan landscape. These savannas form wide, and more or less continuous, treeless grasslands or in some places they are intermingled with forests, thus developing the typical forest–savanna mosaics (Huber, 1994). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b) has led to several hypotheses: (i) the savannas are favoured by poor edaphic (hydrology, nutritional status) conditions (Fölster, 1986; Fölster *et al.*, 2001); (ii) they are relicts of larger savanna extensions, originated in colder and drier epochs (e.g. the Last Glacial Maximum, LGM) (Eden, 1974); (iii) the savannas are the consequence of deforestation by frequent and extensive fires (Dezzeo *et al.*, 2004); or (iv) the present savannas derive from former smaller and scattered savanna patches, the extension of which has been favoured by both climate change and fire (Rull, 1999; Huber, 2006).

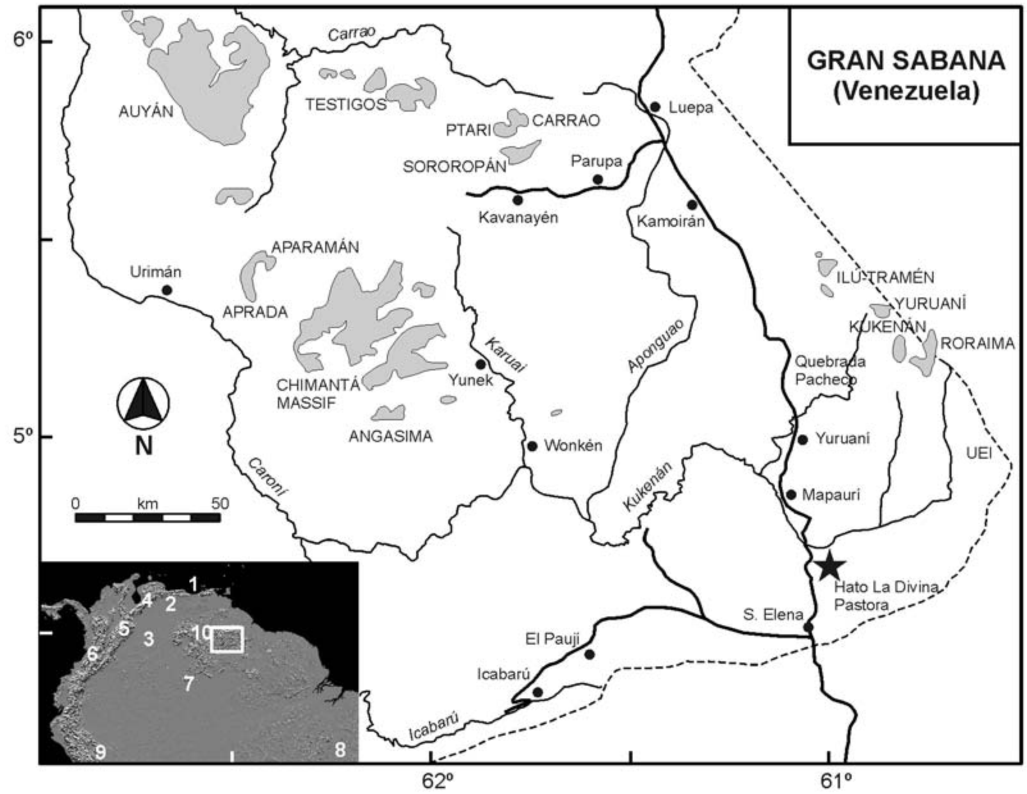

Figure 3.1. Location of the study area and its position within northern South America; radar image courtesy of NASA/JPL-Caltech. The coring site is indicated by a star. Numbers indicate sites with palaeoecological information mentioned in the text: 1, Cariaco Basin (Venezuela); 2, Lake Valencia (Venezuela); 3, Colombian Llanos; 4, Venezuelan Andes; 5, Colombian Andes; 6, Colombian midlands (Cauca Valley); 7, northern Amazon Basin; 8, northern Brazil; 9, Peruvian Andes foothills; 10, Canaima.

The GS savannas are dominated by grasses of the genera *Axonopus* and *Trachypogon* and sedges such as *Bulbostylis* and *Rhyncospora*; woody elements are scarce and rarely emerge above the herb layer (Huber, 1995b). Most GS forests are considered to fall within the category of lower montane forests, because of their intermediate position between lowland and highland forests (Hernández, 1999). Common genera include *Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignoniaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Clathrotropis* (Fabaceae), *Aspidosperma* (Apocynaceae), *Caraipa* (Clusiaceae), *Dimorphandra* (Caesalpiniaceae) and *Byrsonima* (Malpighiaceae), and their composition varies with elevation (Huber, 1995b). The GS shrublands usually occur between 800 and 1500 m elevation and are more frequent at the northern area than at the southern part (Huber, 1995b), where our study site is located. Given the significance of these vegetation types in the present palaeoecological reconstruction, a more detailed description is pertinent. The GS shrublands have been classified into four main types, because of the strong dependence on the substrate type (Huber, 1994, 1995b):

1. Shrublands on rocky soils. Growing on low to moderately inclined sandstone outcrops. The shrub layer is very dense, and is distributed following a density gradient along the rock slope. The herb layer is irregularly and fragmentarily distributed. Dominant taxa are: *Clusia* (Clusiaceae), *Humiria* and *Sacoglottis* (Humiriaceae), *Euceraea* (Flacourtiaceae), *Euphronia* (Euphroniaceae), *Macairea* (Melastomataceae), *Pagamea* (Rubiaceae), and *Notopora* and *Thibaudia* (Ericaceae) (see Appendix B, Table B1).

2. Shrublands on sandy soils. On isolated patches of white sand. The shrub layer is scattered, forming islands in a matrix of bare soil. The herb layer is less developed as in shrublands on rocky soils. Dominant taxa include: *Pera* (Euphorbiaceae), *Emmotum* (Icacinaceae), *Matayba* (Sapindaceae), *Simarouba* (Simaroubaceae), *Gongylolepis* (Asteraceae), *Ternstroemia* (Theaceae) and *Befaria* (Ericaceae) (see Appendix B, Table B2).
3. Shrublands on ferruginous soils. Located upon ferruginous duricrust (millimetric or centimetric, hard and iron-rich layer on top of the soil). A peculiar and isolated shrubland type only found north of GS, north-east of the Yuruaní catchment (Fig. 3.1: Quebrada Pacheco). Both diversity and taxa abundance show great differences with former shrubland types. This formation is organized into three different strata: herbaceous, shrubby and emergent layers. Dominant taxa are: *Bonnetia* (Theaceae), *Phyllantus* (Euphorbiaceae), *Cyrillopsis* (Ixonanthaceae), *Roupala* (Proteaceae) and *Bonyunia* (Loganiaceae) (see Appendix B, Table B3).
4. Shrublands on peaty soils. Located also north of GS, between 1000 and 1300 m elevation, showing more similarities with shrublands from the Guayana Highlands (1500–3000 m elevation) than with other GS shrublands. Dominant taxa are: *Bonnetia* (Theaceae), *Chalepophyllum* and *Pagameopsis* (Rubiaceae), *Digomphia* (Bignoniaceae) and *Meriania* (Melastomataceae) (see Appendix B, Table B4).

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

3.3. Material and Methods

The study site (4.6501 ºN, 61.0157 ºW, 884 m elevation) is located within a private farm called '*Hato Divina Pastora*' near Santa Elena de Uairén, south of the GS region (Fig. 3.1). The annual precipitation in Santa Elena, at 910 m altitude, is about 1700 mm, with a weak dry season from December to March (Huber, 1995a). The study lake lies within a treeless savanna landscape, surrounded by scattered palms of *Mauritia flexuosa* forming small stands locally known as '*morichales*'. In the absence of a local name for the lake, it is here termed Lake Chonita. The core studied (PATAM1 B07; 4.67 m long) was obtained in the deepest part of the lake (3.13 m water depth), using a modified Livingstone squared-rod piston core (Wright *et al*., 1984). The present study is focused on the detailed analysis and palaeoecological interpretation of the Late Glacial to early Holocene interval, ranging from 2.97 to 4.67 m. Nine samples were taken along the whole core for radiocarbon dating, four of them falling within the interval discussed here. Samples were pretreated using standard acid-base-acid procedures (Abbott and Stafford, 1996) and measured at the AMS Radiocarbon Laboratory of the University of California (UCI) and at Beta Analytic (Beta). Calibration was made with CALIB 6.0.1 and the IntCal09.14c database (http://calib. qub.ac.uk./calib/, last accessed June 2010).

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

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

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

3.4. Results and Interpretation

3.4.1. Chronology

The results of accelerator mass spectrometry (AMS) radiocarbon dating (Table 3.1) were used to produce an age-depth model for the whole sequence. The best fit was obtained with a smooth-spline model (Blaauw, 2010), and is represented in Fig. 3.2 for the interval of interest. According to this model, sedimentation rates ranged from 0.03 to 0.16 cm a^{1}, and the mean resolution of our analyses was between 31 and 165 years per sampling interval.

Table 3.1. AMS radiocarbon dates used for the age–depth model for the whole record.

Laboratory	Sample no.	Depth (cm)	Sample type	Age (C14 a BP)	Age (cal a BP), 2s	Age (cal a BP) estimation†
Beta-279600	3	13	Pollen extract	890 ± 40	731–915	803
Beta-277185	11	51	Pollen extract	2850 ± 40	2855–3078	2732
Beta-277184	22	98	Pollen extract	3340 ± 40	3471–3643	3658
UCI-43705	32	144	Wood	4080 ± 40	4497–4655	4642
UCI-43706	49	212	Wood	6465 ± 25	7323–7403	7383
Beta-277186*	70	298	Pollen extract	9590 ± 60	10,738–11,164	10,685
UCI-43537*	87	362	Wood	9720 ± 70	11,063–11,251	11,384
Beta-247284*	93	392	Wood	10,440 ± 40	12,128–12,530	12,342
UCI-43614*	99	402	Wood	11,005± 45	12,699–13,078	12,736

*Dates included in the interval under study. †Weighed average.

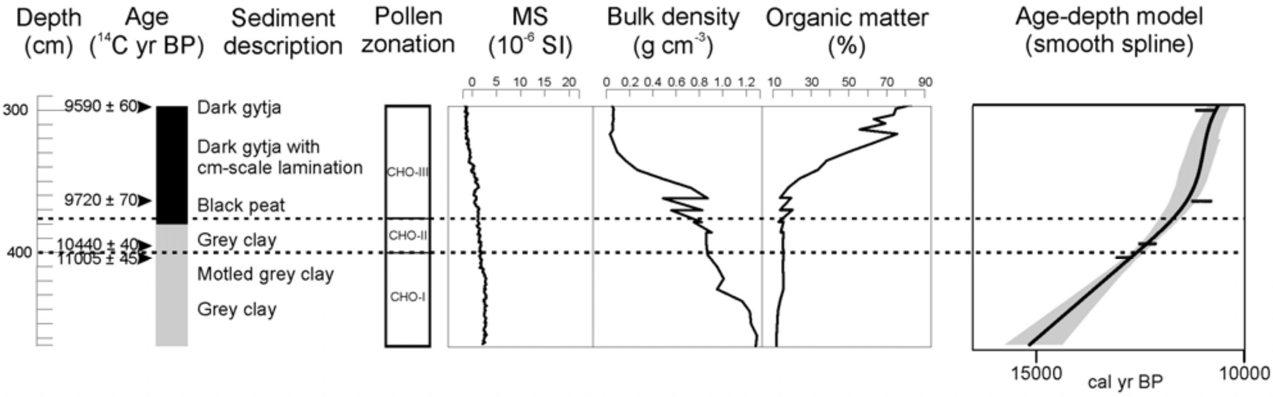

Figure 3.2. Core stratigraphy, with radiocarbon ages and sediment description; pollen zonation; physical parameter curves; and age–depth model of the interval analysed. MS, magnetic susceptibility.

3.4.2. Zonation

The pollen diagram is dominated alternatively by pollen assemblages from two different plant formations: a ligneous community of shrubs, lianas and small trees; and a savanna grassland (Fig. 3.3). The more abundant pteridophyte spores were *Lycopodium cernuun* and psilate triletes, with two prominent peaks around the middle of the diagram (Fig. 3.4). The stratigraphic variations of the pollen and spore assemblages allowed its subdivision into three zones, which are described below for the different proxies analysed.

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

This was characterized by grey clay and mottled grey clay with desiccation features. MS values were the highest of the whole section under study, with a slight decrease in the upper part. The dry BD values were high (0.8-1.3 g cm^3) and the concentration of organic matter was low (<20%) throughout this zone (Fig. 3.2). This section was generally barren for palynomorphs and diatoms, except for several isolated samples with scattered and mostly degraded specimens. At the end of the zone, there was a sudden increase in *Lycopodium cernuun* (Fig. 3.4).

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

3.4.2.2. CHO-II (4.00–3.75 m, 12.7–11.7 k cal a BP, 5 samples)

This intermediate zone is characterized by a shift from grey clay to black peat sediments at the top, a decreasing trend of MS and dry BD values, and increasing amounts of organic matter (Fig. 3.2). The continuous presence of palynomorphs begins in this zone, around 12.7 k cal a BP, and is marked by a sudden increase of *L. cernuum* followed by high percentages of pollen from ligneous taxa such as *Bonyunia*, *Protium*, *Weinmannia*, *Cyrilla*, *Miconia*, *Myrsine*, *Odontadenia*-type and Marcgraviaceae. Poaceae is also present at low concentrations, but increases at the top. Non-identified types show a sudden increase at the beginning of the zone, and are present at low concentrations at the upper part (Fig. 3.3). *L. cernuun* peaks at the base and suddenly decreases until it almost disappears. There is a low frequency of algae and Cyperaceae, while diatom valves are almost absent, except for a single sample at the top showing traces of diatoms (Fig. 3.4). Smaller microcharcoal particles (5–100 mm) are present throughout this section at low concentration, but dramatically increase at the top, together with a slight increase of larger particles (>100 mm) (Fig. 3). Simultaneously, there is a noticeable increase in psilate triletes (Fig. 4) and a change to dark lacustrine sediments (Fig. 3.2). Pollen and spore influx are high in this interval.

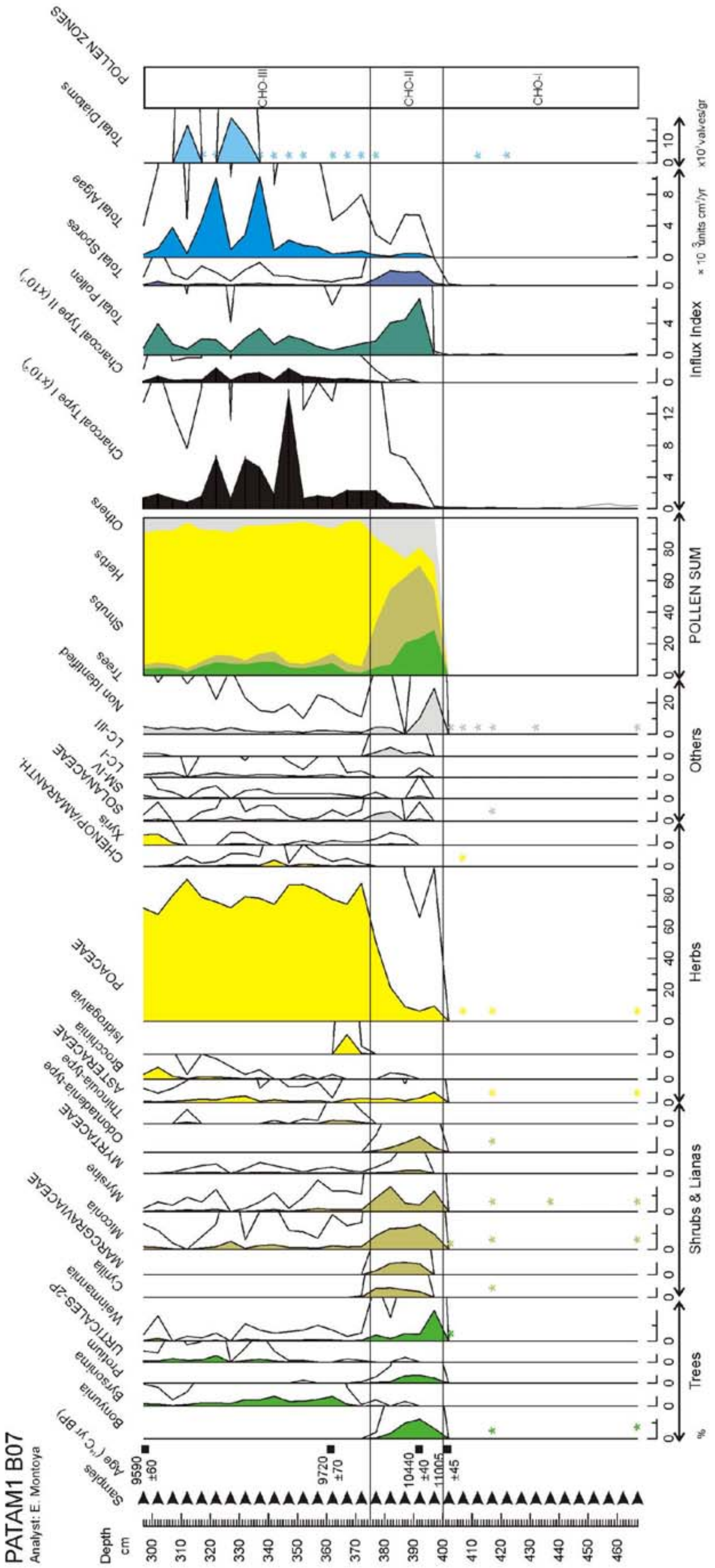

Figure 3.3. General pollen diagram with abundance expressed as percentages. Solid lines represent x 10 exaggeration. *: Low traces or very low (scattered) presence.

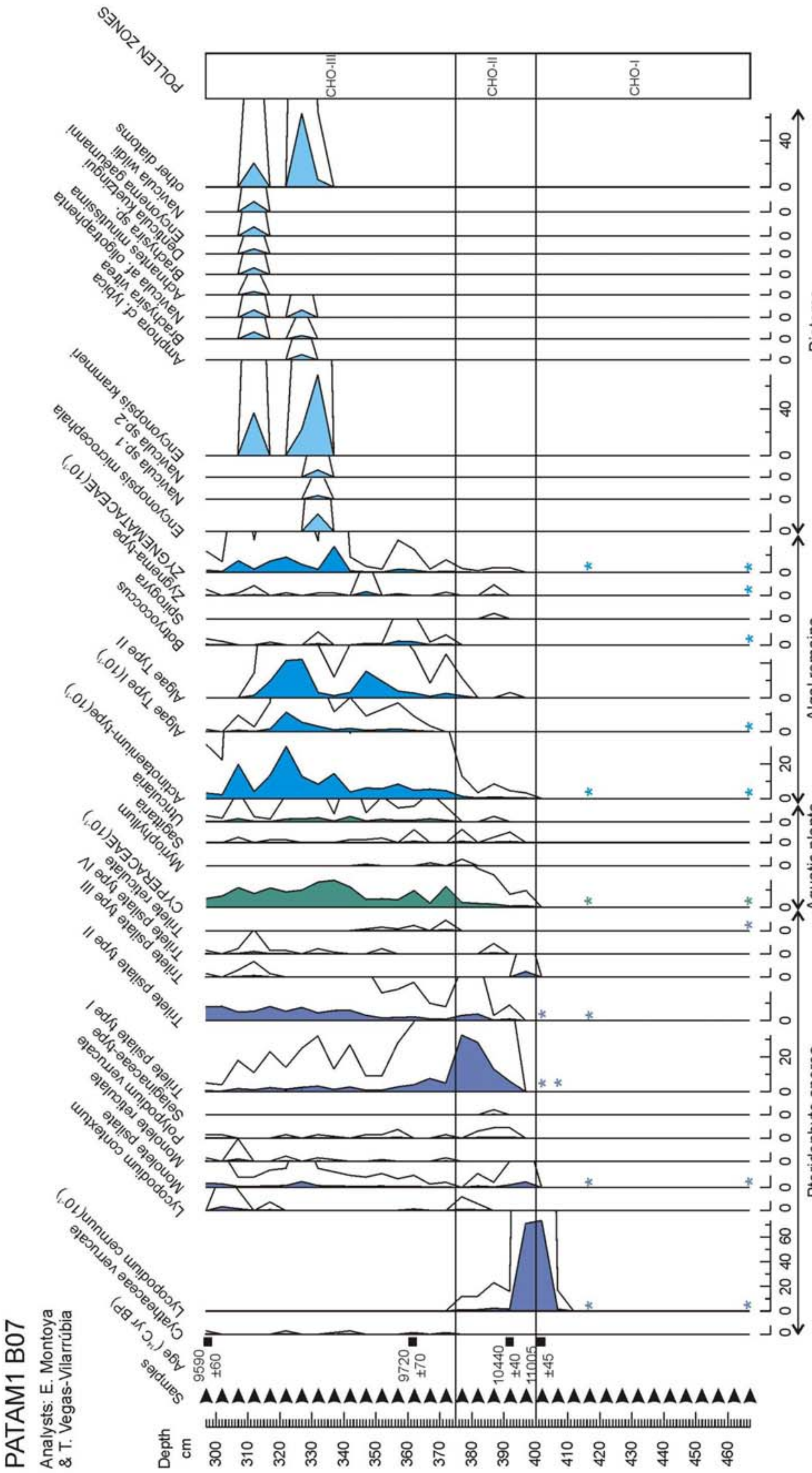

Figure 3.4. Diagram showing the elements outside the pollen sum (pteridophyte spores and aquatic elements). Percentages of pteridophyte spores, aquatic plants and algal remains are based on pollen sum. Percentages of diatoms are based on diatom sum. *: Low traces or very low (scattered) presence.

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

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

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

The sediments of this interval are marked by the transition from black peat to dark organic-rich sediments with centimetre-scale lamination in the lower part; this interval has the lowest MS and BD values of the whole section. It also shows a strong increase in organic matter values, with the highest concentrations of the interval under study (Fig. 3.2). The zone represents a marked change in palynomorph assemblages. At the beginning, there is a sudden drop in all the dominant taxa from the previous zone, and a dramatic increase of Poaceae. Among ligneous elements, *Byrsonima* and, to a lesser extent, Urticales, *Miconia* and Asteraceae become more abundant. At the top of the section, an increase in other herbaceous elements, such as *Brocchinia* and *Xyris*, is recorded (Fig. 3.3). *L. cernuum* is absent and the psilate triletes of the former zone strongly decreases, while another type of psilate triletes slightly increase. Pollen from aquatics plants (Cyperaceae) increases at the beginning and remains at similar percentages through the whole zone. Diatoms and other algae show a similar trend, with a significant increase at the middle to upper part and a decrease at the top (Fig. 3.4). Proportions of both smaller and larger charcoal particles remain at the values attained at the end of the former zone (Fig. 3.3).

At the beginning of this zone, around 11.7 k cal a BP, a dramatic and complete replacement of the former ligneous community by a treeless savanna dominated by grasses is inferred. Diatom assemblages appear for the first time in the record, although valves are found in low quantities (Fig. 3.3). The most frequent diatom species are *Encynopsis krammeri* and *E. microcephala*, but species diversity is high and many species appear with abundances <3% (Fig. 3.4). The species found are commonly reported in peaty environments and suggest the existence of dystrophic and oligotrophic waters with a poor electrolyte content. Other algae (mostly *Actinotaenium*-type) appear regularly and markedly increase from 10.95 to 10.8 k cal a BP coinciding with laminations, and indicating higher water levels and probably an increase in the available moisture. The following decrease of algae remains and the disappearance of diatoms suggest that a shallower water body formed at this time.

The increase of *Brocchinia* and *Xyris* and the characteristics of the sediment (disappearance of laminations and a significant increase of peat) at the top support the existence of more peaty conditions in the site.

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

3.4.3. Correspondence analysis

To compare the ligneous community represented in zone CHO-II (hereafter CHO-II shrubland) with potentially similar present-day communities of the GS, CA was performed using presence/absence data (see Table 3.2 for CHO-II, and Appendix B Tables B1–B4 for data on present-day GS shrublands). A scatter plot using the first two CA axes, which account for 60% of the total variance, is shown in Fig. 3.5. The CHO-II shrubland shows no floristic relationship with the peat shrublands, but it does with the other three. It is most similar to the shrublands on ferruginous soils, situated to the north of the GS. However, this similarity is only partial, and a significant amount of the CHO-II taxa are not present in any of the GS shrublands studied to date.

Table 3.2. Main genera of GS shrublands and pollen assemblages found in CHO-II.

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

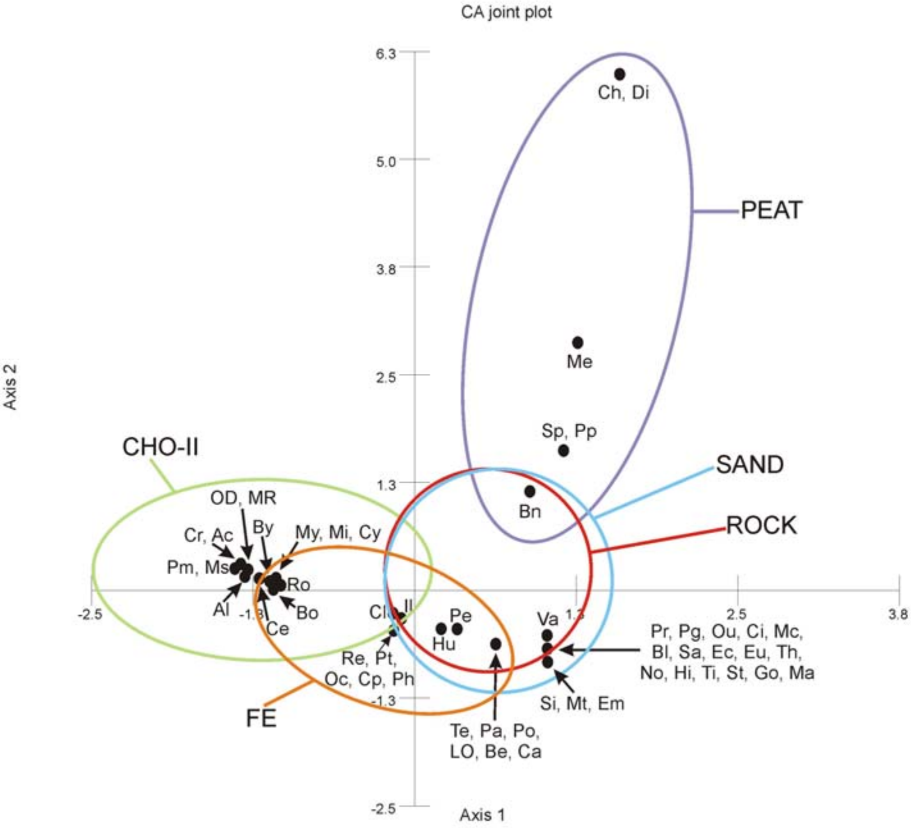

Figure 3.5. Biplot using the first two axes of correspondence analysis, with the genera of the four types of GS shrublands and the pollen assemblage found in Zone CHO-II. PEAT, shrublands on peaty soils; SAND, shrublands on sandy soils; ROCK, shrublands on rocky soils; FE, shrublands on ferruginous soils. See Table 3.2 for genera acronyms.

3.5. Discussion

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

3.5.1. Palaeoecological sequence

3.5.1.1. 15.3–12.7 k cal a BP

This interval coincides with the end of the Oldest Dryas (OD; 18.0–14.6 k cal a BP) and the B/A interstadial (14.6 - 12.85 k cal a BP) of the Northern Hemisphere (Rasmussen *et al*., 2006). The absence of biological proxies was interpreted in terms of dry climates probably unable to support a dense and continuous plant cover or sufficient water to preserve its remains (Fig. 3.6). The lack of sediments of the same age in the Venezuelan–Guayana region prevents the extension of this vegetation cover to a regional level (Rull *et al*., 2010a). The inferred aridity of this period may reflect high temperatures. This inference is supported by different palaeoecological and palaeoclimatical studies developed in other Neotropical regions. For instance, in the Cariaco Basin, a period that was warmer than the LGM and the YD has been proposed, with an average temperature similar or slightly higher than today, probably linked to a northward displacement of the ITCZ (Lea *et al*., 2003; Mertens *et al*., 2009). The Venezuelan Andes (Fig. 3.1) were characterized by warmer climates with sparse vegetation between 13.9 and 12.7 k cal a BP (Rull *et al*., 2005; Stansell *et al*., 2005), coinciding with the Mucubají Warm phase, as documented by Salgado-Laboriau (1989). In the Colombian Andes (Fig. 3.1), van der Hammen and Hooghiemstra (1995) documented the Guantiva interstadial (between 15.1 and 12.8 k cal a BP), with higher average temperatures than the LGM, as equivalent to the European Allerød. In the Colombian midlands (Fig. 3.1), no palaeoecological information could be obtained possibly because of poor preservation until 13.3 k cal a BP, when dry forests expanded (Berrío *et al*., 2002). In the Amazon Basin (Fig. 3.1), Bush *et al*. (2004) documented the occurrence of mesic forests during the last glaciation, and an increase in lianas and dry forest elements during the Late Glacial (22–12 k cal a BP). In northern Brazil (Fig. 3.1), a *Podocarpus* peak was recorded between 15.0 and 14.5 k cal a BP, suggesting cool and moist climatic conditions (Ledru *et al*., 2001). A probably wet and warm climate has been inferred in a few records containing this interval from Central America (Islebe *et al*., 1995; Hodell *et al*., 2008). Therefore, it seems that during the B/A interstadial, climates in the northern South American tropics were probably warmer than during the LGM, but cooler than today and possibly dry.

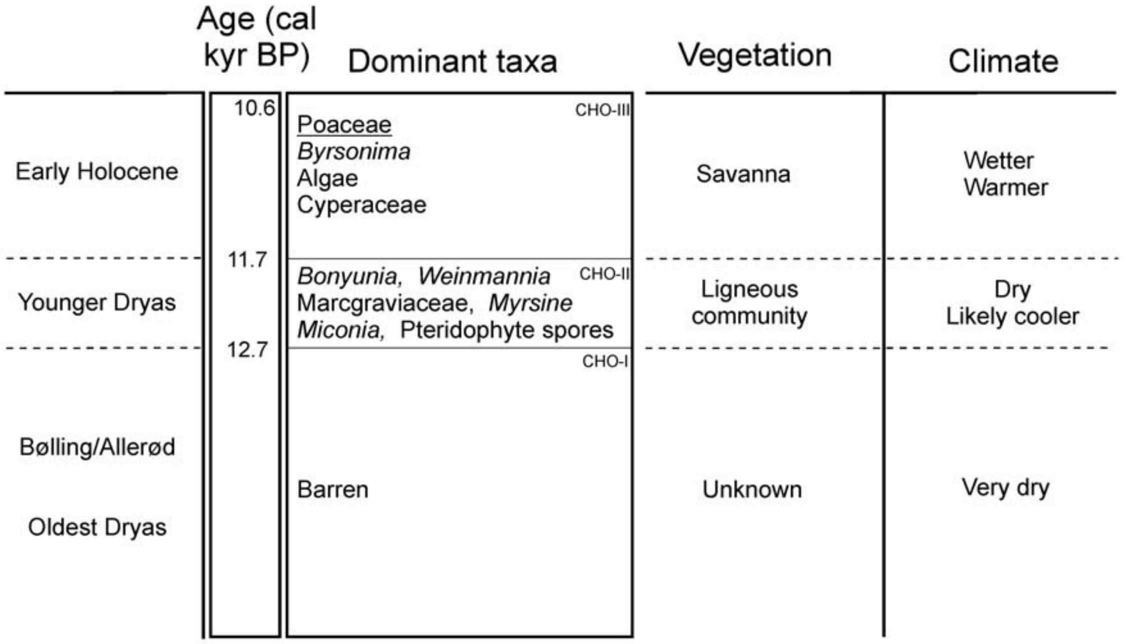

Figure 3.6. Summary of the palaeoecological interpretation.

3.5.1.2. 12.7–11.7 k cal a BP

This phase corresponds to the YD chron of the Northern Hemisphere, dated at 12.85–11.65 k cal a BP (Rasmussen *et al.*, 2006). During this time, the region around Lake Chonita was covered by the CHO-II shrubland mentioned above, and the climate was interpreted as slightly wetter than during the previous interval, but still dry, as the present lake was seasonally desiccated (Fig. 3.6). The basin was occupied by a shrubland with no modern analogues. The most similar extant community known is a shrubland, located at 1000– 1150 m elevation, close to the Quebrada Pacheco (1078 m elevation, Fig. 3.1). As the lake is at 884 m elevation, it could be hypothesized that a northward altitudinal displacement of 115– 265 m with respect to the present occurred during this phase. Using a present-day altitudinal lapse rate of 0.6 ºC/100 m (Huber, 1995a), average temperatures were estimated to be 0.7–1.5 ºC lower than present during this period. Such an inferred decrease in average temperatures during this interval is supported by similar studies in regions closer to the lake. The Cariaco Basin record also showed a decrease in precipitation and sea surface temperatures, which were around 3 - 4 ºC lower than today, between 12.6 and 11.5 k cal a BP (Haug *et al.*, 2001; Hughen *et al.*, 1996; Lea *et al.*, 2003), with lower temperatures during the early YD (until 12.3 k cal a BP). From this, the authors inferred a southward displacement of the ITCZ during the YD chron. In the Venezuelan Andes, a significant altitudinal decline in vegetation was recorded between 12.9 and 11.75 k cal a BP, suggesting a decrease in average temperatures of around 2 - 3 ºC that probably started to increase again after 12.3 k cal a BP, and a more arid climate (Rull *et al.*, 2010b; Stansell *et al.*, 2010). In the Colombian Andes, a sudden drop in average temperatures to about 1 - 3 ºC lower than today, known as El Abra Stadial, was documented between 11 and 10 k ^{14}C a BP (12.8–11.5 k cal a BP) (van't Veer *et al.*, 2000).

At lower elevations, as in the Lake Valencia catchment (Fig. 3.1), the inferred occurrence of intermittent and shallow ponds suggested drier climates between 12.6 and 10 k ^{14}C a BP (14.8–11.5 k cal a BP) (Bradbury *et al.*, 1981; Leyden, 1985; Curtis *et al.*, 1999). In the Colombian midlands, the replacement of dry forests by open grass-dominated vegetation occurred around 10.5 k ^{14}C a BP (12.6k cal a BP) onwards (Berrío *et al.*, 2002). In Amazonia, a wet phase is recorded at southern latitudes (10 ºS) around 12.1 - 11.7 k cal a BP, not wet enough to promote speleothem growth, but sufficient to produce travertine deposits, which the authors also linked to a possible southward displacement of the ITCZ (Wang *et al.*, 2004). In Central America, a likely cold interval with average temperatures 2 - 3 ºC lower than today was suggested between around 11.1 and 10.4 k ^{14}C a BP (13.0 - 12.3 k cal a BP) in Costa Rica (Islebe *et al.*, 1995). In Guatemala, a dry phase was suggested to have been occurred between 12.8 and 10.4 k cal a BP (Hodell *et al.*, 2008).

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

3.5.1.3. 11.7–10.6 k cal a BP

The end of the YD chron and the beginning of the Holocene has frequently been characterized in many northern Neotropical and Atlantic Ocean-influenced records by an increase in temperature and wetter conditions (e.g. Stansell *et al.*, 2005). This phase is known as the EHW in the Northern Hemisphere (Kaufman *et al.*, 2004; Kaplan and Wolfe, 2006). In Lake Chonita, the appearance of diatoms and algae assemblages clearly indicates a shift to a more humid environment.

An evident replacement of the shrubland by a treeless savanna took place at 11.7 k cal a BP in the lake basin, coinciding with an increase of regional fire incidence and the appearance of the first local fires. Therefore, the likely northward migration of the shrublands on ferruginous soils and the rise in water levels was interpreted in terms of a warmer and wetter climate (Fig. 3.6). This inferred warmer climate agrees with different palaeoecological and palaeoclimatic studies from regions to the lake. In the nearby Mapaurí region (Fig. 3.1), a similar increase of regional fires was recorded at the beginning of the Holocene, with an increase in average temperature of about 2 - 3 ºC, as suggested by a forest migration to higher altitudes and its replacement by expanding savannas (Rull, 2007, 2009a). In the Cariaco Basin, an increase of precipitation was observed at *ca.* 11.5 - 10.5 k cal a BP (Haug *et al*., 2001; Lea *et al*., 2003). In the Venezuelan Andes, an increase in temperature and humidity was recorded during this phase (Rull *et al*., 2005; Stansell *et al*., 2010), whereas in the Colombian Andes, average temperatures also increased after the El Abra stadial (van der Hammen and Hooghiemstra, 1995). In the Colombian Llanos (Fig. 3.1), Behling and Hooghiemstra (1998) documented a maximum in the savanna expansion during the early Holocene, whereas also in Colombia, Berrío *et al*. (2002) proposed an increase in aridity starting around 9.9 k cal a BP. Lake levels increased in Lake Valencia between 10 and 8.2 k ^{14}C a BP (11.5 - 9.2 k cal a BP) (Curtis *et al*., 1999). In the Amazon Basin, the continuity of tropical rain forests was reported for the Pleistocene/Holocene boundary and onwards, but with changes in composition with respect to the Pleistocene forests (Bush *et al*., 2004). In Central America, Hodell *et al*. (2008) proposed the occurrence of moist conditions around 10.3 k cal a BP, probably caused by a northward displacement of the ITCZ. Hence, the widespread occurrence of the EHW in the northern Neotropical region seems well supported by the existing evidence.

3.5.2. On the origin of the Gran Sabana

As previously mentioned, the savannas of the GS are considered anomalous, given the warm and wet climate, apparently more suitable for rain forests. This has led to the development of different hypotheses regarding the age and origin of these herbaceous ecosystems (Eden, 1974; Fölster, 1986; Rull, 1999; Fölster *et al*., 2001; Dezzeo *et al*., 2004; Huber, 2006). Among these proposals, those based on climatic (dryness, seasonality) and anthropogenic (frequent and extensive fires) factors are the more accepted. Until recently, the data supporting these hypotheses were from present-day biogeographical and ecological studies, with palaeoecological data beginning to contribute to the discussion about two decades ago (Rull, 1992). So far, the oldest record available for the origin of the GS was from the Mapaurí peat bog, some 35 km north of Lake Chonita. In Mapaurí, the replacement of a *Catostemma*--dominated cloud forest by treeless savanna was recorded around 10.2 k cal a BP, slightly preceding the onset of local and regional fires and supporting a climatic origin for the savannas (Rull, 2007). The causes of fires remain unknown, but the possibility of early human occupation of the GS has been suggested (Rull, 2009a).

The Chonita record is around 5000 years older, but the treeless savanna was not documented until 11.7 k cal a BP, around 1500 years earlier than in Mapaurí. In this case, regional fires were already occurring, even at low intensity/frequency, whereas local fires began more or less at the same time as the shrubland/savanna replacement occurred. Therefore, fire seems to have been influential in the observed vegetation change, which is supported by the abrupt shrubland decline just after regional fire initiation, and the subsequent peak of fern spores commonly associated with secondary colonization of burnt areas in the GS (Rull, 1999). Moisture indicators (diatoms and other algae) did not show any significant change linked to the vegetation shift, suggesting that water balance was less influential.

If the previously suggested EHW was real, it could have had some influence but, at this stage, empirical support is not sufficient for a definitive assessment. Despite a significant increase in water balance, the same savanna vegetation remained until 10.6 k cal a BP, probably caused by local and regional fires. This is supported by the continued medium to high abundance of charcoal and the increase in *Byrsonima*, a common fire-resistant small tree in Neotropical savannas (Marchant *et al.*, 2002). Therefore, in contrast to the Mapaurí record, fire appears to have been a determinant in the origin and expansion of savanna vegetation in the Lake Chonita area. The more likely scenario for the Pleistocene/Holocene boundary and the early Holocene in the present GS region could be a complex vegetation composed of forests, shrublands and patches of savannas progressively changing to a treeless savanna under the influence of climate (warming) and fire (Rull, 2009b). Moisture seems to have played a minor role, if any.

An increase in fire incidence immediately after the YD, after around 11.7 k cal a BP, has been reported in several Neotropical regions and elsewhere (e.g. Haberle and Ledru, 2001; Ledru *et al.*, 2002; Daniau *et al.*, 2007). Marlon *et al.* (2009) documented a general increase in fire incidence in North America at the boundaries of the YD, being greater around the end of the YD (11.7 k cal a BP), both in the amount of burnt localities and in fire magnitude. Owing to the synchrony of fire occurrence along widespread regions, this has been related to abrupt climate change (Alley, 2000; van der Hammen and van Geel, 2008; Marlon *et al.*, 2009). The Lake Chonita record has documented a similar, well-dated increase in fire frequency at the end of the YD. The sudden fire increase around Lake Chonita might be caused by climate, but human presence cannot be dismissed, even in the absence of land-use changes (Bush *et al.*, 2007), as was tentatively proposed in the nearby Mapaurí area (Rull, 2009a). The onset of regional fire incidence around Lake Chonita has been dated to 12.4 k cal a BP, the oldest fire evidence in the GS so far (Fig. 3.3). The two discussed GS sequences (Chonita and Mapaurí) have clearly shown the presence of fire in the region since at least the late Pleistocene, in agreement with the situation in Central and northern South America, where both rapid climatic changes or early human activity have been suggested for the increase in fire incidence along the YD interval and onwards (Bush *et al.*, 1992; Haberle and Ledru, 2001). This potential early human occupation of the GS is supported by archaeological studies in areas closer to the lake (Fig. 3.1), where preceramic human evidence, such as spearheads and bifacial worked knives, has been found around the Late Pleistocene/Early Holocene boundary (Gassón, 2002).

3.6. Conclusions

The Neotropical, mid-altitude Lake Chonita sequence analysed here has been subdivided into three palaeoecological/palaeoclimatic intervals (CHO-I, CHO-II and CHO-III), which are coeval with the Northern Hemisphere OD-B/A, YD and EHW, respectively. During the OD-B/A, very dry conditions have been inferred, in good agreement with other widespread northern Neotropical records. A dry and probably cold phase was documented between 12.7 and 11.7 k cal a BP, coinciding with the Northern Hemisphere YD cold reversal. During this period, a shrubland with no modern analogues was the dominant vegetation in the catchment area. This shrubland is absent today and it has been proposed, as a working hypothesis, that it could have migrated northwards at slightly higher altitudes where a similar, but different, shrubland occurs today. Such displacement would imply an increase in averaged temperatures of 0.7–1.5 ºC. At the end of the YD, the shrubland was replaced by a treeless savanna similar to that at present. This coincides with the onset of local fires, suggesting that they could have influenced the vegetation change. Therefore, both climate and fire seem to have induced the shrubland/savanna turnover.

The following phase (after 11.7 k cal a BP) coincides with the quasi-global EHW and is characterized, in Lake Chonita, by the establishment of treeless savannas and a significant increase in water levels, suggesting wetter and warmer conditions than during the YD. The continuity of savannas despite the increase in humidity suggests that fire prevented shrubland recovery, thus favouring savanna expansion. The manifest fire increase after 11.7 k cal a BP could have been related to climatic change or early Holocene human occupation of the region, or both. This supports the hypothesis of a mixed origin of the GS savannas, due to both climate and fire, and the important role of fire in their further persistence. This record is unique for northern South America midlands and lowlands. The analysis of other sequences of similar age is in progress to verify the local or regional extent of the documented trends.

3.7. Acknowledgements

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APPENDIX B

Main genera of the current shrublands of GS.

Table B1. Dominant taxa in rocky soils shrublands (Huber, 1994; 1995b).

Layer	Family	Genus
Shrubs	Asteraceae	*Gongylolepis* sp.
	Clusiaceae	*Clusia* spp.
	Ericaceae	*Bejaria* sp.
		Notopora sp.
		Thibaudia sp.
	Euphroniaceae	*Euphronia* sp.
	Humiriaceae	*Humiria* sp.
		Vantanea sp.
	Melastomataceae	*Macairea* sp.
	Theaceae	*Bonnetia* sp.
		Ternstroemia sp.
Herbaceous	Cyperaceae	*Lagenocarpus* sp.
	Poaceae	*Axonopus* sp.
		Echinolaena sp.
		Paspalum sp.
		Trachypogon sp.
	Rapateaceae	*Stegolepis* sp.
	Velloziaceae	*Vellozia* sp.
Emergents	No present	

Table B2. Dominant taxa in sandy soils shrublands (Huber, 1994; 1995b).

Layer	Family	Genus
Shrubs	Asteraceae	*Gongylolepis* sp.
	Clusiaceae	*Clusia* spp.
	Ericaceae	*Bejaria* sp.
	Euphorbiaceae	*Pera* sp.
	Euphroniaceae	*Euphronia* sp.
	Humiriaceae	*Humiria* sp.
	Icacinaceae	*Emmotum* sp.
	Sapindaceae	*Matayba* sp.
	Simaroubaceae	*Simauroba* sp.
	Theaceae	*Ternstroemia* sp.
Herbaceous	Asclepiadaceae	*Cynanchum* sp.
	Asteraceae	*Ichthyopthere* sp.
	Caesalpiniaceae	*Chamaecrista* sp.
	Eriocaulaceae	*Paepalanthus* sp.
	Poaceae	*Axonopus* sp.
		Trachypogon sp.
Emergents	Ericaceae	*Befaria* sp.
	Simaroubaceae	*Simauroba* sp.

Table B3. Dominant taxa in ferruginous soils shrublands (Huber, 1994; 1995b).

Layer	Family	Genus
Shrubs	Aquifoliaceae	*Ilex* sp.
	Asteraceae	*Calea* sp.
	Clusiaceae	*Clusia* sp.
	Cyrillaceae	*Cyrilla* sp.
	Ericaceae	*Befaria* sp.
	Euphorbiaceae	*Phyllantus* sp.
	Humiriaceae	*Humiria* sp.
	Ixonanthaceae	*Cyrillopsis* sp.
	Malpighiaceae	*Byrsonima* sp.
	Melastomataceae	*Miconia* sp.
	Myrtaceae	*Myrcia* sp.
	Proteaceae	*Roupala* sp.
	Rubiaceae	*Remijia* sp.
	Theaceae	*Bonnetia* sp.
		Ternstroemia sp.
Herbaceous	Cyperaceae	*Bulbostylis* sp.
		Hypolytrum sp.
		Rhynchospora sp.
		Scleria sp.
	Orchidaceae	*Epidendrum* sp.
	Poaceae	*Axonopus* sp.
		Echinolaena sp.
		Paspalum sp.
		Trachypogon sp.
	Rubiaceae	*Declieuxia* sp.
		Sipanea sp.
	Scrophulariaceae	*Buchnera* sp.
Emergents	Ixonanthaceae	*Ochthocosmus* sp.
	Loganiaceae	*Bonyunia* sp.
	Ochnaceae	*Poecilandra* sp.

Table B4. Dominant taxa in peaty soils shrublands (Huber, 1994; 1995b).

Layer	Family	Genus
Shrubs	Bignoniaceae	*Digomphia* sp.
	Melastomataceae	*Meriana* sp.
	Rubiaceae	*Chalepophyllum* sp.
		Pagameopsis sp.
	Theaceae	*Bonnetia* sp.
Herbaceous	Bromeliaceae	*Brocchinia* sp.
	Rapateaceae	*Stegolepis* sp.
Emergents	No present	

CHAPTER 4:

Paleoecología del Holoceno en la Gran Sabana, SE Venezuela: Análisis preliminar de polen y microcarbones en la Laguna Encantada.

Pare digueu-me què li han fet al bosc que no hi ha arbres.
A l'hivern no tindrem foc ni a l'estiu lloc per aturar-se.
Pare que el bosc ja no és el bosc.
Pare abans de que no es faci fosc ompliu de vida el rebost.
Joan Manuel Serrat; Pare.

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RESUMEN

La región de la Gran Sabana, al SE de Venezuela, se caracteriza por la presencia de extensas sabanas neotropicales, en un clima cálido y húmedo, que parece más propicio para la existencia de bosques húmedos. Existen dos grandes grupos de hipótesis para explicar esta configuración vegetal: las naturales (cambios climáticos, pobreza de suelos) y las antrópicas (incendios provocados). El presente estudio utiliza el análisis de polen y microcarbones para reconstruir las tendencias paleoambientales, de la vegetación y del régimen de incendios, en la turbera litoral de la Laguna Encantada, durante los últimos 7.500 años. Las sabanas han dominado el paisaje durante todo este tiempo, a pesar de que los incendios locales no afectaron el área hasta hace unos 1.200 años, momento en el cual se establecen las comunidades actuales. Hacia los 4.000 años antes del presente tuvo lugar una expansión de los bosques de galería, causada por cambios climáticos, seguida de una evidente deforestación debida al fuego, que culminó en la situación actual. Estos resultados, junto con estudios anteriores, sugieren que las sabanas actuales de la Gran Sabana son el resultado de la interacción de diversos factores, estando el clima muy asociado a su origen y los fuegos provocados a su gran expansión actual.

Palabras clave: Fuego; *Mauritia*; Microcarbones; Paleoecología; Polen; Sabanas; Venezuela.

ABSTRACT

Holocene paleoecology of the Gran Sabana, SE Venezuela: preliminary pollen and microcharcoal analysis at Laguna Encantada.- The Gran Sabana region (SE Venezuela) is characterized by extensive neotropical savannas, in a warm and wet climate, apparently more suitable for the existence of rain forests. Two main types of hypotheses have been proposed to explain this situation: natural factors, such as climate changes or soil poverty, and burning by humans. This study analyzes the pollen and charcoal content of a 7,500 years old peat bog, at the shore of Laguna Encantada. The savanna landscape has dominated the area during the whole interval, but local fires did not appear until around 1,200 years ago, when the present communities began to establish. An expansion of gallery forests, likely due to a climatic shift, has been recorded around 4,000 years ago, followed by a deforestation triggered by fire, leading to present-day situation. These results, together with former similar studies, suggest that the present Gran Sabana landscape resulted from the interaction of diverse factors, being climate changes more related to its origin and human induced fires more linked to the recent expansion.

Keywords: Fire; *Mauritia*; Microcharcoal; Palaeoecology; Pollen; Savannas; Venezuela.

4.1. Introducción

El estudio de restos biológicos (polen, esporas, algas, hongos, etc.), como indicadores de situaciones pasadas en sedimentos lacustres, turberas, etc., ha despertado un creciente interés desde la segunda mitad del siglo pasado (Birks & Birks, 1980). Muchos de estos estudios paleoecológicos están basados en análisis palinológicos. La identificación de taxones vegetales a partir de los granos de polen y esporas no sólo permite reconstruir las comunidades vegetales del pasado, sino que contribuye a establecer la evolución climática de una determinada región (Faegri *et al.,* 1989). Otro de los indicadores frecuentemente utilizados en paleoecología son los microcarbones. Estas partículas se encuentran en el sedimento como consecuencia de los incendios que tienen lugar en la zona de influencia. Se trata, en su mayoría, de restos de cenizas, generalmente procedentes de material vegetal quemado. El uso de carbones macro- y microscópicos como apoyo a estudios paleoecológicos ha ido en aumento durante los últimos 20 años. Su estudio, junto con el de polen y esporas, nos proporciona información acerca del clima, la vegetación, el régimen de incendios y las actividades humanas en el pasado (Kangur, 2002; Hammond *et al.*, 2006; Enache & Cumming, 2007; Duffin *et al.*, 2008).

El presente estudio se desarrolla en una turbera de la Gran Sabana (GS), situada en el SE de Venezuela (Fig. 4.1). Las sabanas han despertado gran interés por su característica distribución geográfica y por la gran extensión que ocupan (aproximadamente 3 millones de km^2 sólo en el trópico americano [Huber, 1987]). Existen numerosos estudios paleoecológicos realizados en sabanas neotropicales o zonas de mosaico bosque-sabana, cuyo propósito es determinar el origen de este tipo de vegetación e inferir los mecanismos que han actuado para la continuidad en el tiempo de la misma (por ejemplo, Wymstra & Van der Hammen, 1966; Servant *et al.,* 1993; Van der Hammen & Absy, 1994; Bush *et al.,* 2004). Un aspecto importante en el estudio del origen y extensión de estas sabanas ha sido su relación con el fuego, ya que estas comunidades sufren una alta presión por incendios (Beerling & Osborne, 2006; Ramírez *et al.,* 2007). En la GS, por ejemplo, se registran más de 10.000 incendios de origen antrópico cada año (Huber, 1995*b*), causados principalmente por agricultores, indígenas y mineros. Diversos estudios indican que, teniendo en cuenta los regímenes de temperatura y precipitación de la GS (ver apartado de área de estudio), esta región posee un bioclima típico de bosque montano perennifolio (Huber, 1995*c*; Ramírez *et al.,* 2007). Sin embargo, su vegetación actual se caracteriza por vastas extensiones de sabana y mosaicos bosque-sabana (Baruch, 2005), lo que ha llevado a plantearse las posibles causas de la presencia y extensión de esta formación vegetal. Las principales causas propuestas hasta ahora son:

- Las condiciones edáficas, sobre todo la pobreza en nutrientes y las relaciones hídricas (Fölster, 1986; Fölster *et al.,* 2001).
- Que las sabanas actuales sean un relicto de extensiones de esta formación en épocas pasadas, como durante el último máximo glaciar (*ca.* 20.000 años) (Eden, 1974).
- La acción directa del fuego (Dezzeo *et al.,* 2004).
- La expansión de sabana a partir de núcleos aislados preexistentes debido a la presión humana, principalmente a través de los incendios (Rull, 1999; Huber, 2006).

Figura 4.1. Localización del área de estudio. Recuadro externo: Mapa ampliado de la Gran Sabana, donde el asterisco señala el lugar del sondeo. Recuadro interno: Imagen de radar del norte de Sudamérica (NASA/ JPL-Caltech). El rectángulo amarillo señala la región de la Gran Sabana, mientras que los diferentes números muestran regiones bajas donde se han llevado a cabo los estudios paleoecológicos mencionados en el texto, siendo: (1) Cuenca de Cariaco (Venezuela); (2) Lago Valencia (Venezuela); (3) Llanos Orientales de Colombia; y (4) Sabanas de Guyana.

Los trabajos efectuados hasta el momento han puesto de manifiesto la baja resiliencia de los ecosistemas forestales de la GS. Se ha manifestado el escaso o nulo poder de recuperación del bosque con posterioridad a eventos de deforestación, a corto y largo plazo, bien sea por causas naturales o antrópicas (Fölster, 1992; Rull, 1992, 1999; Fölster *et al.,* 2001; Dezzeo & Chacón, 2005; Dezzeo & Chacón, 2006). La capacidad de regeneración del bosque estaría limitada por la influencia de los factores edáficos y la rápida colonización por plantas herbáceas a partir de sabanas cercanas, así como por la alta frecuencia de incendios. El resultado de este conjunto de factores es una sucesión secundaria que, a largo plazo, termina en la instalación de sabanas inarboladas o morichales (comunidades monoespecíficas de palmeras dominadas por *Mauritia flexuosa*, frecuentes en suelos mal drenados como los alrededores de las lagunas y a lo largo de los ríos), según sean las condiciones de humedad (Rull, 1992).

En la GS y sabanas neotropicales cercanas, el Holoceno (los últimos 11.500 años) constituye una época de fluctuaciones ambientales, lo que ha afectado a la vegetación del entorno (Rull *et al.*, en prensa). El inicio del Holoceno se caracterizó, en la Gran Sabana, por un aumento en las temperaturas medias de 2 - 3ºC posterior al Último Máximo Glacial, y que muy probablemente repercutió en la sustitución de la vegetación dominante hasta ese momento, un bosque mesófilo húmedo, por una sabana inarbolada (Rull, 2007). Esta interpretación discrepa con la hipótesis propuesta por Eden (1974), que afirma que la vegetación de sabana constituye un relicto del último máximo glacial. Otros estudios ilustran como las oscilaciones ambientales y el fuego han influido fuertemente en el paisaje vegetal en los últimos milenios (véase por ejemplo, Rull, 1991). En general, las consecuencias de las fases de clima más seco y las de mayor incidencia de fuegos han sido similares, manifestándose en ambos casos en una reducción de los bosques y expansión de las sabanas (Rull, 1992). Prácticamente toda la información paleoecológica de que se dispone para la región corresponde a los últimos 4.000 años, fecha desde la cual, la incidencia de fuegos ha aumentado considerablemente (Rull, 1991; Fölster, 1992). En estos estudios, se ha observado que después de cada perturbación causada indistintamente por el clima o el fuego, se desencadenan procesos de sucesión secundaria que terminan en el establecimiento de sabanas, con o sin morichales. El retorno de condiciones húmedas después de las fases climáticas secas o los incendios no ha conducido a la regeneración de los bosques, sino que en su lugar, se han establecido comunidades casi monoespecíficas de *Mauritia flexuosa* (Rull, 1992, 1999). Estos morichales han aumentado en los últimos milenios y se ha propuesto que están en expansión desde la última glaciación, favorecidos por el fuego (Rull, 1998*a*).

El propósito de este trabajo es reconstruir la vegetación y sus cambios a escala de milenios en una secuencia continua de 7.500 años de antigüedad, con especial interés en determinar las causas del establecimiento de la comunidad actual de sabanas con morichales en la zona de estudio. Se pretende reconstruir la dinámica de la vegetación durante el Holoceno y analizar el papel del clima y del fuego, con el fin de evaluar las hipótesis sobre el origen y el mantenimiento de la actual Gran Sabana.

4.2. Área de Estudio

La Gran Sabana es una extensa región de unos 18.000 km^2 situada al SE de Venezuela (4,6089 - 6,6331 N y 61,0679 - 74,0478 W, Fig. 4.1), aunque las sabanas continúan más allá de estas fronteras, penetrando en Guyana y Brasil, con una extensión total de aproximadamente 30.000 km^2. Esta región se extiende entre los 750 y 1.450 m de altitud, con un gradiente descendente de N a S. Desde el punto de vista fisiográfico, forma parte de las llamadas “tierras medias” o *uplands* que, en la región de Guayana, se sitúan entre 500 y 1.500 m de altitud (Huber, 1995*a*). Desde el punto de vista geológico, la GS se encuentra enteramente sobre el sector nororiental del Escudo de Guayana, uno de los núcleos terrestres más antiguos del continente americano. Dependiendo de la geología predominante, la geomorfología de la zona varía notablemente, desde llanuras onduladas asociadas a sustratos de arenisca, a colinas y lomas bajas sobre diabasa (Huber & Febres, 2000). Dentro de las seis superficies de erosión que se han descrito para el Escudo de Guayana, la GS se encuentra en su mayoría incluida en la de Wonkén, de 900 a 1.200 m de altitud (Briceño & Schubert, 1990). El clima de la región es de tipo submesotérmico, con una temperatura media anual de 18 - 20ºC. El régimen pluviométrico es de tipo ombrófilo (2.500 - 4.000 mm anuales), existiendo notables variaciones locales. La distribución anual de la precipitación está condicionada por la variación estacional de la Zona de Convergencia Intertropical (ITCZ), lo que se traduce en una alternancia anual de las precipitaciones que determina la existencia de una estación lluviosa entre abril y noviembre, y otra más seca entre diciembre y marzo.

Ambos parámetros climáticos muestran un claro gradiente en sentido N-S, siendo ascendente para la temperatura y descendente para la precipitación (Galán, 1984; Huber & Febres, 2000). Según Huber (1995*c*), la vegetación de la GS se puede dividir en cuatro tipos principales: 1) formación boscosa, en la cual se pueden diferenciar bosques de tipo montano y bosques de galería; 2) formación arbustiva, con las comunidades de mayor diversidad en la zona (Huber, 1986; Huber, 1995*c*); 3) formación herbácea, en la que se pueden distinguir los herbazales gramíneos o sabanas, y los herbazales no gramíneos o praderas; y 4) formación pionera, caracterizada por una vegetación dispersa y una alta especialización de arbustos y herbáceas. Dentro de las sabanas, se pueden distinguir a su vez tres tipos (Huber, 1995*c*): 1) Sabanas abiertas o lisas, el tipo más extendido, llamadas también sabanas inarboladas. En estas sabanas existe un estrato herbáceo de hasta 1 m de alto, de densidad variable. Son comunidades pobres en especies (20 - 30 especies), donde pueden aparecer elementos leñosos (arbustos o sufrútices) aislados, que no superan la altura alcanzada por las plantas herbáceas. 2) Sabanas con morichales, estacionalmente inundadas, donde se forma un denso estrato herbáceo de hasta 2 m de alto con parches más o menos dispersos de morichales. 3) Sabanas arbustivas, en suelos extremadamente pobres en nutrientes y ácidos. El estrato herbáceo aparece disperso e irregular, y dominan taxones de la familia *Cyperaceae*.

4.3. Matrerial y Métodos

La turbera objeto de este estudio se encuentra en el margen de la Laguna Encantada (4,7110 N 61,0821 W; 867 m altitud), dentro de la finca privada denominada “Hato Santa Teresa”, cercana a la ciudad de Santa Elena de Uairén (Fig. 4.1). Esta ciudad se ubica en la zona sur de la GS a unos 910 m de altitud. Sus registros pluviométricos señalan una precipitación total anual de 1.700 mm (Galán, 1984). La laguna se encuentra rodeada por una extensa sabana abierta que, en sus orillas, se transforma en una turbera con individuos dispersos de *Mauritia flexuosa*. El sondeo PATAM4_D07 se realizó en una de estas turberas en enero de 2007, utilizando una sonda rusa (Jowsey, 1966), con la que se obtuvo una secuencia total de 392 cm de profundidad. En ella se realizaron un total de 10 dataciones de ^{14}C mediante la técnica de espectometría de aceleración de masas (AMS), sobre macrorrestos vegetales o extractos polínicos, en los laboratorios UCI (Laboratorio de Radiocarbono de la Universidad de California, USA) y Beta Analytic (Laboratorio comercial, USA). La calibración de estas dataciones se llevó a cabo con el software CALIB 5.0.2 y la base de datos IntCal04.14c (http://calib.qub. ac.uk./calib/, última consulta en mayo del 2008). Las edades obtenidas se expresaron finalmente como años calibrados antes del presente o cal BP (Wolff, 2007). El modelo de profundidad-edad del sedimento se realizó mediante el software R (http://www.r-project.org, última consulta en mayo del 2008), utilizando el paquete de datos age.R (http://chrono.qub.ac.uk/blaauw/, última consulta en mayo de 2008). El modelo se basó en la interpolación lineal de las edades obtenidas en la calibración (Blaauw *et al.*, en prep.). Para el presente análisis polínico preliminar de la secuencia se analizaron 25 muestras con una separación de entre 15–20 cm entre cada una. El tratamiento de laboratorio consistió en sucesivas digestiones con KOH, HCl, HF y mezcla de acetólisis (anhídrido acético y ácido sulfúrico en proporción 9:1) (Faegri *et al.,* 1989; Moore *et al.,* 1991). El medio de montaje empleado fue aceite de silicona, por lo que las muestras pasaron por un proceso previo de deshidratación, por imbibición secuencial en etanol y butanol terciario. Antes del tratamiento, se introdujeron tabletas con esporas de *Lycopodium* (*batch* 124.961, con 12.542 ± 2.081 esporas por comprimido), según Benninghoff (1962) y Stockmarr (1971). Para la identificación de palinomorfos se utilizaron las siguientes referencias: Hooghiemstra (1984); Moore *et al.* (1991); Roubik & Moreno (1991); Tryon & Lugardon (1991); Herrera & Urrego (1996); Rull & Vegas-Vilarrúbia (1997); Rull (1998*b*); Colinvaux *et al.* (1999) y Rull (2003). El conteo se hizo siguiendo las relaciones de calidad/esfuerzo propuestas en Rull (1987). La suma de polen incluye todos los taxones polínicos identificados, excepto las especies acuáticas.

No se incluyeron en el diagrama los taxones con proporciones inferiores al 0,1%. Para la construcción y zonación de los diagramas polínicos, se utilizó el software PSIMPOLL 4.26 (http://www. chrono.qub.ac.uk/psimpoll/psimpoll.html, última consulta realizada en marzo del 2008) y los criterios de Bennett (1996). La interpretación de los espectros polínicos se basó en estudios previos de sedimentación polínica actual en relación con la vegetación (Rull, 1991). Los cálculos del índice de diversidad de Shannon (H´), la equitabilidad (E) y la riqueza de especies (S) (Pielou, 1966; Hurlbert, 1971), se llevaron a cabo mediante el programa MVSP versión 3.13. El conteo de microcarbones se efectuó en las mismas preparaciones destinadas al análisis palinológico. Se contaron las partículas mayores de 5 µm y se establecieron tres grupos diferentes dependientes del tamaño, siguiendo la clasificación para la Gran Sabana de Rull (1999):

1. Microcarbones menores de 100 µm (Tipo I): como indicadores de fuegos regionales, al ser fácilmente transportados por el viento.
2. Microcarbones comprendidos entre 100 y 500 µm (Tipo II): indicadores de incendios locales o cercanos a la zona de sondeo.
3. Microcarbones mayores de 500 µm (Tipo III): indicadores de incendios locales e intensos.

4.4. Resultados

4.4.1. Cronología

De las 10 dataciones realizadas, se utilizaron 7 para establecer el modelo de profundidad-edad (Tabla 4.1, Fig. 4.2). Las otras 3 dataciones fueron descartadas por presentar edades incongruentes, debido probablemente a contaminación por material más joven procedente de niveles superiores El modelo sedimentario muestra un testigo continuo con distintas velocidades de acumulación, en el que se diferencian tres zonas principales (Fig. 4.2):

1. La parte más profunda (390 - 310 cm, 7.500 - 7.095 años cal BP), con una rápida velocidad de acumulación (0,223 cm/año).
2. El tramo intermedio (310 - 240 cm, 7.095 - 3.400 años cal BP), con una velocidad marcadamente inferior (0,0178 cm/año).
3. El tramo superior (240 - 10 cm, 3.400 años cal BP al presente), con una tasa de acumulación intermedia (0,069 cm/año).

La naturaleza y composición del sedimento no es homogénea a lo largo de la secuencia (Fig. 4.2). El testigo comienza siendo una turba oscura con contenido arcilloso (391,5–384,5 cm). Seguidamente, se observa un intervalo (384,5–306 cm) de arcillas grisáceas con intercalaciones de arena. A continuación (306–200 cm), comienza de nuevo un sedimento turboso, el cual contiene al inicio una porción arcillosa oscura. La parte más reciente del testigo (200–10 cm), se caracteriza por una turba oscura, poco compactada y con elevado contenido en agua. Se consideró la posibilidad de un hiatus a 300 cm, en el contacto entre arcilla y turba, pero se aceptó el modelo de sedimentación continua por ser el más significativo estadísticamente.

Tabla 4.1. Resultados de las dataciones (Acrónimo de los laboratorios responsables: UCI: Universidad de California; y Beta: Laboratorio comercial Beta Analytic Inc.). Las muestras utilizadas para el modelo de profundidad-edad se han marcado con un asterisco.

Nº Laboratorio	Muestra	Profundidad (cm)	Tipo muestra	Edad (años ^{14}C BP)	Edad (años cal BP) con 2σ
UCI – 43721 *	PATAM4_D07/10	55-60	Macrofósil	655 ± 35	555-609
UCI – 43694 *	PATAM4_D07/22	115-120	Macrofósil	1.235 ± 20	1.079-1.188
UCI – 43695	PATAM4_D07/34	175-180	Macrofósil	790 ± 20	680-732
Beta – 242280 *	PATAM4_D07/35	180-185	Macrofósil	2.090 ± 40	1.949-2.152
Beta – 243846 *	PATAM4_D07/46	235-240	Extracto polínico	3.140 ± 40	3.335-3.404
UCI – 43696	PATAM4_D07/47	240-245	Macrofósil	1.930 ± 20	1.825-1.903
UCI – 43697	PATAM4_D07/59	300-303	Macrofósil	445 ± 20	487-524
Beta – 242281 *	PATAM4_D07/60	303-306	Extracto polínico	6.170 ± 40	6.949-7.169
Beta – 242282 *	PATAM4_D07/74	362-367	Extracto polínico	6.530 ± 40	7.414-7.511
UCI – 37498 *	PATAM4_D07/81	388-393	Macrofósil	6.530 ± 20	7.422-7.476

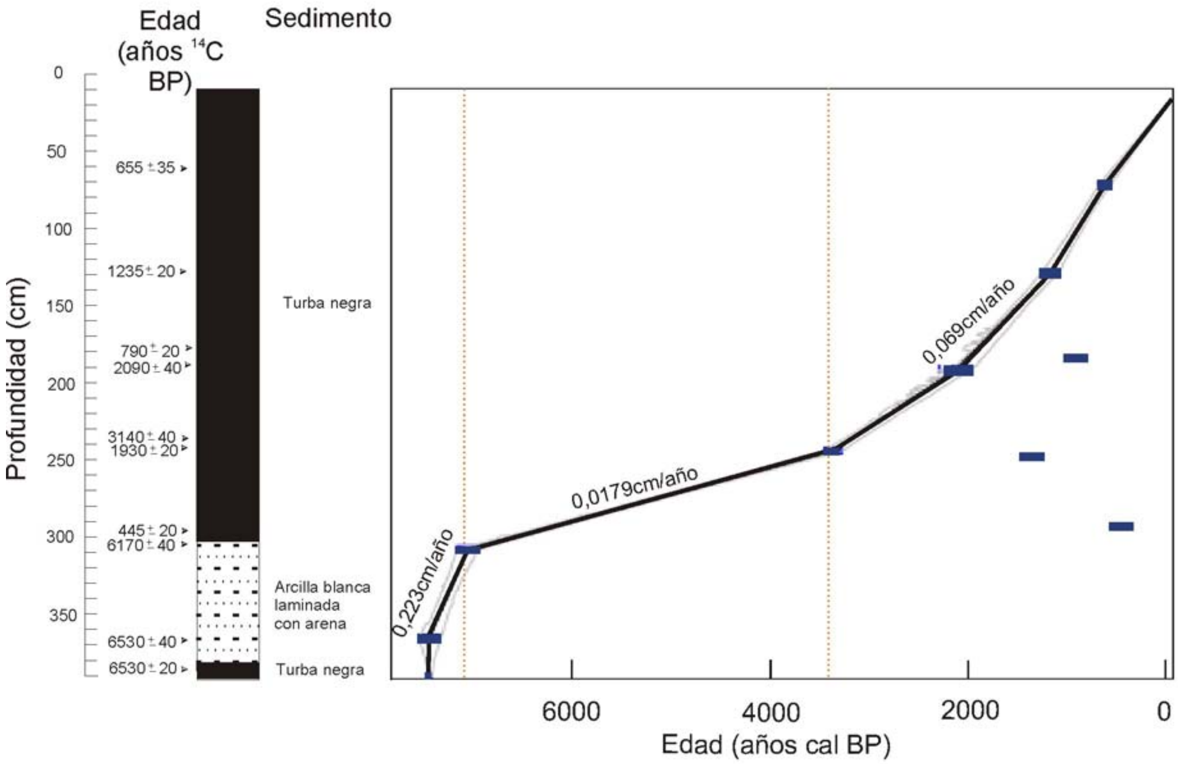

Figura 4.2. Columna estratigráfica del testigo analizado, con las dataciones realizadas (edades no calibradas) y la descripción de la columna sedimentaria, junto con el modelo de profundidad-edad, con las tasas de sedimentación de cada intervalo. Los cuadros azules representan las dataciones realizadas con sus respectivos errores.

4.4.2. Polen y esporas

El diagrama polínico (Fig. 4.3) se subdividió en tres zonas polínicas que se describen a continuación. La muestra de la base de la secuencia se describe aisladamente pese no a no ser significativamente distinta, debido a las diferencias sedimentológicas y palinológicas que presenta con el resto de la secuencia. La distancia entre muestras (15–20 cm) supone una diferencia de edad de entre 280 y 350 años, por lo que la resolución de esta reconstrucción es a escala de milenios.

Muestra 81 (392–389 cm, 1 muestra)

Caracterizada por su alto contenido orgánico y por sus elevados porcentajes de gramíneas y otros elementos herbáceos como *Xyris*, así como algunos taxones leñosos (*Byrsonima, Miconia*) y, en una menor proporción, *Urticales*. El resto de taxones arbóreos y arbustivos se encuentran en baja proporción o están ausentes.

4.4.2.1. Zona SM-I (389–198 cm, 12 muestras)

En general, se aprecia un aumento de elementos forestales y algas con respecto a la muestra anterior. Entre los taxones leñosos destacan *Brosimum* y otras *Urticales*, *Weinmannia*, *Malpighiaceae* y *Miconia.* Estos elementos se alternan en abundancia con las gramíneas en la mitad inferior de la zona, mientras que en la mitad superior aumentan notablemente, coincidiendo con una mayor abundancia de algas. En esta mitad superior, también aumentan otros elementos forestales como *Schefflera, Acalypha* y *Alchornea*. *Mauritia* está ausente en esta parte de la secuencia.

4.4.2.2. Zona SM-II (198–120,5 cm, 5 muestras)

Caracterizada por una disminución de la mayoría de taxones leñosos (*Acalypha, Alchornea, Byrsonima, Schefflera*, *Urticales, Malpighiaceae*, *Miconia* y *Myrsine*). Los taxones herbáceos sufren un aumento evidente, sobre todo las gramíneas y *Xyris,* y en menor medida *Eriocaulaceae*. Las esporas también aumentan, sobre todo los triletes psilados. En esta zona se registran las primeras apariciones de *Mauritia*, aunque en una baja proporción. Las algas mantienen niveles similares o ligeramente inferiores a la parte final de la anterior zona.

4.4.2.3. Zona SM-III (120,5–10 cm, 7 muestras)

La mayoría de taxones leñosos y esporas de pteridófitos desaparecen casi totalmente a excepción de *Mauritia,* que experimenta un notable y súbito aumento hasta convertirse en el taxón subdominante después de las gramíneas. Las gramíneas aumentan de nuevo en la primera parte de esta zona, y otras herbáceas como *Eriocaulaceae* y *Xyris* se mantienen en proporciones similares a la zona anterior. Las algas disminuyen en esta zona.

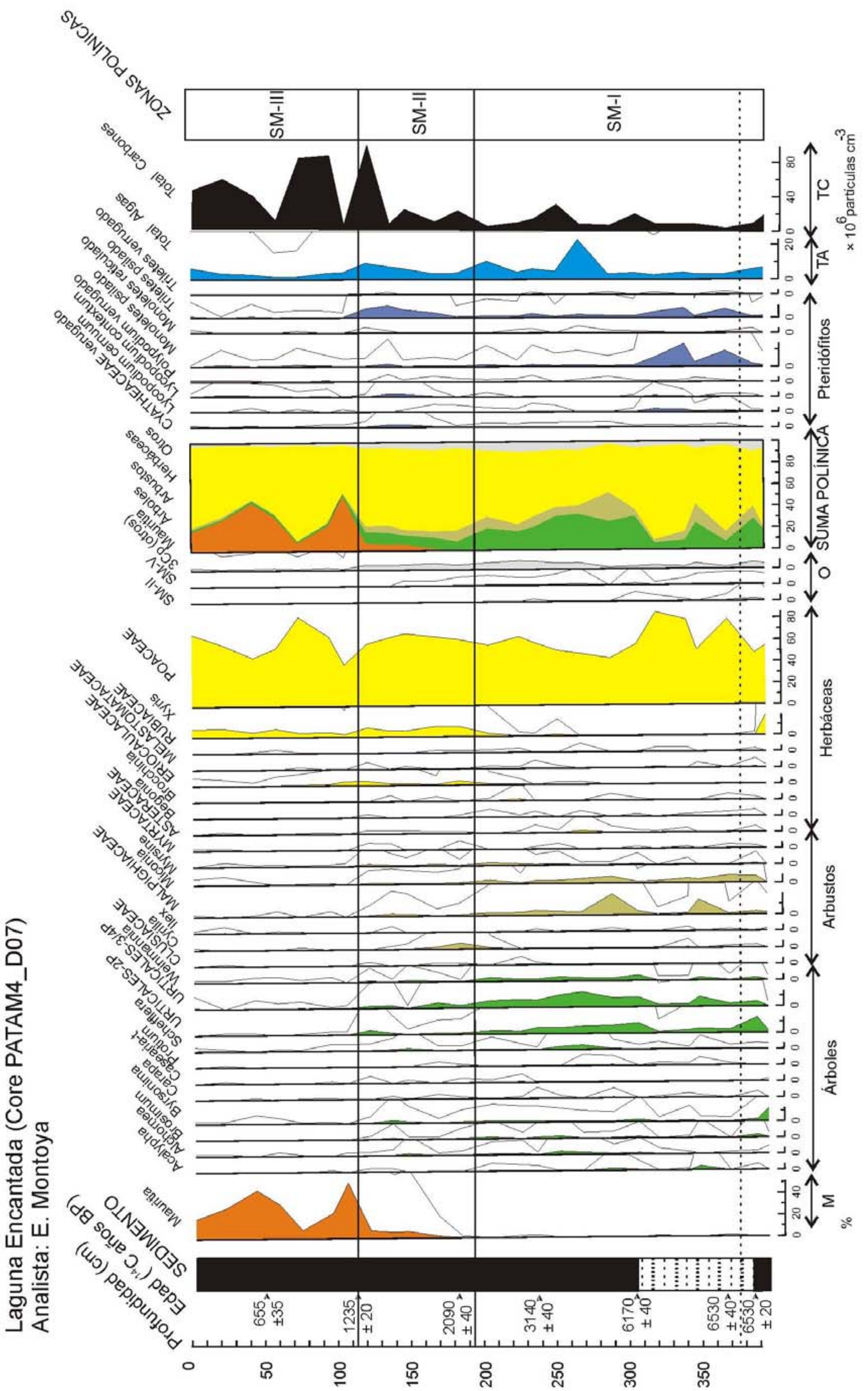

Figura 4.3. Diagrama polínico de la secuencia, expresado en porcentaje con respecto a la suma polínica. M, *Mauritia*; O, otros; TA, total de algas; TC, total de carbones; SM-II y SM-V, morfotipos polínicos indeterminados; 3Cp, polen tricolporado no identificado.

4.4.3. Algas

Las algas y los macrófitos acuáticos se representan en un diagrama separado para ilustrar las variaciones del medio acuático (Fig. 4.4). Algunos taxones muestran una presencia más o menos continua a lo largo del sedimento (*Zygnemataceae*, *Cyperaceae* y *Sagittaria*), mientras que otros aparecieron sólo de manera puntual en un tramo de la secuencia (*Botryococcus*, *Utricularia* y *Spirogyra*). Existe un marcado pico de *Zygnemataceae* a 270 cm, en la Zona SM-I, simultáneo con la aparición de *Botryococcus*, que no está acompañado por cambios en las plantas acuáticas. Sin embargo, otro aumento de las algas, registrado en la mitad superior de la Zona SM-II, sí que coincide con picos de *Cyperaceae* y *Sagittaria*. En la Zona SM-III, se aprecia una disminución general de los taxones acuáticos mayoritarios.

4.4.4. Microcarbones

La presencia de microcarbones es continua durante toda la secuencia, apareciendo con menores concentraciones en la Zona SM-I y primera mitad de la SM-II. En la segunda mitad de la Zona SM-II aumentan de forma muy acusada, manteniéndose en valores similares (aunque con grandes fluctuaciones) en la Zona SM-III (Fig. 4.5). En la Zona SM-I, los microcarbones de menor tamaño (I) son los más abundantes, mientras que los de tamaño intermedio (II) están presentes en muy baja proporción y la clase III está ausente. En la Zona SM-II, aumentan ligeramente los intermedios y los menores se mantienen similares, a excepción de la última muestra en la que experimentan un gran aumento. Por último, en SM-III, se produce el mayor aumento en los microcarbones, debido principalmente a los de menor tamaño, aunque los intermedios aumentan también su concentración. Los microcarbones de mayor tamaño (tipo III) se mantienen constantes en cantidades insignificantes durante toda la secuencia.

4.4.5. Riqueza y diversidad

El índice de diversidad de Shannon oscila en la mitad inferior de SM-I y se estabiliza en valores altos en la parte superior de esta zona (Fig. 4.5). En la Zona SM-II, este índice sufre una progresiva disminución, que sigue hasta la Zona SM-III, donde alcanza su mínimo. El valor de equitabilidad también oscila en la mitad inferior de SM-I y posteriormente se estabiliza hasta experimentar una ligera disminución en SM-II y un mínimo en SM-III. La riqueza de taxones se mantiene en un rango similar desde la base del diagrama hasta SM-III, donde se evidencia una ligera disminución. En general, las tres curvas presentan una tendencia descendente a lo largo de la secuencia, que se acentúa en SM-III.

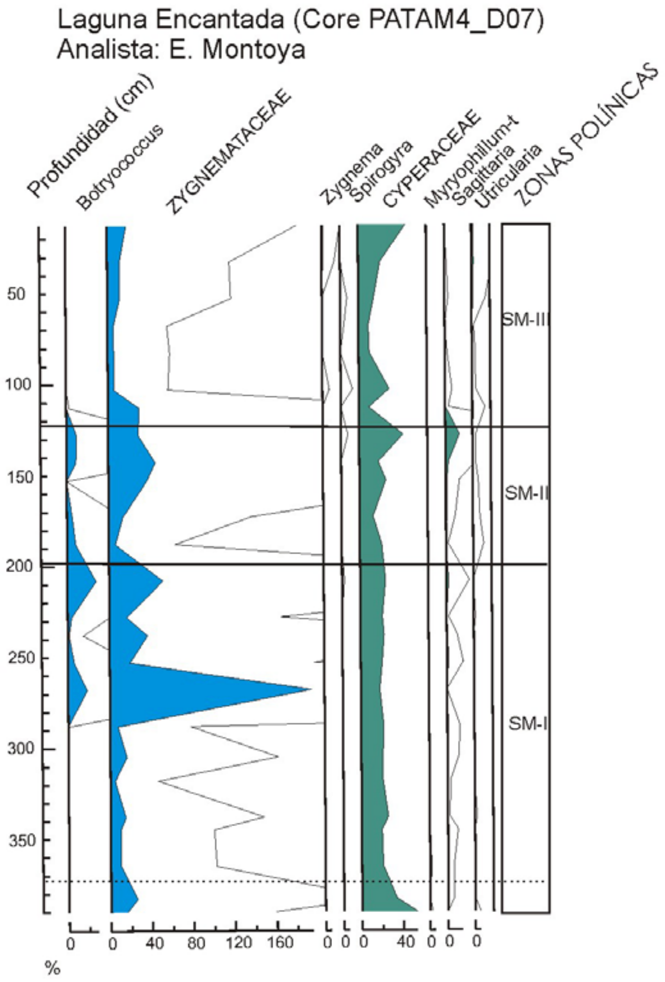

Figura 4.4. Diagrama polínico de taxones acuáticos y algas, expresados en porcentajes con respecto a la suma polínica.

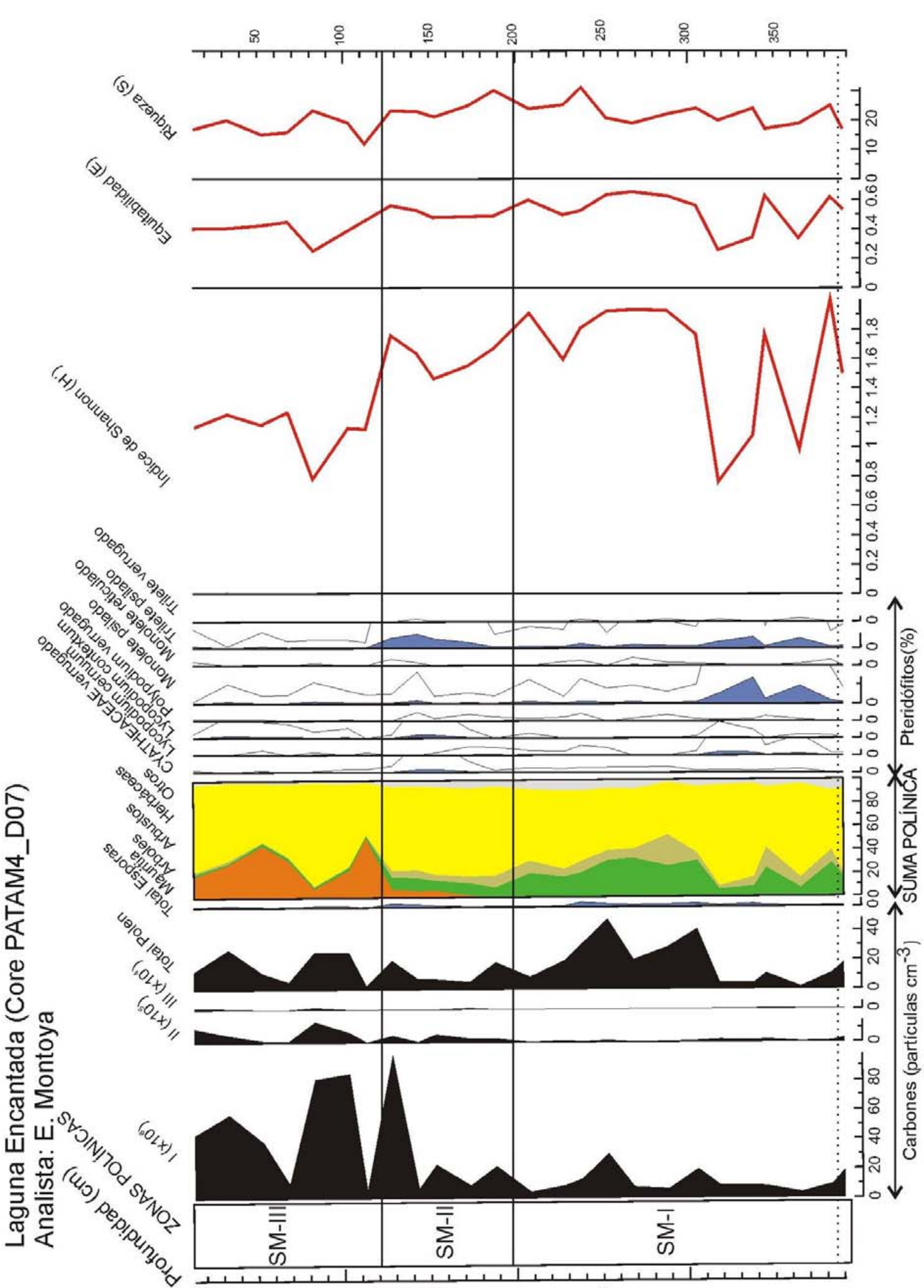

Figura 4.5. Diagrama de microcarbones, expresados en concentración. También se muestran las esporas de pteridófitos (en porcentaje) y los índices calculados.

4.5. Interpretación y Discusión

La secuencia estudiada refleja la dinámica de la vegetación alrededor de la Laguna Encantada en los últimos 7.500 años. Los cambios observados se pueden interpretar en términos de variaciones ambientales, sobre todo en el balance hídrico (P/E), entendido como la relación entre la precipitación (P) y la evapotranspiración (E), y del régimen de incendios. La interpretación paleoecológica resultante se resume en la Fig. 4.6 y se describe a continuación, comparándola con otros estudios de áreas neotropicales vecinas.

4.5.1. Reconstrucción paleoambiental y de la vegetación

4.5.1.1. 7.500 - 7.450 cal BP (Muestra 81)

La abundancia de taxones herbáceos junto a la presencia, en baja proporción, de algunos elementos leñosos se interpreta como indicativa de una formación de sabana herbáceo-fruticosa o de sabana mixta. La baja proporción de esporas y algas sugiere un balance hídrico similar al actual o ligeramente más seco. Este tipo de vegetación, por lo demás pobre en taxones, es consistente con climas menos pluviosos o más estacionales que los actuales, como proponen Behling & Hooghiemstra (1998*b*) para regiones cercanas. Trabajos realizados en zonas similares como las sabanas de los Llanos de Colombia o el Lago Valencia (Fig. 4.1), también ponen de manifiesto condiciones más secas que las actuales durante el Holoceno Temprano, cuando las formaciones de sabana predominaban sobre las formaciones boscosas en el norte de Sudamérica (Wymstra & Van der Hammen, 1966; Leyden, 1985; Behling & Hooghiemstra, 1998*b*; Berrío *et al.,* 2002).

Figura 4.6. Esquema resumen de la secuencia, con la zonación e interpretación del diagrama polínico.

4.5.1.2. 7.450 - 2.470 cal BP (Zona SM–I)

El cambio sedimentológico desde la turba orgánica de la muestra anterior a las arcillas con intercalaciones de arena de la base de este intervalo, indica la presencia de un curso de agua de baja energía, lo que sugiere un aumento en el balance hídrico. En esta parte del testigo, la velocidad de sedimentación es muy rápida, lo cual es consistente con una mayor tasa de aporte de sedimentos clásticos alóctonos, debida a un aumento de la escorrentía. El aumento de taxones leñosos en este mismo intervalo se puede interpretar como una mayor extensión de los bosques de galería. Esta situación se había mantenido en una primera etapa, hasta los 7.180 años cal BP. En el segundo tramo de la zona (7.180–2.470 cal BP), la tasa de sedimentación es muy inferior (Fig. 4.2) y el sedimento vuelve a caracterizarse por un alto porcentaje de la fracción orgánica (autóctona), aunque con contenido en arcillas, lo que podría estar ocasionado por la formación de una laguna similar a la actual. El aumento de los elementos forestales (que indica mayor extensión o proximidad de los bosques) y el aumento de los taxones acuáticos alrededor de *ca*. 4.000 años cal BP, apoyan la interpretación de un mayor balance hídrico, que estaría de acuerdo con la hipótesis de Marchant & Hooghiemstra (2004), del predominio de climas húmedos a escala del trópico sudamericano, hacia los 4.000 años cal BP. El final del Holoceno Temprano y comienzos del Holoceno Medio parece haberse caracterizado, en las zonas bajas del Norte de Sudamérica, por un aumento del balance hídrico, paralelamente con un aumento en la extensión de las formaciones forestales (Berrío *et al.,* 2002; Marchant & Hooghiemstra, 2004; Behling & Hooghiemstra, 1998*b*). En el Lago Valencia, esta fase corresponde a niveles lacustres altos (Curtis *et al.,* 1999), mientras que en la cuenca de Cariaco (Fig. 4.1), las evidencias isotópicas y geoquímicas apuntan a un aumento de la precipitación hacia el mismo periodo, que se relacionan con un desplazamiento hacia el norte de la Zona de Convergencia Intertropical (ITCZ), que regula el régimen de precipitaciones (Haug *et al*., 2001).

4.5.1.3. 2.470 - 1.220 cal BP (Zona SM–II)

La disminución de los elementos arbóreos y las algas, junto con la gran dominancia de los taxones herbáceos se interpreta como una expansión de las sabanas y una retracción de los bosques. Dado que no se observa aumento de la concentración de microcarbones, estos cambios vegetales se interpretan como de origen climático. Todo ello sugiere una disminución del balance hídrico y niveles lacustres más bajos. Hacia la mitad de esta zona, los primeros individuos de *Mauritia* llegaron a la Laguna Encantada, pero sin formar todavía morichales. La existencia de condiciones más secas a nivel regional se manifiesta en un descenso de los niveles lacustres en el Lago Valencia (Leyden, 1985; Curtis *et al.,* 1999), al mismo tiempo que se ha documentado una expansión de las sabanas circundantes y una disminución de la precipitación en la cuenca de Cariaco, debido a un aumento de la intensidad de los ciclos de El Niño-La Niña (ENSO) (Haug *et al*., 2001; Tedesco & Thunell, 2003). Una expansión similar de las sabanas se ha registrado también en otros sondeos de la GS (Rull, 1991, 1992), de Colombia (Behling & Hooghiemstra, 1998*a*) y de Guyana (Fig. 4.1) (Wymstra & Van der Hammen, 1966). La hipótesis climática es que la ITZC, y con ella el cinturón lluvioso ecuatorial, se habría desplazado de nuevo hacia el sur (Curtis *et al*., 1999; Haug *et al*., 2001).

4.5.1.4. 1.220 años cal BP hasta el presente (Zona SM–III)

El cambio de vegetación más notable de la secuencia se produce en esta zona. Las gramíneas (y por lo tanto, la sabana) siguen siendo dominantes, pero esta vez los elementos arbóreos desaparecen casi del todo de una forma simultánea, reflejando una reducción drástica de los bosques, a la vez que se establecen los morichales.

Este cambio ya se había anticipado al final de la zona anterior, cuando se observa el primer gran pico de microcarbones, que coincide con el de los triletes psilados, interpretados como indicadores de incendios (Rull, 1999). A partir de este momento, los picos de *Mauritia* se alternan con los de gramíneas y microcarbones. A juzgar por el descenso de las algas, los niveles lacustres también parecen haber descendido ligeramente, hasta los actuales. El panorama general es de deforestación, disminución de la riqueza y la diversidad vegetal (sobre todo de taxones arbóreos), expansión de la sabana, establecimiento de morichales y aumento significativo del fuego, a escala regional. Se podría afirmar que es el principio del establecimiento de la Gran Sabana, tal como la conocemos hoy en día. Según Behling & Hooghiemstra (1998*a*, 2001), esta configuración vegetal se debe a un incremento general de la intervención humana, a nivel de las sabanas neotropicales.

4.5.2. Efectos del fuego y expansión de los morichales

En otras áreas tropicales, se ha visto que la alta incidencia de fuegos parece crear un ambiente propicio para la expansión de la formación de sabana, en lugares donde las condiciones climáticas y edáficas serían, en principio, más adecuadas para el desarrollo de una formación forestal (San Jose & Fariñas, 1983; Bond *et al.,* 2005; Bowman, 2005). Sin embargo, el presente estudio permite observar que el origen de la sabana de los alrededores de la Laguna Encantada fue muy anterior a la aparición de fuegos locales. Este hecho podría deberse a que el fuego no fuese el único factor que explique el origen de la sabana, aunque pueda favorecer su expansión. También cabe la posibilidad de que se hayan producido incendios locales anteriores al inicio de esta secuencia (~7.500 cal BP). La primera hipótesis estaría apoyada por el hecho de que en la localidad de Mapaurí (GS), situada unos 30 km al N de la Laguna Encantada, se observó la sustitución de bosques por sabanas debido a condiciones más cálidas y secas hacia los 10.000 años cal BP (Rull, 2007), sin la intervención de fuegos locales. Así, a consecuencia de un aumento en las temperaturas medias de 2 - 3ºC, se produjo un desplazamiento altitudinal de la vegetación forestal (unos 500 m aproximadamente) hacia las laderas de las montañas próximas, mientras que la sabana se expandió en las áreas anteriormente ocupadas por el bosque. Con respecto a la segunda posible explicación, existen estudios donde se ha reportado la existencia de una alta correlación positiva entre la abundancia del polen de gramíneas y los microcarbones de origen regional (Rull, 2008), sugiriendo una relación entre incendios y expansión de sabanas. Sin embargo, en este estudio, se ha observado que la sabana se ha mantenido, pese a la inexistencia de fuegos locales, durante más de 5.000 años. Esto sugiere que, a pesar de poder favorecer la expansión de la sabana, el fuego no ha sido el único factor influyente en su mantenimiento, lo cual aboga por otras causas, como por ejemplo factores edáficos (Dezzeo & Chacón, 2005). Así pues, aunque en la actualidad se reconoce al fuego como factor decisivo tanto de la expansión como del mantenimiento de la sabana (Fölster *et al.,* 2001), los estudios paleoecológicos indican que otros factores, como el clima o las características del suelo (contenido en nutrientes, agua, etc.), pueden tener las mismas consecuencias.

En este estudio se observan las dos situaciones mencionadas anteriormente, es decir, la extensión de sabana con y sin incendios locales, con un punto de inflexión en los ~1.200 años cal BP. Antes de esa fecha, la sabana se mantenía y los bosques aumentaban o disminuían en importancia obedeciendo principalmente a cambios en el balance hídrico.

Después de esa fecha, la sabana se ha mantenido en condiciones similares, pero el bosque ha desaparecido o se ha reducido drásticamente y han aparecido los morichales, a causa de un aumento notable de la frecuencia de los incendios locales. Una situación similar se observó en la localidad de Urué, a unos 40 km de la Laguna Encantada, donde se registraron incendios locales intensos hasta los 1.000 años BP y después prácticamente cesaron (Rull, 1999). A pesar de ello, el bosque no se recuperó, ni siquiera con la llegada de un período de clima más húmedo que, por el contrario, llevó al establecimiento de un morichal. La explicación podría estar, una vez más, en la degradación progresiva del suelo (Fölster *et al.,* 2001; Dezzeo & Chacón, 2005). Una conclusión extraída de la secuencia de Urué es la condición de *Mauritia* como colonizadora secundaria de terrenos quemados, en caso de existir la suficiente humedad como para mantener el suelo saturado de agua. El efecto del fuego consistiría básicamente en eliminar las especies de bosque potencialmente competidoras y dejar el terreno libre para los morichales (Rull, 1998*a*). En la Laguna Encantada, las condiciones necesarias de humedad para el establecimiento de los morichales se dieron en más de una ocasión, especialmente durante el Holoceno Medio, pero estas comunidades sólo prosperaron a partir de ~1.200 años cal BP, a pesar de la ausencia de bosques *in situ*. Esto sugiere que el clima no es el único condicionante y apoya indirectamente la hipótesis de Rull (1998*a*), según la cual, el área de distribución de *Mauritia* se habría reducido mucho durante la última glaciación, de forma que su lenta expansión postglacial no habría alcanzado la GS hasta el Holoceno Tardío.

4.6. Conclusiones

La formación dominante en la zona de estudio desde el Holoceno Temprano (*ca*. 7.500 cal BP), hasta el presente ha sido una sabana, que ha sufrido cambios en su composición taxonómica debido a variaciones en las condiciones ambientales y al régimen de incendios. Las variaciones paleoambientales y de vegetación registradas durante el Holoceno se han correlacionado con registros paleoambientales de otras áreas del norte de Sudamérica, lo que ha permitido reconocer tendencias regionales neotropicales a escala de milenios, como por ejemplo el periodo de mayor balance hídrico del Holoceno Medio (*ca*. 4.000 cal BP), y de condiciones más secas a partir de2.500 años cal BP. El incremento del balance hídrico del Holoceno Medio coincide con un aumento de la riqueza y la diversidad taxonómica, sobre todo en elementos de bosque. Las variaciones ambientales, principalmente los cambios en el balance hídrico, no han sido las únicas responsables de los cambios de vegetación, ya que el fuego ha ejercido un efecto de perturbación, sobre todo durante los últimos 1.200 años. Las comunidades vegetales actuales se establecieron más o menos en esa fecha, coincidiendo con la intensificación de los incendios locales. La estrecha relación entre la presencia de fuegos locales y la aparición y expansión de los morichales, observado en diversas localidades de la GS, sugiere que *Mauritia* podría considerarse una planta pirófila. El efecto que el fuego ha tenido sobre la vegetación difiere, según la comunidad que se considere. Así, en los bosques provoca una reducción e impide su posterior reexpansión, mientras que favorece la expansión de sabanas y morichales. En el caso de los últimos, podría afirmarse incluso que es necesario, a la vista de las evidencias recopiladas hasta el momento en la GS. La sabana, por su parte, no sólo es favorecida por el fuego, sino también por las condiciones climáticas y la degradación del suelo, sobre todo en relación a los nutrientes. Los resultados de este trabajo, junto con estudios anteriores, apoyan la hipótesis de un origen mixto, con el clima y el fuego como principales factores, de las actuales sabanas de la GS. Para una visión ecológica más precisa de los procesos implicados en los cambios de vegetación, es necesario aumentar la resolución del registro, mediante el análisis de muestras intermedias a las utilizadas en este estudio.

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CHAPTER 5:

Forest-savanna-morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia.

> *Ninguna orden de inteligencia divina une*
> *a las especies. Los lazos naturales son genealógicos*
> *junto a caminos contingentes en la historia.*
> Stephen Jay Gould.

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ABSTRACT

The southern Gran Sabana (SE Venezuela) holds a particular type of neotropical savanna characterized by the local occurrence of *morichales* (*Mauritia* palm swamps), in a climate apparently more suitable for rain forests. We present a paleoecological analysis of the last millennia of Lake Chonita (4º39'N - 61º0'W, 884 m elevation), based on biological and physico-chemical proxies. Savannas dominated the region during the last millennia, but a significant vegetation replacement occurred in recent times. The site was covered by a treeless savanna with nearby rainforests from 3640 to 2180 cal yr BP. Water levels were higher than today until about 2800 cal yr BP. Forests retreated since about 2180 cal yr BP onwards, likely influenced by a higher fire incidence that facilitated a dramatic expansion of *morichales*. The simultaneous appearance of charcoal particles and *Mauritia* pollen around 2000 cal yr BP supports the potential pyrophilous nature of this palm and the importance of fire for its recent expansion. The whole picture suggests human settlements similar to today -in which fire is an essential element- since around 2000 years ago. Therefore, present-day Gran Sabana landscapes seem to have been the result of the synergy between biogeographical, climatic and anthropogenic factors, mostly fire.

Keywords: Fire; Gran Sabana; Human occupation; Last millennia; Charcoal; *Mauritia*; Neotropics; Paleoecology; Vegetation change.

5.1. Introduction

Savannas are among the most important vegetation formations of the American tropics (Huber, 1987). Palynological studies show that neotropical savannas have been common during the Holocene, especially in the lowlands (e.g. Wymstra and van der Hammen, 1966; Behling and Hooghiemstra, 2001), and emphasize the importance of the last millennia for the shaping of present savanna landscapes (Rull, 1992, 1999; Behling and Hooghiemstra, 1998). In northern South America, neotropical savannas are mainly shared between Colombia (Llanos Orientales) and Venezuela (Orinoco Llanos). In addition, there is another relatively large savanna extension between Venezuela, Brazil and Guyana, which in Venezuela is called the Gran Sabana (Huber, 1995b), lying on a mid-altitude plateau, where the present study is located (Figure 5.1).

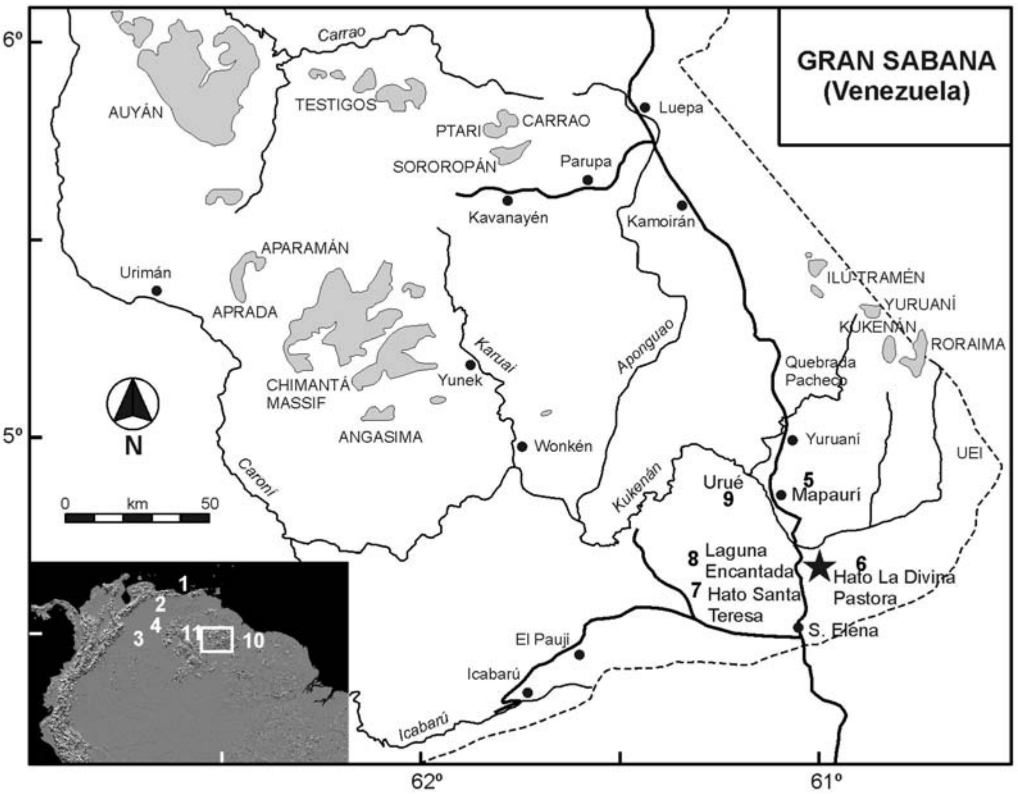

Figure 5.1. Location of the study area and its position within northern South America. (Radar image courtesy of NASA/JPL-Caltech). The coring site is indicated by a star. Numbers indicate the sites with paleoecological information mentioned in the text: 1 - Cariaco Basin (Venezuela); 2 - Lake Valencia (Venezuela); 3 - Colombian Llanos; 4 - Orinoco savannas (Venezuela); 5 - Mapaurí (Gran Sabana); 6 - Divina Pastora (Gran Sabana); 7 - Santa Teresa (Gran Sabana); 8 - Lake Encantada (Gran Sabana); 9 - Urué (Gran Sabana); 10 - Rupununi savannas (Guyana); and 11 - Canaima (Gran Sabana).

Although there are several high resolution paleoecological and paleoclimatic studies of the last millennia in Venezuela (e.g. Rull *et al.*, 2010a), records of this type are scarce in the Gran Sabana (GS). Previous paleoecological studies reveal that during the Late Glacial and Holocene, the GS experienced several climatic and vegetation changes. For example, a pronounced and relatively rapid vegetation shift occurred during the Younger Dryas, which ended with the establishment of treeless savanna. This coincided with variations in the hydrological balance (precipitation/evaporation ratio) and possibly with temperature (Montoya *et al.*, 2011). The Mapaurí record (Fig. 5.1), showed a dramatic change from cloud forests to savannas at the beginning of the Holocene, also linked to temperature and moisture changes (Rull, 2007).

In both cases, fire seems to have played a potentially important role in the vegetation change. Two other middle Holocene records from the Divina Pastora (DV) and Santa Teresa (ST) localities show that, during the last five thousand years, the landscape was dominated by treeless savannas. However, forests were located close to these sites and/or expanded their range between 5400 and 4100 cal yr BP in DV, and 5100 to 3900 cal yr BP in ST. After this time, the climate became drier and the forest extension decreased in size (Rull, 1992). Wetter conditions returned by 2700 cal yr BP, which resulted in the establishment of modern *morichales* (palm swamps dominated by the palm *Mauritia flexuosa*), rather than the expansion of forests. Similar results were obtained in the Encantada pollen record, with the initiation of *morichal* around 1200 cal yr BP (Montoya *et al*., 2009). In a nearby site called Urué (Fig. 5.1), the vegetation trends during the last two millennia could be reconstructed in more detail. At the beginning of this period, around 1700 cal yr BP, several recurrent forest fire events triggered a secondary succession that determined a significant forest reduction and the expansion of savannas, as well as the establishment of *morichales* (Rull, 1999). This study highlighted the effect that fires had upon Gran Sabana vegetation and the low resilience of its forests. Based on the available evidence, it could be assumed that both climatic oscillations and fire have had similar effects over the GS vegetation, that is, the reduction of forest cover and the expansion of savannas, with the establishment of *morichales*, thus shaping the nowadays GS landscape (Rull, 1992). According to Rull (1998b), the *morichales*, a unique neotropical vegetation type strongly linked to poorly drained and seasonally flooded soils at altitudes below around 1000 m, would have been expanding their range since the Last Glacial Maximum, favored by both climate and fire. Montoya *et al*. (2009) hypothesize that *M. flexuosa* would be considered a pyrophilous element, as it is an active colonizer of river margins where gallery forests have been removed by fire.

In this paper, we report the paleoecological study of a lake sediment core from Lake Chonita, in the southern GS, based on pollen and spore analysis, as well as charcoal and non-pollen palynomorphs (NPP), and some physico-chemical measurements (magnetic susceptibility, bulk density and organic matter concentration). The aim is to reconstruct the vegetation changes that occurred during the last three millennia, to analyze the savanna/*morichal* dynamics and the shaping of present-day GS landscapes, as well as to discuss the potential paleoclimatic and/or anthropogenic forcings involved, with emphasis on human occupation timing and fire regimes. The implications of these results for *Mauritia* biogeography, in a regional northern South America context, are also discussed.

5.2. Study Area

The GS is a vast region of about 18,000 km^2 located in SE Venezuela (4º36’ to 6º37’N and 61º4’ to 74º2’W, Fig. 5.1). The GS is part of an undulated erosion surface developed on the Precambrian Roraima quartzites and sandstones, and forms an *altiplano* slightly inclined to the south, ranging from about 750 to 1450 m elevation (Briceño and Schubert, 1990; Huber, 1995a). The climate has been described as submesothermic ombrophilous, with annual average temperatures of around 18 to 22ºC and precipitation values of 1600 - 2000 mm yr^{-1}, with a dry season (<60 mm/month) from December to March (Huber and Febres, 2000). Concerning vegetation, the GS is a huge island of savanna within the normally forested Guayana landscape. These savannas form wide and more or less continuous treeless grasslands, locally intermingled with forests developing typical forest-savanna mosaics (Huber, 1994). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b) has lead to several hypotheses related to edaphic conditions, climate changes, and anthropogenic fires (Eden, 1974; Fölster, 1986; Rull, 1999; Fölster *et al*., 2001; Dezzeo *et al*., 2004; Huber, 2006).

The GS savannas are dominated by C_4 grasses of the genera *Axonopus* and *Trachypogon*, with sedges such as *Bulbostylis* and *Rhyncospora*; woody elements are scarce and rarely emerge above the herb layer (Huber, 1995b). According to Huber (1994), there is a special type of plant formation (locally called *morichal*) where the herbaceous stratum remains ecologically dominant (treeless savanna), but the palm *Mauritia flexuosa* forms characteristic monospecific stands. This association is especially common around lakes, and in the bottom of river valleys and flooded depressions of the southern GS, up to about 1000 m elevation (Huber, 1995b). Most GS forests are considered to fall within the category of lower montane forests (also called submesothermic forests, between 800 and 1500 m elevation), because of their intermediate position between lowland and highland forests (Hernández, 1999). Common genera include: *Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignoniaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Clathrotropis* (Fabaceae), *Aspidosperma* (Apocynaceae), *Caraipa* (Clusiaceae), *Dimorphandra* (Caesalpiniaceae), *Byrsonima* (Malpighiaceae), etc., and their composition varies with elevation (Huber, 1995b). The GS shrublands usually occur between 800 and 1500 m elevation and are more frequent at the northern area than at the southern part (Huber, 1995b), where our study site is located. The more common shrub genera are: *Euphronia* (Euphroniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Ochthocosmus* and *Cyrillopsis* (Ixonanthaceae), *Thibaudia, Notopora* and *Befaria* (Ericaceae), *Spathelia* (Rutaceae), *Byrsonima* (Malpighiaceae), etc. They usually grow on a rocky, sandstone substrate or deep white sands of alluvial origin (Huber, 1995b).

The GS region is the homeland of the Pemón indigenous group, from the Carib-speaking family. Today they are sedentary, living in small villages, usually in open savannas. Though the GS population density is currently low, the indigenous settlements have experienced an expansion since the arrival of European missions, and today, more than 17,000 people live in the GS (Medina *et al*., 2004). Fire is a key component of the Pemón culture as they use it every day to burn wide extensions of savannas, and occasionally, forests (Kingsbury, 2001). The reasons for the extent and frequency of these fires are related to activities such as cooking, hunting, fire prevention, communication, magic, etc (Rodríguez, 2004; 2007). Surprisingly, land use practices, such as extensive agriculture or cattle raising, typical of other cultures strongly linked to fire, are not characteristic of the Pemón culture (Rodríguez, 2004). According to the available evidence, the Pemón seem to have reached the GS very recently, probably around 300 years ago (Thomas, 1982; Colson, 1985), but an early occupation could not be dismissed. There is some archaeological evidence consisting of pre-Hispanic remains (spearheads and bifacial worked knives) similar in style to others from about 9000 years old found at other Venezuelan localities (Gassón, 2002; Rostain, 2008). In addition, palynological evidence indicating the occurrence of intense and extensive fires during the Younger Dryas (around 12,400 cal yr BP), suggested a potential early human occupation of the GS (Montoya *et al*., 2011). However, a definitive assessment is not yet possible.

5.3. Materials and Methods

Lake Chonita (4º39’N - 61º0’W, 884 m elevation) is located within a private farm called “Hato Divina Pastora” near Santa Elena de Uairén, at the south of the GS region (Fig. 5.1). The annual precipitation in Santa Elena, at 910 m altitude, is about 1700 mm, with a weak dry season from December to March (Huber, 1995a). The lake is within a treeless savanna landscape, surrounded by scattered *morichal* patches. In the absence of a known local name for the lake, it will be called Lake Chonita for the purposes of the present study, to be consistent with previous studies developed at the same site (Montoya *et al*., 2011).

The core (PATAM1 B07; 4.67 m long) was obtained in the deepest part of the lake (3.13 m water depth), using a modified Livingstone squared-rod piston core (Wright *et al.,* 1984). The present study is focused on the detailed analysis, and paleoecological interpretation, of the last three millennia interval (0.03 to 0.97 m). A total of 9 samples were taken along the whole core for radiocarbon dating, 3 of them falling within the interval discussed here. Samples were pretreated using standard acid-base-acid procedures (Abbott and Stafford, 1996) and measured at the AMS Radiocarbon Laboratory of the University of California, Irvine (UCI) and Beta Analytic (Beta). Calibration was made using CALIB 6.0.1 and the IntCal09.14c database (http://calib.qub.ac.uk./calib/, last accessed on April 2010).

Twenty-eight volumetric samples (2 cm^3) were taken in the section studied, at 2-5 cm intervals, for pollen analysis. These samples were processed using standard palynological techniques slightly modified according to the sediment nature (Rull *et al.*, 2010b), after spiking with *Lycopodium* tablets (batch 177745, average 18,584 ± 1853 spores/tablet). The slides were mounted in silicone oil without sealing. Pollen and spore identification was made according to Hooghiemstra (1984), Roubik and Moreno (1991), Tryon and Lugardon (1991), Herrera and Urrego (1996), Rull (1998a; 2003) and Colinvaux *et al*. (1999). Counts were conducted until a minimum of 300 pollen and spores were tabulated (excluding Cyperaceae and aquatic plants: *Myriophyllum*, *Sagittaria* and *Utricularia*), but counting continued until the saturation of diversity was reached (Rull, 1987). Final counts averaged 533 grains per sample. Pollen taxa were grouped according to the vegetation types previously described (Huber, 1986; 1989; 1994; 1995b; Huber and Febres, 2000). All identified pollen taxa were included into the pollen sum, except for Cyperaceae and the aquatic plants mentioned above. Pollen diagrams were plotted with *PSIMPOLL 4.26*, using a time scale derived from an age-depth model based on radiocarbon dating, developed with the *clam.R* statistical package (Blaauw*,* 2010). The pollen zonation was performed by Optimal Splitting by Information Content (OSIC), and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Only pollen types over 0.4% were considered for zonation. Interpretation was based on comparison with modern samples from previous studies (Rull, 1992, 1999) and the known autoecology of taxa found (Marchant *et al*., 2002; Rull, 2003). NPP were analyzed on pollen slides, and plotted in percentages based on pollen sum. NPP identification was made according to Montoya *et al*. (2010) and literature therein. Charcoal counts were carried out in the same pollen slides, considering two size classes (Rull, 1999):

- Type I (smaller microcharcoal particles: 5 - 100 µm): used as proxy for mostly regional fires, because of their easy dispersion by wind.
- Type II: (larger microcharcoal particles: >100 µm): used as proxy for local fires.

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

5.4. Results

5.4.1. Lithology and chronology

The lacustrine sequence is characterized, in the studied section, by dark-brown organic-rich sediments. The upper part of the section is characterized by slightly higher magnetic susceptibility values than the lower one, with a major peak between ~30-24 cm and a minor peak in the upper 10 cm (between 8.5 and 1.5 cm). The organic matter data shows changes in the relative amounts of organic matter and terrigenous (mineral) sediments in the core (Fig. 5.2). Generally, sections with high dry bulk density (Fig. 5.2) also have lower organic matter and high in terrigenous sediments. Dry BD shows a high variability and presents its maximum values between ~30-24 cm, coinciding with the major MS peak. Organic matter is characterized by a fluctuating trend followed by an abrupt increase in the upper 20-10 cm of the record.

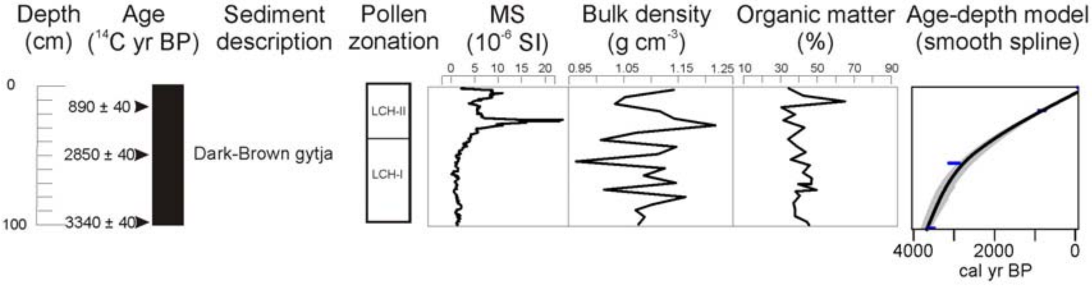

Figure 5.2. Core stratigraphy, with radiocarbon ages (in radiocarbon years, uncalibrated ages) and sediment description; pollen zones, physical parameters curves and age-depth model of the study section. MS: Magnetic susceptibility.

The results of AMS radiocarbon dating were used to produce an age-depth model for the sequence (Table 5.1). The best fit was obtained with a smooth-spline function (Blaauw, 2010), and is represented in Figure 5.2 only for the interval of interest of this study. The sedimentation rate of the whole sequence varies between 0.02 and 0.17 cm yr^{-1}. For the interval studied here, the sedimentation rate ranges between 0.02 and 0.08 cm yr^{-1}. The time interval between samples ranges from 60 to 150 years.

Table 5.1. AMS radiocarbon dates used for the age-depth model for the whole record. Asterisks mark the dates included in the interval under study. The estimated ages have been extracted from the calibrated ages (WA: Weighed average).

Laboratory	Sample	Depth (cm)	Sample Material	Age (yr C^{14} BP)	Age (cal yr BP) 2σ	Age (cal yr BP) estimation(WA)
Beta - 279600*	PATAM1_B07/3	13	Pollen extract	890 ± 40	731 - 915	800
Beta - 277185*	PATAM1_B07/11	51	Pollen extract	2850 ± 40	2855 - 3078	2730
Beta - 277184*	PATAM1_B07/22	98	Pollen extract	3340 ± 40	3471 - 3643	3660
UCI - 43705	PATAM1_B07/32	144	Wood	4080 ± 40	4497 - 4655	4640
UCI - 43706	PATAM1_B07/49	212	Wood	6465 ± 25	7323 - 7403	7380
Beta - 277186	PATAM1_B07/70	298	Pollen extract	9590± 60	10,738 - 11,164	10,690
UCI - 43537	PATAM1_B07/87	362	Wood	9720 ± 70	11,063 - 11,251	11,380
Beta - 247284	PATAM1_B07/93	392	Wood	10,440 ± 40	12,128 - 12,530	12,340
UCI - 43614	PATAM1_B07/99	402	Wood	11,005 ± 45	12,699 - 13,078	12,740

5.4.2. Palynological zonation

The pollen diagram is dominated by pollen assemblages from two different herbaceous plant formations: a treeless savanna, with a nearby forest in the lower part; and a savanna with *morichal*, coinciding with a decrease in forest elements, in the upper half (Figure 5.3). The pteridophyte spores are not very abundant, though psilate triletes and monoletes are better represented than others. Regarding NPP, *Botryococcus, Coniochaeta cf. ligniaria* and *Neorhabdocoela* oocites are the more abundant (Figure 5.4). The stratigraphic variations of the pollen and spore assemblages allowed subdivision of the diagram into two zones:

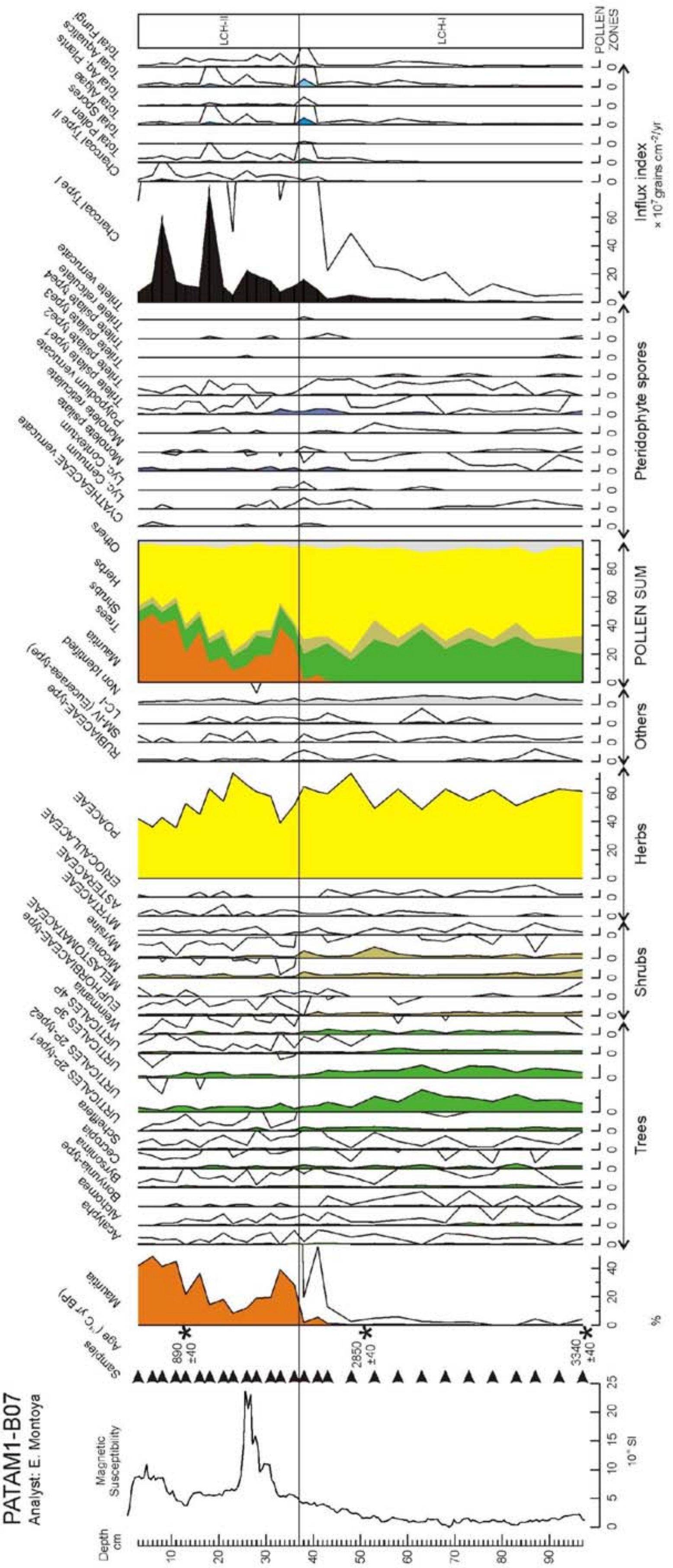

Figure 5.3. General pollen diagram expressed in percentages. Solid lines represent x10 exaggeration.

5.4.2.1. LCH-I (97 - 37 cm, 14 samples)

The pollen assemblage is clearly dominated by Poaceae, which presents fluctuating values ranging from 40 to 70% of the total pollen sum, followed by trees (mainly Urticales) (Fig. 5.3). Some forest elements are also present at high to medium abundances, as for example Urticales (the more abundant of them), *Alchornea*, *Byrsonima*, *Cecropia*, Euphorbiaceae-type, *Miconia*, *Myrsine* and *Weinmannia*. *Mauritia* appears at the top of the zone, though with low abundance. The percentages of pteridophyte spores are low, but a slight increasing trend can be observed in psilate monoletes and psilate triletes at the top of the zone. Smaller charcoal particles (5 - 100 µm) remain at low abundances, with an increase at the top of the zone, coinciding with the first appearance of larger particles (> 100 µm). Regarding influx index, it can be observed that all proxies studied show local peaks of different magnitude at the top of the zone. Among aquatic elements (algal remains and aquatic or semi-aquatic plants; Figure 5.4), *Botryococcus* is the dominant, with strong fluctuations in its concentration and a sharp decrease in the upper part of the zone. Type 91 (HdV. 91) shows an increase at the upper part of the zone, and *Spirogyra* peaks at the top. Cyperaceae are also abundant, with minor variations, and *Sagittaria* shows a slightly decreasing trend at the upper part of the zone. Regarding fungal spores and other NPP, the more abundant are *Coniochaeta* cf. *ligniaria*, *Neorhabdocoela* oocites, *Cercophora*-type and *Sordaria*-type, thought Sordariales also presents a peak at the lower part of the zone (Fig. 5.4).

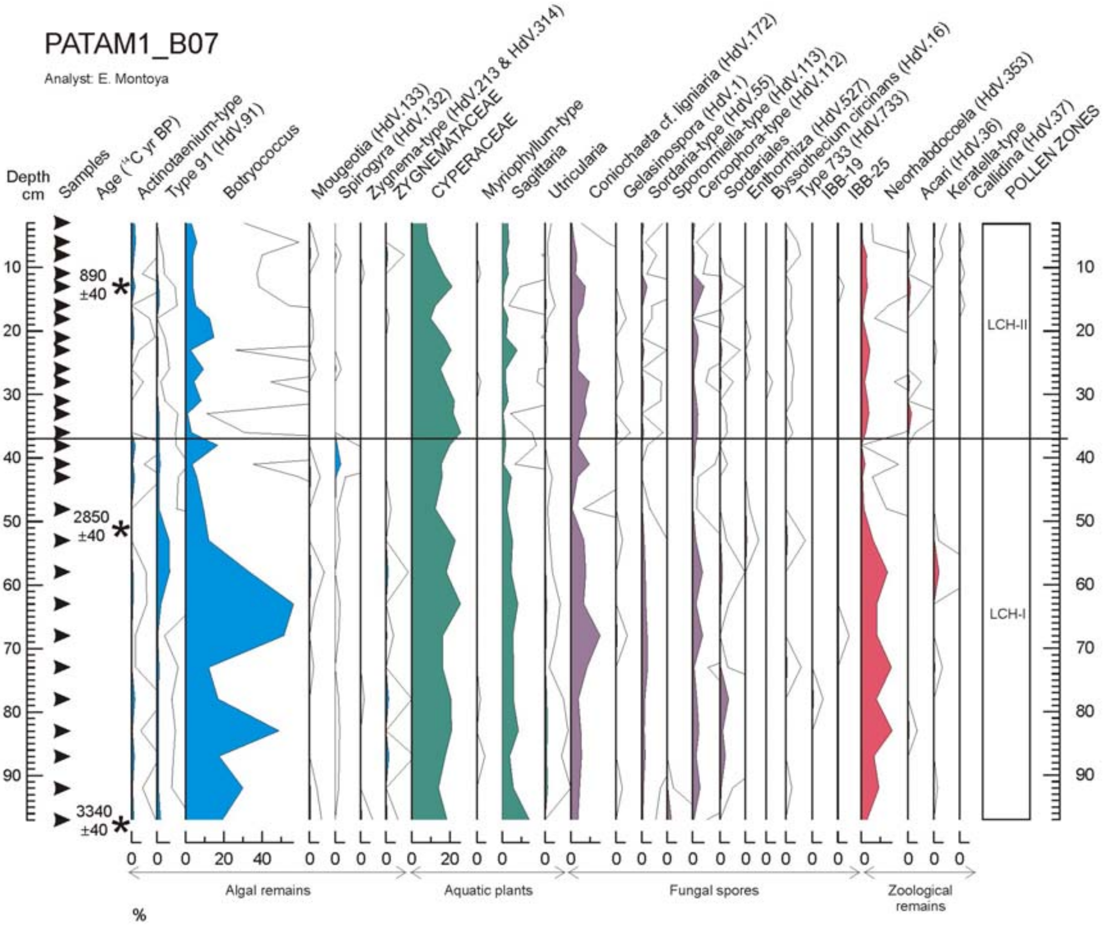

Figure 5.4. General non-pollen palynomorphs (extra pollen sum taxa) diagram expressed in percentages respect to pollen sum. Solid lines represent x10 exaggeration. HdV: Hugo de Vries Lab; IBB: Institut Botànic de Barcelona.

5.4.2.2. LCH-II (37 - 3 cm, 14 samples)

The pollen assemblage is marked by an abrupt increase of *Mauritia* likely at the expense of trees, in the lower half of the zone, and of trees and Poaceae in the upper part, from around 35 cm upwards (Fig. 5.3). There is a decrease of *Mauritia* and a return to the former higher values of Poaceae in the intermediate part of the zone (32 - 18 cm). Above this depth, *Mauritia* increases again synchronously with a decrease in Poaceae. There is a general decreasing trend of nearly all the forest elements, which in some taxa, as *Alchornea* and *Bonyunia*-type, represent almost their complete disappearance. Pteridophyte spores remain at similarly low values to the previous zone. Psilate triletes has higher values at the base of the zone, showing a slightly decreasing trend from ~30 cm upwards. Smaller charcoal particles maintain the increasing trend initiated at the upper part of the previous zone, and experience three abrupt peaks, the first one around 32 to 23 cm, and the other two, of higher magnitude, at 18 and 8 cm, respectively (Fig. 5.3). Larger charcoal particles remain low at the beginning of the section, and show a pattern similar to smaller particles, but significantly lower in magnitude, throughout the zone. All the biological proxies analyzed show an increase in their influx indices, except for pteridophyte spores. Aquatic elements and fungal spores and other NPP are characterized by lower abundances respect to the former zone, except for Cyperaceae, which show similar values (Figure 5.4). The correlation between *Mauritia* and total charcoal influx index curves (Figure 5.5) was performed, obtaining an R value of 0.718, which is significant for $\alpha < 0.001$.

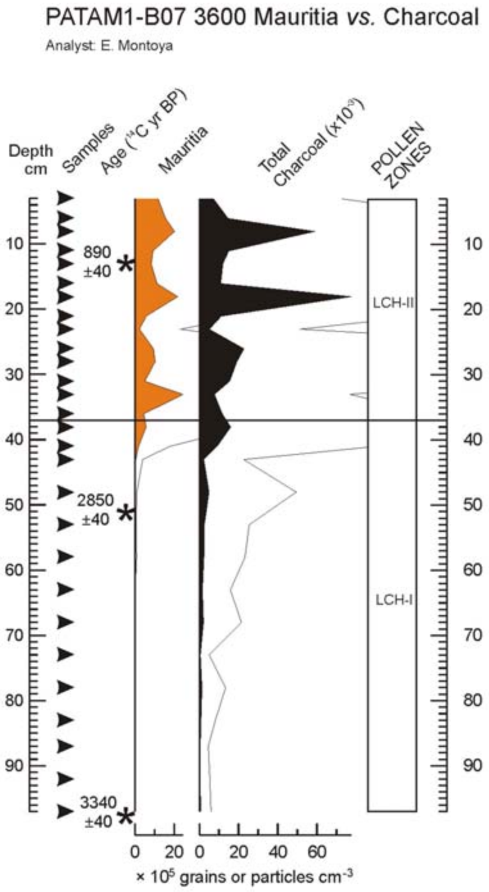

Figure 5.5. Influx index diagram of *Mauritia* pollen and total charcoal particles. Solid lines represent x10 exaggeration.

5.5 Discussion

The region around Lake Chonita has remained a savanna during the last three millennia, but a significant vegetation change occurred around 2000 years ago. Indeed, prior to 2180 cal yr BP, a treeless savanna landscape with nearby forests dominated the site, but the last two millennia have been characterized by forest retraction and the establishment of a *morichal*, which remains until present. The paleoecological sequence is discussed in the following sections in the context of northern South American savannas, and the contribution of these results to the understanding of the fire-vegetation relationships at South GS.

5.5.1. Paleoecological interpretation

5.5.1.1. 3640 to 2180 cal yr BP

The sedimentary features and the presence of aquatic organisms indicate that the lake probably was already established prior to 3640 cal yr BP. The pollen assemblage of this zone indicates a treeless savanna landscape without *morichales*. The abundance of forest elements suggests that this formation was probably closer and/or more expanded than today. The continued presence of smaller charcoal particles -indicative of regional fires- together with the continuous presence of *Cecropia* -a secondary colonizer- may indicate some regional fires of low intensity occurred. The lack of coarse charcoal indicates local fires did not occur. The first appearance of larger microcharcoal particles, as proxies for local fires, were recorded at ~2400 cal yr BP. This occurred synchronously with the first appearance, though at low values, of *Mauritia* pollen, and an increase in psilate triletes. These spores have been related with early stages of secondary succession after fire, in other sites of the GS (Rull, 1999). The high values of *Botryococcus* and *Neorhabdocoela* oocites from 3640 to 2800 cal yr BP suggest that lake levels were stable. During this time period climate might have varied from a higher water balance prior to 2800 cal yr BP to lower moisture availability from this date to the end of the interval, as indicated by the lower values of aquatic organisms, mainly *Botryococcus* and *Neorhabdocoela*. This is in agreement with the Encantada record (Montoya *et al*., 2009), but it does not coincide exactly with other GS records, as for example DV or ST (Rull, 1992). Dating inconsistencies in previous records derived from the use of large quantities of bulk sediment for dating using conventional radiocarbon methods instead of AMS techniques, and the few dates available for a sound age-depth model can not be dismissed for this time interval.

Similar trends regarding water levels and climate have been observed in some paleoecological and paleoclimatic records from northern South America. For instance, Lake Valencia (Fig. 5.1) had higher water levels from 6000 to 3000 ^{14}C yr BP (~6840 to 3200 cal yr BP), except for a short interval of lower lake levels centered at 3300 ^{14}C yr BP (~3550 cal yr BP) (Bradbury *et al*., 1981; Leyden, 1985; Curtis *et al*., 1999). From this, some of these authors inferred a high precipitation/evaporation ratio (P/E) determined by higher insolation and changes in the latitudinal position of the Intertropical Convergence Zone (ITCZ) (Curtis *et al*., 1999). Haug *et al*. (2001) inferred a decrease in precipitation from 5350 cal yr BP in the Cariaco Basin (Fig. 5.1), with large century-scale variations between ~3750 to 2750 cal yr BP. In the Colombian Llanos Orientales, a wetter interval was suggested for the middle Holocene, peaking around 4000 cal yr BP (Marchant and Hooghiemstra, 2004). Such climatic inferences were supported by evidence of forest expansion in different records (e.g. Behling and Hooghiemstra, 1998, 1999, 2000; Berrío *et al*., 2002). Contrarily, the Rupununi savannas of Guyana (Fig. 5.1), would have had a continuous presence of treeless savanna since the middle Holocene, with an increase in Poaceae around 3000 ^{14}C yr BP (~3200 cal yr BP) (Wymstra and van der Hammen, 1966).

Therefore, a likely forest expansion in the present savanna areas of northern South America prior to 3000 cal yr BP, probably linked to an increase in moisture, seems to be supported by the available evidence. The regional differences found in nearby locations could be related to local climate variations.

5.5.1.2. 2180 cal yr BP to present

The beginning of this time interval was marked by an abrupt local vegetation change, though the general GS landscape continued to be dominated by treeless savannas. The sudden increase of *Mauritia* coincides with a decrease of Poaceae and forest elements. While Poaceae abundance returned to former values at *ca.* 1920 cal yr BP, the forest did not show any recovery until the present. The increase in fire incidence during this interval could have been decisive in this sense, favoring the establishment of *morichal* communities, as suggested by several former studies (Rull, 1992, 1998b, 1999; Montoya *et al*., 2009). The potential establishment of a drier regional climate since 2800 cal yr BP (Bradbury *et al*., 1985; Curtis *et al*., 1999; Berrío *et al*., 2000, 2002; Behling and Hooghiemstra 2001; Wille *et al*., 2003), might indicate some level of climatic influence (or a synergistic fire-climate coupling) on forest retraction. The treeless savanna expanded again from 1920 to 1120 cal yr BP, synchronously with a decrease of *Mauritia* abundance. At the same time, there is a major peak in MS and BD curves. Such synchrony could be interpreted as a higher input of terrigenous sediments to the watershed due to erosion processes caused by the existence of a more open landscape resulting from *Mauritia* clearing. After that, two major charcoal peaks recorded at *ca.* 1120 and 480 cal yr BP coincide with the *morichal* expansion. Thus, it is suggested that the present-day landscape around Lake Chonita was established around 1120 cal yr BP. The MS minor peak occurred this time paralleled the *Mauritia* increase and is dated *ca*. 500 to 50 cal yr BP, which is synchronous with the Little Ice Age (LIA) recorded in the Venezuelan Andes, as a cool and humid interval linked to solar activity cycles (Polissar *et al*., 2006). In Lake Chonita, the only potential evidence for more humid conditions is the *Mauritia* increase at the top. However, aquatic elements indicate that during the whole interval moisture conditions were more or less stable, and similar to present-day, with minor variations, so a definitive interpretation can not be made.

The recent appearance and sudden increase of *Mauritia*, or the establishment of present-day *morichales*, coinciding with an increased fire incidence have also been reported in most sequences in the GS (e.g.: DV, ST, Urué and Encantada) (Rull, 1992, 1999; Montoya *et al*., 2009). Sudden increases of *Mauritia* and/or slightly drier climate than mid Holocene relative to the last millennia have also been reported in several studies in nearby areas. In the Venezuelan Llanos, *Mauritia* presence was also reported only for the last two millennia, in a climate likely more humid than the previous interval (Leal *et al*., 2002, 2003). In the Colombian Llanos, the same trends have been observed, during the last two millennia, in several localities (Behling and Hooghiemstra, 1998, 1999, 2000, 2001; Berrío *et al*., 2000, 2002; Wille *et al*., 2003). Hence, there is a general agreement regarding the influence of increased human impact, usually through fire, in the establishment of *morichales*, and the shaping of the present savanna landscapes during the last two millennia.

5.5.2. *Mauritia*, climate, fire, and human occupation in the GS

Several studies developed in the GS have revealed the continuous persistence of savannas since at least the early Holocene (Rull, 2007; Montoya *et al*., 2011). However, the taxonomic composition of this biome has shown the dynamic nature of its plant communities.

This is the case of *morichales*, whose occurrence has been traditionally considered indicative of warm and wet lowlands (and midlands) of northern South America. As a consequence, *morichal* expansions observed in paleoecological records have been generally interpreted in terms of wetter climate (e.g. Rull, 1992, 1999; Behling and Hooghiemstra, 1999; Berrío *et al*., 2000; Leal *et al*., 2002, 2003). The appearance and expansion of *Mauritia*-dominated communities in the Colombian Llanos Orientales (Fig. 5.6), likely agree with this climatic interpretation. Thereby, this palm was recorded for first time around the middle Holocene, where a wet period was documented for the region (Marchant and Hooghiemstra, 2004). In our study, however, the recent *morichal* expansion occurred in a climate drier than the preceding phase which, at first, seems contradictory. Nevertheless, this evidence also suggests that climate is not the only factor affecting the *morichal* occurrence and distribution at GS, which appears to be linked more strongly to fire incidence or to fire-climate synergies (Fig. 5.5). The synchrony between increased fire frequency and *morichal* establishment recorded in several GS sequences together with the correlation degree obtained, as well as the common presence of charcoal particles in palynological slides, supports this view. This is in agreement with the absence of *Mauritia* palm swamps during the Holocene in the GS, despite the occurrence of periods of higher moisture availability, and its later expansion during phases of high fire incidence (e.g. Montoya *et al*., 2009). This supports the assumed pyrophilous character of *Mauritia* and the *morichales* it forms (Montoya *et al*., 2009). Another potential factor involved would be geographical. According to Rull (1998b) *Mauritia* has been expanding its range since the end of last glaciation, so it is possible that this palm did not reach the GS until the last two millennia. This would also help to explain its former absence in the GS during Holocene periods, with assumedly optimal ecological conditions, when it was indeed present in the Colombian Llanos Orientales (Fig. 5.6). Overall, this suggests that the present-day distribution of this palm could be the result of a synergism between biogeography (post-glacial expansion), climate (humid conditions) and human disturbance (fire). Unfortunately, the lack of charcoal data for most of the available neotropical records prevents a regional synthesis of the potential effect of fire upon *Mauritia* communities.

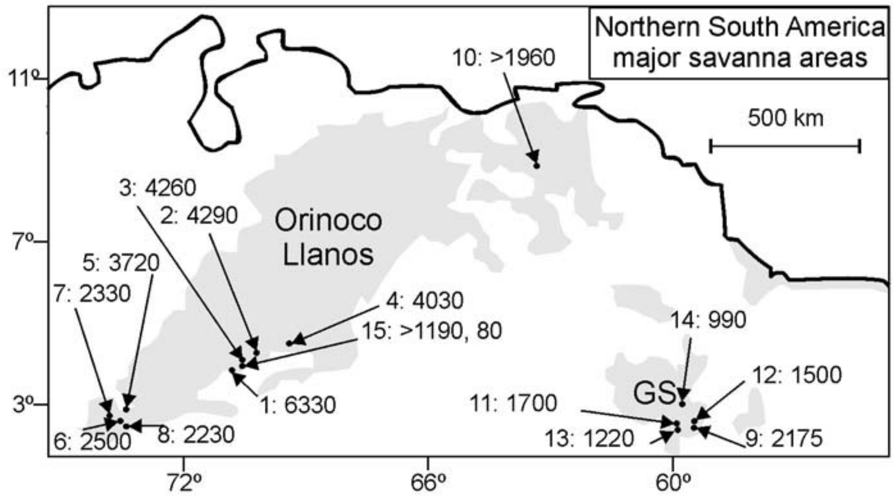

Figure 5.6. Location of sequences where *morichal* establishment has been reported in northern South American savannas. Map extracted from Behling and Hooghiemstra (2001) and Eva *et al*. (2004); present-day savanna areas are marked in grey. Numbers are referred to: *(i)* the sequences properly, they are ordered chronologically and showed at Appendix C; and *(ii)* the age (expressed in cal yr BP) of the *morichal* establishment. GS: Gran Sabana; > marks those localities where *morichales* were present at the beginning of the record, so the palm establishment must have occurred earlier. See Appendix C for all information related.

The existing evidence suggests that fire is a key factor to understand the GS environmental history. As mentioned before, the GS has been the homeland of the Pemón indigenous group at least during the last 300 yr. The intensive and extensive use of fire by this culture is well documented (Kingsbury, 2001; Rodríguez, 2004; 2007), and has been often related to the current extension of savannas and forests (Dezzeo *et al.*, 2004; Huber, 2006). The results presented here do not show any increase in fire frequency during the last 300 years, rather a slight decreasing trend (Figs. 5.3 & 5.5). However, a higher resolution study of the upper section would clarify this point. The last charcoal peak recorded in the sequence is dated around *ca.* 480 cal yr BP (8 cm depth), prior to the assumed Pemón arrival, and coeval with the first Spanish colonizers. The high amount of charcoal in different neotropical records has been postulated as indicative of human settlements, even in the absence of changes in land use (Bush *et al.*, 2007). Moreover, there is some archaeological evidence of human populations synchronous with charcoal peaks around the Orinoco Basin, frequently located close to water courses (e.g.: Saldarriaga and West, 1986). The continuous presence of local fires at Lake Chonita since about 2000 years ago (Figs. 5.3 & 5.5), suggests an earlier human occupation of the lake catchment. If so, one possible scenario is that once humans arrived, they made fires for different reasons, and the forest suppression favored the *morichal* establishment where edaphic conditions were suitable. In this case, humidity seems to have played a minor role in the palm establishment, due to the time elapsed between the decrease in water levels and the *Mauritia* expansion (Figs. 5.3 & 5.4). Conversely, the synchrony between increases in charcoal and *Mauritia* after 2000 yr ago point to this possible early human settlement at South GS, not necessarily of the Pemón culture, but a similar culture at least in regard to the use of fire. The extensive use of palms by many indigenous cultures from the Neotropics supports this assumption (Heckenberger and Neves, 2009).

5.5.3. Biogeographic considerations on *Mauritia*

Given the results presented here, some considerations regarding *morichal* communities seem pertinent. Figure 5.6 shows the age of modern-day *Mauritia* community establishment in different paleoecological records from northern South American savannas. *Mauritia* pollen can be present both in monospecific palm formations (with percentages from 10 to 30% or more), and in mixed or gallery forests (with percentages from 1 to 4%) (Rull, 1992). Thus, the age marks not the first appearance of *Mauritia* pollen in the record, but the formation of a modern *morichal* community (see Study area for palm formation definition). In a northern South American context, the Holocene colonization of the GS by *Mauritia* seems to have occurred later than in the savannas from the Orinoco lowlands (Fig. 5.6). This would be due in part to anthropogenic factors (i.e. time of arrival of fire-prone cultures), but the physical isolation of the GS from any other savanna patch would have also played a role. *Mauritia* has no long-distance dispersal by wind, and its seeds are commonly transported by animals (mousses, opossums, squirrels, agoutis, peccaries, and others) or by water (Ponce, 2002). Therefore, a physical connection is needed for *Mauritia* expansion. At present, there is no such connection in the GS. One possibility is that *Mauritia* reached the GS during a phase of a general savanna expansion, which would have caused a less fragmented pattern, but there is no any paleoecological record suggesting such a framework after around 2000 years ago. It is also possible that humans were the dispersal agents, as it is known that this palm is widely and intensively used by indigenous cultures for housing, food, and other relevant activities (Henderson *et al.*, 1995; Gomez-Beloz, 2002; Heckenberger and Neves, 2009). In this case, physical connection is not mandatory, as humans could have migrated from one savanna patch to another through the rainforest. Concerning the source, colonization from the north is unlikely because the northern GS is a physical barrier due to its elevation, around 400-500 m higher than required for *Mauritia*, whose upper limit is around 1000 m altitude.

For *Mauritia* to reach such elevations and cross this barrier, an increase of *ca.* 2.5-3.0 ºC in the annual average temperatures would be needed by 2000 cal yr BP, but this has not been found in the GS records to date. Therefore, the GS populations of this palm species should come from elsewhere. With the presently available -though very scarce- data, the more likely source seems to be the Amazon Basin (Rull, 1998b). This should be considered a working hypothesis, which needs further palynological analysis (including charcoal records) combined with anthropological and archaeological studies. Emphasis should be placed on the precise delimitation of present-day *Mauritia* distribution, which is still largely unknown, and the design of a coring strategy able to produce a network of sites with dated first appearances of the *Mauritia* pollen, in order to follow the spatio-temporal colonization patterns. Intra-specific phylogeographic studies would also help to reconstruct migrational patterns and potential genetic variability among populations, to help test biogeographical hypotheses based on paleoecological results.

5.6. Conclusions

The palynological study of the upper part of the lake Chonita sequence, from southern GS, allows for the reconstruction of vegetation changes during the last three millennia. Although savannas were the dominant vegetation type, two different savanna landscapes are recognized: a treeless savanna with forests more extensive and/or closer than today prior to 2180 cal yr BP (with likely higher water levels prior to 2800 cal yr BP), and a savanna with *morichal*, under intensive fire regimes thereafter. The abrupt and dramatic increase of *Mauritia*, and the concomitant decrease of forest elements occurred around 2000 cal yr BP could have been caused by fire. At the same time, a shift to drier conditions than in the mid-Holocene has been reported in nearby localities suggesting that a regional climate change should also be considered, but given the preference of *Mauritia* for humid climates, the hypothesis of fire is better supported. The synchronous appearance of *Mauritia* and charcoal, together with the disappearance of forests, support the hypothesis of a potential pyrophilous nature of this palm (Montoya *et al*., 2009). The continuous occurrence of local fires during the last two millennia around Lake Chonita suggests the presence of human settlements well before the assumed colonization around AD 300 (Thomas, 1982; Colson, 1985). The results presented here highlight the importance of the interplay between climate and fire to explain the present-day GS vegetation. The colonization of the GS by *Mauritia* appears to have occurred later than in the Colombian Orinoco Llanos, probably because of a later human occupation and the physical isolation of these savanna patches with respect to the main northern South American savanna areas. Further studies are require to test this hypothesis, but it seems that the present geographical patterns of *Mauritia,* and the monospecific communities it forms, are the result of the synergy between biogeographic, climatic and anthropogenic factors, with human-made fires as a major cause.

5.7. Acknowledgments

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5.8. References

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APPENDIX C

Localities depicted in Figure 5.6. The different sequences are ordered chronologically, by the time of appearance *Mauritia* or *Mauritiella* palm stands or *morichales*, expressed as cal yr BP. Fire column refers to the coincidence between *morichal* pollen and charcoal increase. > marks those localities where *morichales* were already present at the beginning of the record. Elev.: Elevation (in meters); Carim: Carimagua; ND: no data; GS: Gran Sabana.

N	**Locality**	**Coordinates**	**Elev**	**Region**	***Morichal***	**Fire**	**Reference**
1	Chenevo	4º5’N - 70º21’W	150	Colombia	6330	ND	Berrío *et al.*, 2002
2	Angel	4º28’N - 70º34’W	200	Colombia	4290	ND	Behling and Hooghiemstra, 1998
3	Carimagua	4º4’N - 70º14’W	180	Colombia	4260	ND	Behling and Hooghiemstra, 1999
4	Sardinas	4º58’N - 69º28’W	80	Colombia	4030	ND	Behling and Hooghiemstra, 1998
5	Mozambique	3º58’N - 73º3’W	175	Colombia	3720	ND	Berrío *et al.*, 2002
6	Margaritas	3º23’N - 73º26’W	290	Colombia	2500	Yes	Wille *et al.*, 2003
7	Loma Linda	3º18’N - 73º23’W	310	Colombia	2330	ND	Behling and Hooghiemstra, 2000
8	Agua Sucia	ND	260	Colombia	2230	ND	Wijmstra and van der Hammen, 1966
9	Chonita	4º39’N - 61ºW	884	Venezuela, GS	2175	Yes	This publication
10	Sta. Barbara	9º33’N - 63º40’W	80	Venezuela	> 1960	ND	Leal *et al.*, 2002, 2003
11	Sta. Teresa	4º43’N - 61º5’W	880	Venezuela, GS	1700	ND	Rull, 1992
12	Div. Pastora	4º42’N - 61º4’W	800	Venezuela, GS	1500	ND	Rull, 1992
13	Encantada	4º42’N - 61º4’W	867	Venezuela, GS	1220	Yes	Montoya *et al.*, 2009
14	Urué	5º2’N - 61º10’W	940	Venezuela, GS	990	Yes	Rull, 1999
15	Carim-Bosque	4º4’N - 70º13’W	180	Colombia	> 1190, 80	ND	Berrío *et al.*, 2000

CHAPTER 6:

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.

> *El desarrollo del hombre depende fundamentalmente de la invención. Es el producto más importante de su cerebro creativo. Su objetivo final es el dominio completo de la mente sobre el mundo material y el aprovechamiento de las fuerzas de la naturaleza a favor de las necesidades humanas.*
> Nikola Tesla.

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ABSTRACT

This paper shows a Holocene paleoecological reconstruction based on a peat bog sequence (El Paují, 4º28'N - 61º35'W, 865 m elevation) located in the transition zone between the Gran Sabana (SE Venezuela) savannas and the Amazon rainforests. Paleoecological trends are based on the analysis of pollen and pteridophyte spores, algae and animal remains, fungal spores, and charcoal particles. The whole record embraces the last *ca.* 8000 cal years BP, and was subdivided into five pollen zones, representing the following vegetation succession: savanna/rainforest mosaic (8250-7715 yr BP), dense rainforests (7715-5040 yr BP), savanna/rainforest mosaic (5040-2690 yr BP), secondary dry forests (2690-1440 yr BP), and peat bog in an open savanna landscape (1440 yr BP-present). These vegetation changes have been attributed to the action of either climate and land-use changes, as well as the corresponding synergies between them. Fire has been one of the main drivers of landscape evolution. Based on the reconstructed fire and vegetation shifts, a changing land-use pattern could have been recognized. Between the early and the mid Holocene (*ca.* 8.3-5.0 kyr BP), land-use practices seem to have been more linked to shifting agriculture in a rainforest landscape -as is usual in Amazon cultures- with medium fire incidence affecting only local forest spots or surrounding savannas. More extensive forest burning was recorded between *ca.* 5.0 and 2.7 kyr BP, followed by land abandonment and the dominance of drier climates between 2.7 and 1.4 y BP. The modern indigenous culture, which prefers open environments and makes extensive use of fire thus preventing forest re-expansion, seem to have established during the last 1500 years. Therefore, a significant cultural replacement has been proposed for the region, leading to the present-day situation. Changing human activities have been instrumental for ecological evolution in this savanna-rainforest transitional region, as well as for the shaping of modern landscapes.

Keywords: Fire; Gran Sabana; Amazon rainforests; Indigenous land management; Savanna/forest boundary; Ecological succession.

6.1. Introduction

The paleoecological and paleoclimatological research developed in northern South America has been continuously improving (e.g.: Behling and Hooghiemstra, 2001; Bush *et al*., 2004; Rull *et al*., 2010a) since pioneer works began several decades ago (e.g.: Wymstra and Van der Hammen, 1966). However, given the vast extension and the different ecosystems present (Colinvaux *et al*., 2000), many areas remain barely studied, and in some cases prevent a regional perspective about vegetation-climate-human interactions over time. Indeed, in northern South America (North of equator) efforts have been focused mainly on: 1) mountains or highlands (vertical landscapes), where the altitudinal distribution of vegetation can allow the reconstruction of temperature shifts (e.g.: Hooghiemstra, 1984; Stansell, 2009); and 2) generally flat lowlands and midlands (horizontal landscapes), where the vegetation changes have been usually interpreted as responses to mainly moisture trends (e.g.: Behling and Hooghiemstra, 2001; Berrío *et al*., 2002a; de Toledo and Bush, 2007). Within these horizontal landscapes, large extensions of forests intermingle with savanna patches, which in some places can become the dominant plant formation (Huber, 1995a; Behling and Hooghiemstra, 2001). In Amazonia, variations in the coverage of both plant formations have been documented since the Last Glacial interval, interpreted as result of mainly past climatic oscillations (e.g.: Behling, 1996; Colinvaux, *et al*., 1996). Besides climate, humans have been an important forcing factor in shaping the present-day landscape in northern South American lowlands (Sanford *et al*., 1985; de Toledo and Bush, 2007). Contrary to previously thought, Amazonia has suffered different levels of pressure due to anthropogenic disturbances prior to the European arrival (Bush and Silman, 2007). Human presence has been reported for the region since the Late Glacial, followed by a Holocene expansion (Cooke, 1998). In this sense, several paleoecological studies have been addressed, mainly in Amazonia, to discern the possible anthropogenic impact of ancient cultures by themselves or coupled with climate shifts (e.g.: Bush *et al*., 2000; Bush *et al*., 2007a,b). Nevertheless, the scarcity and scattered nature of the surveys prevent a full regional view, though it is a growing field.

Forest edges and forest-savanna ecotonal boundaries have proven to be good places for paleoecological research due to their sensitivity to climatic shifts, even when such changes are small or of local origin and/or effect (Desjardins *et al*., 1996; Pessenda *et al*., 2001; Mayle and Power, 2008). In Venezuela, the Gran Sabana (GS) is characterized by extensive savannas with gallery forests, and forest savanna mosaics (Huber and Febres, 2000). Previous paleoecological studies revealed that during the Late Glacial and Holocene, the GS experienced several climatic and vegetation changes. For example, a pronounced and relatively rapid vegetation shift occurred during the end of Younger Dryas and early Holocene that ended with the replacement of forest and shrubland formations by treeless savannas (Rull, 2007; Montoya *et al*., 2011). This landscape shift coincided with variations in the water balance (precipitation/evaporation or P/E ratio) and possibly also in temperature. In both cases, fire seems to have played a potentially important role in the vegetation change (Rull, 2007, 2009; Montoya *et al*., 2011). Several records show that, during the Holocene, the landscape was dominated by treeless savannas, while forests locally expanded or contracted following moisture variations. Present-day environmental conditions and vegetation established during the last millennia, and the typical gallery forests called *morichales* (palm swamps dominated by the palm *Mauritia flexuosa*) occupied the GS only in the last 2000 yr onwards, under a high fire incidence regime (Rull, 1992, 1998a, 1999; Montoya *et al*., 2009). Based on the available evidence, it could be assumed that both climatic fluctuations and fire have had similar effects on the GS vegetation, that is, the reduction of forest cover and the expansion of savannas, with the establishment of *morichales*, thus shaping the currently GS landscape (Rull, 1992).

The incidence of fires in GS during the last millennia has promoted the hypothesis of an early timing arrival of people to this region; highlighting the important role that human could have in shaping the present-day GS landscape (see Section 6.2 for further information).

In this paper, we present the paleoecological study of a peat bog sediment core located south of the GS (SE Venezuela), near the Brazilian boundary, which coincides with the Orinoco-Amazon watershed boundary. The research is based on pollen and spore analysis, combined with charcoal and non-pollen palynomorphs (NPP). The main aims were: (*i*) to reconstruct vegetation dynamics and its potential links with local and/or regional climatic changes; (*ii*) to discern the role played by either climate or fire, or the synergy of both, on plant communities; and (*iii*) to look for evidence about potential pre-Columbian human settlements and the corresponding land use practices.

6.2. Study Area

The GS covers a region of about 18,000 km^2 located in SE Venezuela (4º36’ to 6º37’N and 61º4’ to 74º2’W, Fig. 6.1). Geomorphologically, the GS lies on an undulated erosion surface developed on the Precambrian Roraima quartzites and sandstones, and forms an *altiplano* slightly inclined to the south, ranging from about 750 to 1450 m elevation (Briceño and Schubert, 1990; Huber, 1995a). The climate has been defined as submesothermic ombrophilous, with annual average temperatures of around 18 to 22ºC and precipitation values of 1600 - 2000 mm yr^{-1}, with a dry season (<60 mm/month) from December to March (Huber and Febres, 2000). Regarding vegetation, the GS present large extensions of savannas within the normally forested Guayana landscape. These savannas form wide and sometimes almost continuous cover of treeless grasslands intermingled with forests, developing the typical forest-savanna mosaics (Huber, 1995b). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b) has lead to several hypotheses, basically encompassed in three main categories related to edaphic conditions, climate change and fires (see: Eden, 1974; Fölster, 1986; Rull, 1999; Fölster *et al*., 2001; Dezzeo *et al*., 2004; Huber, 2006).

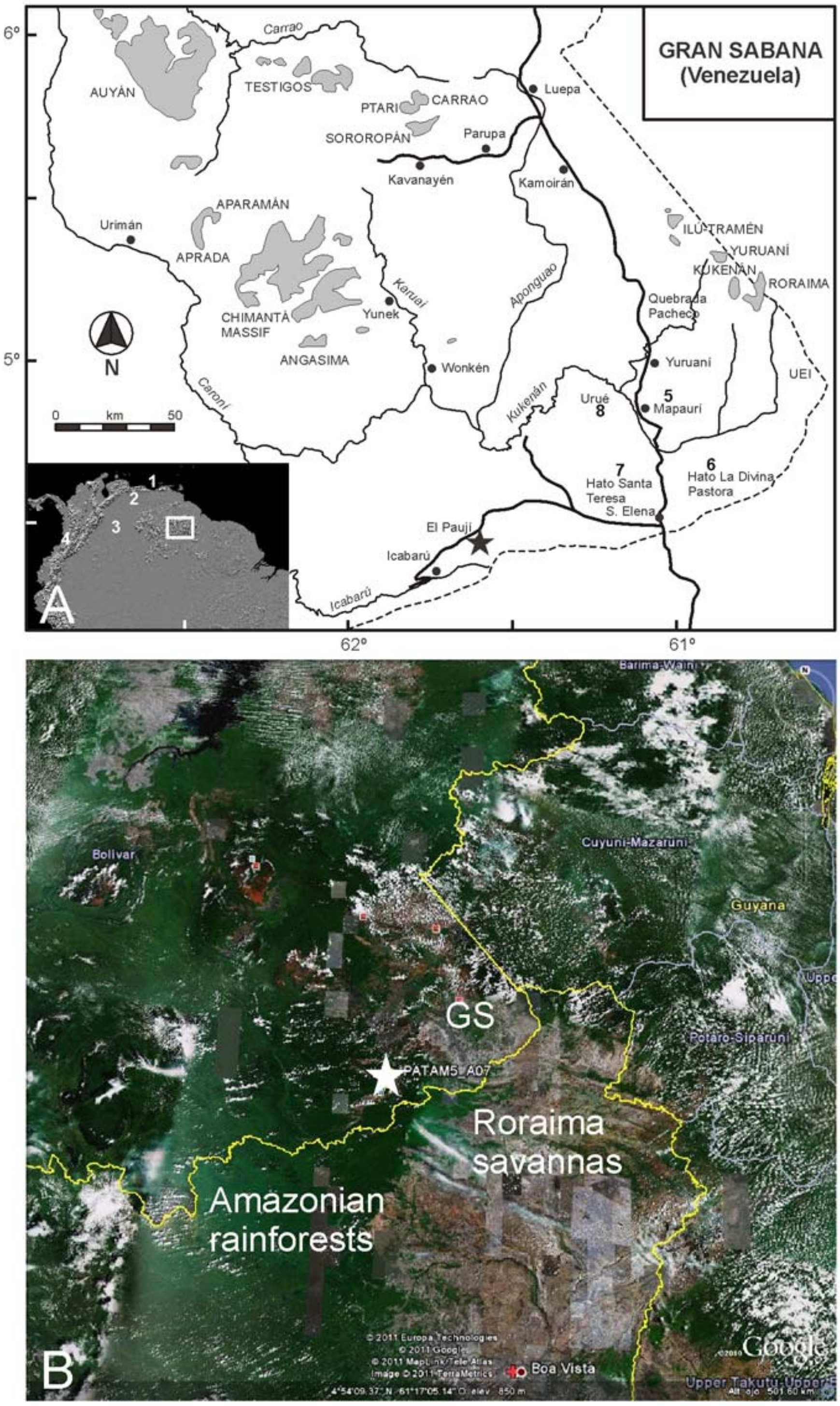

Figure 6.1. A. Location of the study area and its position within northern South America. (Radar image courtesy of NASA/JPL-Caltech). The coring site is indicated by a black star. Numbers indicate the sites with palaeoecological information mentioned in the text: 1 - Cariaco Basin (Venezuela); 2 - Lake Valencia (Venezuela); 3 - Colombian Llanos; 4 - Cauca Valley (Colombia); 5 - Mapaurí (Gran Sabana); 6 - Lake Chonita (Gran Sabana); 7 - Lake Encantada (Gran Sabana); and 8 - Urué (Gran Sabana). B. Google-earth image of present-day forest/savanna contact at the study. The coring site is marked with a white star. GS: Gran Sabana.

The GS savannas are dominated by grasses of the genera *Axonopus* and *Trachypogon* and sedges such as *Bulbostylis* and *Rhyncospora*; woody elements are scarce, and rarely emerge above the herb layer (Huber, 1995b). Most GS forests are considered to fall within the category of lower montane forests, because of their intermediate position between lowland and highland forests (Hernández, 1999). Common genera include: *Virola* (Myristicaceae), *Protium* (Burseraceae), *Tabebuia* (Bignoniaceae), *Ruizterania* (Vochysiaceae), *Licania* (Chrysobalanaceae), *Clathrotropis* (Fabaceae), *Aspidosperma* (Apocynaceae), *Caraipa* (Clusiaceae), *Dimorphandra* (Caesalpiniaceae), *Byrsonima* (Malpighiaceae), etc., and their composition varies with elevation (Huber, 1995b). The GS shrublands usually occur between 800 and 1500 m elevation and are more frequent in the northern area than in the southern part (Huber, 1994, 1995b), where our study site is located. The most common genera of this association are: *Euphronia* (Euphroniaceae), *Bonyunia* (Loganiaceae), *Bonnetia* and *Ternstroemia* (Theaceae), *Clusia* (Clusiaceae), *Gongylolepis* (Asteraceae), *Macairea* (Melastomataceae), *Humiria* and *Vantanea* (Humiriaceae), *Ochthocosmus* and *Cyrillopsis* (Ixonanthaceae), *Thibaudia, Notopora* and *Befaria* (Ericaceae), *Spathelia* (Rutaceae), *Byrsonima* (Malpighiaceae), etc. They usually grow on a rocky, sandstone substrate or deep white sands of alluvial origin (Huber, 1995b).

The GS region is the homeland of the Pemón indigenous group, from the Carib-speaking family. Today, they are sedentary, living in small villages, usually in open savannas. Though the GS population density is currently low, the indigenous settlements have experienced an expansion since the arrival of European missions, and today, more than 17,000 people live in the GS (Medina *et al*., 2004). Fire is a key component of the Pemón culture as they use it every day to burn wide extensions of savannas, and occasionally, forests (Kingsbury, 2001). The reasons for the extent and frequency of these fires are related to activities such as cooking, hunting, fire prevention, communication, magic, etc (Rodríguez, 2004; 2007). Surprisingly, land use practices, such as extensive agriculture or cattle raising, typical of other cultures strongly linked to fire, are not characteristic of the Pemón culture (Rodríguez, 2004). According to the scarce available evidence, the Pemón seem to have reached the GS very recently, probably between 300 and 600 years ago (Thomas, 1982; Colson, 1985; Huber, 1995a), but an early occupation could not be dismissed. There is some archaeological evidence consisting of pre-Columbian remains (spearheads and bifacial worked knives) similar in style to others from about 9000 years old found in other Venezuelan localities (Gassón, 2002). Moreover, palynological evidence indicating the occurrence of intense fires since the Younger Dryas (around 12,400 cal yr BP), suggested a potential early human presence in the GS (Rull, 2009; Montoya *et al*., 2011). In addition, the continued high fire incidence documented during the last two millennia in several southern GS records points to a prior settlement (Montoya *et al*., in prep.).

6.3. Material and Methods

The study site (4º28'N - 61º35'W, 865 m elevation, Figure 6.1) is located near the El Paují indigenous (Pemón) community, in the southernmost part of the GS region, and close to Brazilian boundary (Fig. 6.1). The closest town is Santa Elena de Uairén (910 m elevation), though there is a closer small village called Icabarú (Fig. 6.1). The annual precipitation in Santa Elena is about 1700 mm in average, with a weak dry season from December to March (Huber, 1995a). The sampled peat bog is situated in a gentle slope surrounded by forests and savannas, and its local vegetation is dominated by *Brocchinia* (Bromeliaceae), *Orectanthe* and *Xyris* (Xyridaceae). Contrarily to most of the Gran Sabana the site is nowadays within the forest domain, with patches of savanna at both sides of the road from Santa Elena to Icabarú. This locality is representative of a major forest-savanna ecotone between the GS savannas and the Amazon rainforests.

In the absence of a local name for the sample site, it will be called El Paují peat bog for the purposes of the present study. The core studied (PATAM5 A07; 2.19 m long) was obtained in the deepest part of the peat bog, using a Russian corer (Jowsey, 1966). A total of 4 samples were taken along the whole core for radiocarbon dating, which was carried out by Beta Analytic (Beta). Calibration was made with CALIB 6.0.1 and the IntCal09.14c database (http://calib.qub.ac.uk./calib/, last accessed on December 2010).

Forty-three samples were taken in the section studied, at 5 cm interval for pollen analysis. These samples were processed using standard palynological techniques (KOH, HF and HCl digestion, and acetolysis) slightly modified according to the sediment nature (Rull *et al.*, 2010b), after spiking with *Lycopodium* tablets (batch 177745, average 18,584 ± 1853 spores/tablet). The slides were mounted in silicone oil without sealing. Pollen and spore identification was made according to Roubik and Moreno (1991), Herrera and Urrego (1996), Rull (1998b; 2003), Colinvaux *et al.* (1999) and Leal (2010). Counts were conducted until a minimum of 300 pollen and spores were tabulated (excluding Cyperaceae and aquatic plants: *Myriophyllum*, *Sagittaria* and *Utricularia*), but counting continued until the saturation of diversity was reached (Rull, 1987). Final counts averaged 357 grains/spores per sample. Pollen taxa were grouped according to the vegetation types previously described (Huber, 1986; 1989; 1994; 1995b; Huber and Febres, 2000). Only identified pollen taxa were included in the pollen sum (spores were excluded), except for Cyperaceae and the aquatic plants mentioned above. Pollen diagrams were plotted with *PSIMPOLL 4.26*, using a time scale derived from an age-depth model based on radiocarbon dating, developed with the *clam.R* statistical package (Blaauw, 2010). The zonation was performed by Optimal Splitting by Information Content (OSIC), and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Only pollen types over 0.1% were considered for zonation. Interpretation was based on comparison with modern samples from previous studies (Rull, 1992, 1999) and the known autoecology of taxa found (Marchant *et al.*, 2002; Rull, 2003). NPP were analyzed on pollen slides, and plotted in percentages based on pollen sum. NPP identification was made according to Montoya *et al*. (2010) and literature therein. Descriptions and illustrations of new morphotypes are included in the Appendix D. Charcoal counts (only for particles larger than 5 mm) were carried out in the same pollen slides, considering three size classes (Rull, 1999):

- Type I (smaller microcharcoal particles: 5 - 100 µm): used as proxy for mostly regional fires, because of their easy dispersion by wind and/or water.
- Type II: (larger microcharcoal particles: 100 - 500 µm): used as proxy for local fires.
- Type III: (largest microcharcoal particles: > 500 µm): used as proxy for high virulence local fire events. Due to the low concentration presented, only presence/absence data were recorded (Figures 6.3 and 6.4).

6.4. Results

Figure 6.2 represents the age-depth model produced with the results of AMS radiocarbon dating (Table 6.1). The best fit was obtained with a smooth-spline model (Blaauw, 2010). Peat accumulation rates were relatively low between 0.02 and 0.07 cm yr^{-1}, therefore, the resolution of this study is multidecadal to centennial (160 years per sampling interval in average). This accumulation rate is in concordance with other GS late Holocene sediments (Leal, 2010; Montoya *et al.*, in prep.), and slightly lower than a Late Glacial lake sediment and a Holocene peat sequence (Montoya *et al.*, 2009, 2011).

Table 6.1. AMS radiocarbon dates used for the age-depth model (WA: Weighed average).

Laboratory	Sample	Depth (cm)	Sample Type	Age (yr C^{14} BP)	Age (cal yr BP) 2σ	Age (cal yr BP) estimation(WA)
Beta - 247285	PATAM5_A07/10	45 - 50	Wood	990 ± 40	898 - 1006	957
Beta - 247286	PATAM5_A07/20	95 - 100	Wood	3170 ± 40	3341 - 3480	3405
Beta - 247287	PATAM5_A07/33	160 - 165	Wood	6130 ± 40	6890 - 7164	6918
Beta - 251877	PATAM5_A07/43	210 - 215	Wood	7280± 40	8013 - 8174	8144

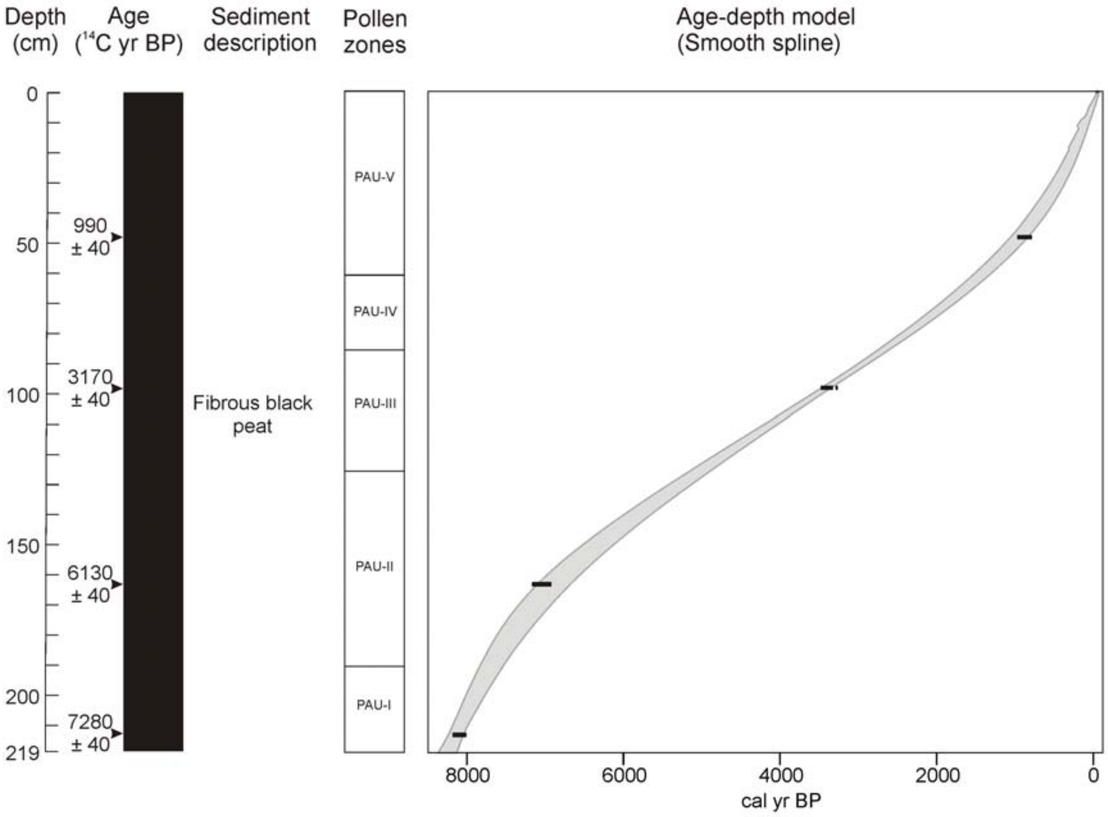

Figure 6.2. Core stratigraphy, with radiocarbon ages, sediment description, pollen zones and age-depth model of the sequence.

The pollen diagram is characterized by the alternation between Poaceae, as the dominant herbaceous taxa, and forest elements, mainly Urticales and *Alchornea* (Figure 6.3). The whole record suggests a forested landscape surrounded by open vegetation, except for the upper part, in which open savannas established. Fire has been common during the whole time period under study, especially in the upper levels, where savannas dominated. Remains of aquatic organisms indicate fluctuating flooding, with increased moisture availability towards the top (Figure 6.4). The pollen sequence has been subdivided into five zones:

6.4.1. PAU-I (219 - 190.5 cm, 6 samples)

The pollen assemblage is dominated by herbaceous elements, but the tree pollen is also abundant. Poaceae are the dominant herbs, with percentages fluctuating between 40 and 60%, followed by forest elements, notably Urticales belonging to several morphological types which identification is still uncertain. Minor herbaceous elements are *Drosera, Brocchinia* and *Xyris*. Among trees, *Alchornea*, *Cecropia*, and *Weinmannia* are also worth mentioning. Shrubs are very scarce. Charcoal particles show intermediate values. The more abundant spores are *Lycopodium contextum*, followed by psilate monoletes and triletes. Cyperaceae dominate among aquatic plants and *Mougeotia* among algae. Regarding other NPP, *Coniochaeta* cf. *ligniaria*, is the more well represented, followed by *Gelasinospora reticulispora*, IBB-37, IBB-39 and IBB-42.

6.4.2. PAU-II (190.5 - 125.5 cm, 13 samples)

This zone is characterized by the marked increase in forest elements (mainly Urticales, which reached 50% of the pollen sum, but also *Alchornea*) at the expense of herbs, notably Poaceae, which fell to percentages around 30% and, in minor extent, *Eriocaulaceae*, *Xyris* and *Genlisea*. No changes in the dominant taxa are recorded with respect to the previous zone. *Centrolobium* appears more continuously, but still with low values. Charcoal particles are also similar in concentration to PAU-I but with a local peak at the beginning and a consistent lowering trend since the middle towards the top of the zone. Aquatic plants also initiate a decreasing trend and *L. contextum* experiences a remarkable decrease, which extends throughout the whole zone. Among algae, *Mougeotia* shows an increasing tendency from the middle towards the top of the zone. Other NPP show abundances similar to PAU-I, except for a dramatic increase in a likely animal remain (IBB-42), a lower but conspicuous increase of a fungal spore (IBB- 41), and the occurrence of several peaks of *Assulina*.

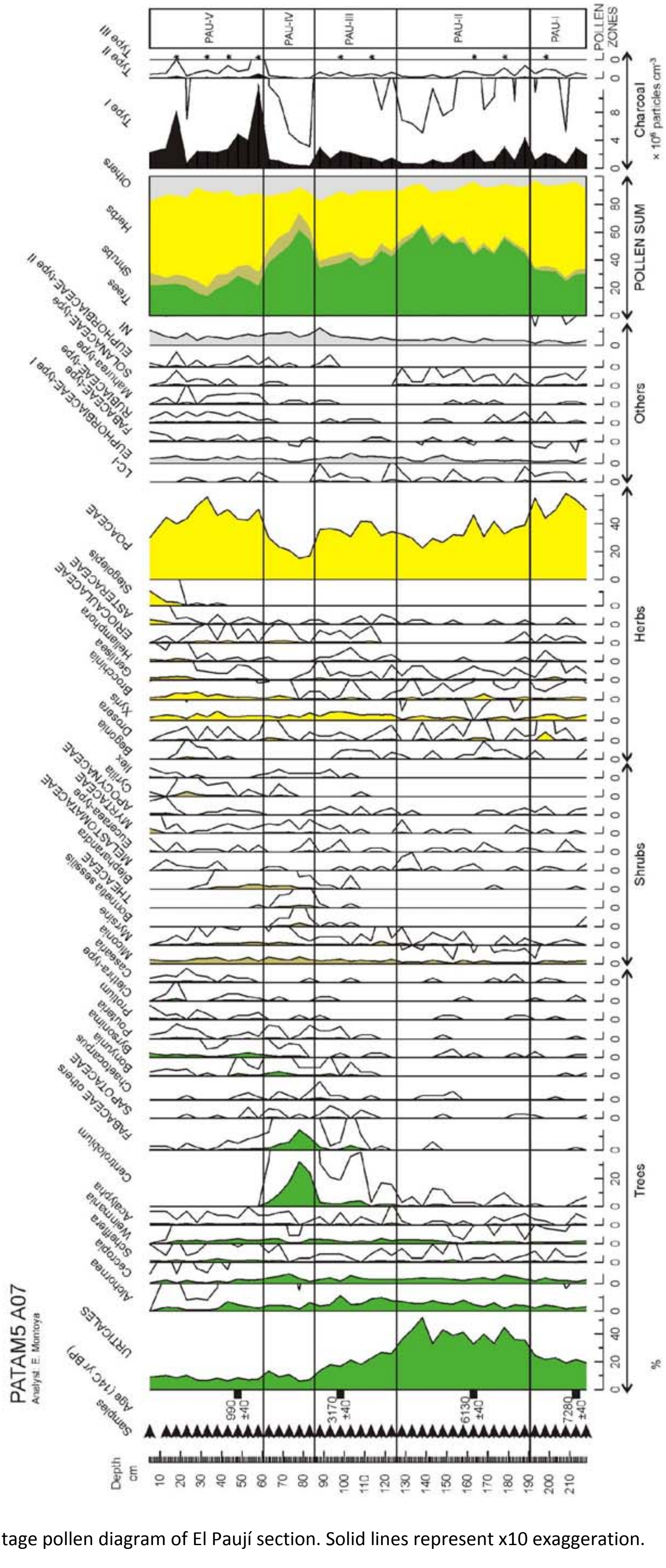

Figure 6.3. Percentage pollen diagram of El Paují section. Solid lines represent x10 exaggeration.

6.4.3. PAU-III (125.5 - 85.5 cm, 8 samples)

The pollen assemblage of this zone shows a reversal to values similar to PAU-I, with some slight differences. Poaceae increases up to 40%, without reaching values typical of PAU-I (60%). Urticales experienced a noticeable decrease from around 50% (PAU-II) to less than 20%. Other trees as for example *Alchornea*, *Weinmannia*, *Bonyunia*, *Pouteria*, *Centrolobium* and Fabaceae (others) slightly increase. There is also a subtle increase in herbs such as *Heliamphora*, and *Xyris*. Charcoal particles increase until the top of the zone reaching intermediate values again. Similar raising trends are also observed in several pteridophyte spores, mainly *L. cernuun* and *L. contextum*. Among algae, *Mougeotia* has a local maximum in this zone. The more conspicuous changes in other NPP are the abrupt and dramatic declines of *Coniochaeta* cf. *ligniaria*, *Gelasinospora reticulispora* and IBB-42, coeval with an increase in IBB-43.

6.4.4. PAU-IV (85.5 - 60.5 cm, 5 samples)

This zone is characterized by an abrupt and conspicuous change in the pollen assemblages. A sudden decline in Poaceae coincides with a steep increase of *Centrolobium*, reaching a pronounced peak and disappearing at the top of the zone, where Poaceae show a recovery. Fabaceae (others) shows exactly the same trends than *Centrolobium*, but with lower percentages. Other trees show values similar to PAU-I and PAU-III, except for *Cecropia*, which has a small local peak around the middle of the zone. Urticales are in their minimum values. There is also a consistent increase in shrubs, though none of them is important individually. Charcoal particles decline to their minimum values at the beginning of the zone and remain low over it. Among pteridophyte spores, psilate triletes and *L. cernuum*, increase while *L. contextum* and psilate monoletes show a subtle decrease. *Mougeotia* abruptly declines in a similar fashion than Poaceae, whereas *Actinotaenium*-type consistently appears and increases in this zone. Regarding other NPP, IBB-43 peaks and then declines in a similar fashion that *Centrolobium* and others Fabaceae, IBB-37 increases and peaks at the top of the zone, and IBB-41 declines and almost disappears at the top.

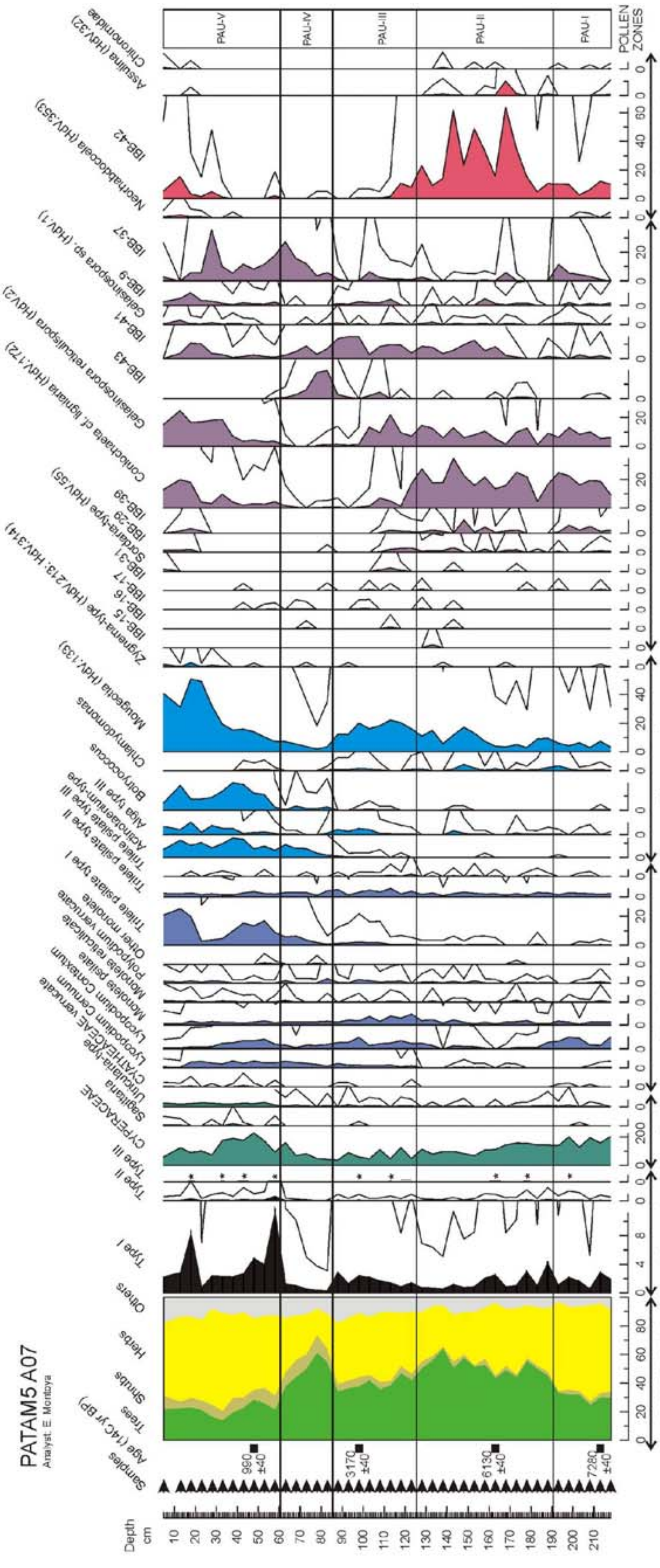

Figure 6.4. Diagram showing the elements outside the pollen sum, namely aquatic and semi-aquatic plants, pteridophyte spores, algae remains, and non-pollen palynomorphs. The abundances are expressed in percentage respect to the pollen sum. Solid lines represent x10 exaggeration. AQ. PLANTS = Aquatic and semi-aquatic plants; HdV = Hugo de Vries Lab; IBB = Institut Botànic de Barcelona.

6.4.5. PAU-V (60.5 - 0 cm, 11 samples)

Another significant shift in pollen assemblages occurs in this zone. *Centrolobium* disappears from the record permanently, Fabaceae (others) abruptly declines, and the pollen assemblage is dominated by grasses again, reaching percentage similar to PAU-I. All trees are in their minimum values while shrubs maintain the percentages attained in the former zone. Some herbs, notably *Brocchinia* and *Stegolepis*, increase. Charcoal concentration reaches its maximum values, showing two major peaks, one at the base of the zone and the other near the top. The more remarkable change in pteridophyte spores is the increase of psilate triletes, which mimics the charcoal curve. There is a general increase in Cyperaceae and algae remains, notably *Actinotaenium*-type, *Mougeotia* and *Botryococcus*, which was scarce or absent in the former zones. Among fungal spores, IBB-43 notably declines, following similar trends than *Centrolobium* and others Fabaceae. *Coniochaeta* cf. *ligniaria* and *Gelasinospora reticulispora* show a recovery to values typical of PAU-I and PAU-II, whereas *Gelasinospora* sp. and IBB-9 slightly increase. IBB-37 remains similar to the former zone, and IBB-41 is scarce until the middle of the zone, from where a slight increase occurs. The animal remain IBB-42 shows a comparatively small peak at the top.

6.5. Paleoecological interpretation

According to the former results, the vegetation around El Paují peat bog has experienced significant changes during the last 8000 cal yr BP. Forests and savannas have been recurrently expanding and retreating, likely due to climate shifts, human activities, or synergies between both. This section deals with the paleoecological interpretation in terms of vegetation, climate and human pressure. Comparison with other records from the GS and northern South America are also addressed, in order to evaluate the spatial extent of the recorded changes. The time intervals discussed correspond to the pollen zones of the diagram (Figs. 6.3 and 6.4).

6.5.1. 8250 to 7715 cal yr BP

The dominance of Poaceae upon forest elements suggests that during this interval open savannas surrounded by forests dominated by several Urticales, or forest-savanna mosaics, characterized the coring site. The landscape would have been similar to the present, but with closer or more extended forests. Fires seem to have been present since the beginning, as an important vegetation disturbance element. The parallelism between charcoal curves corresponding to Type I and Type II suggest a moderate incidence of local fires (Leal, 2010). The presence of fungal spores usually associated with death and charred plant material after fire (mainly *Coniochaeta* cf. *ligniaria* and *Gelasinospora reticulispora*) (van Geel and Aptroot, 2006), together with the occurrence of *Cecropia* -a common pioneer tree in early successional stages after fire disturbance (Behling and Hooghiemstra, 1999; Marchant *et al.*, 2002; Mayle and Power, 2008)-, supports the common occurrence of local fires during this time interval. Aquatic elements suggest a hydrological balance (P/E ratio) lower than present. Conditions drier than today have been also reported at Lake Valencia (Fig. 6.1), for the same interval (Leyden, 1985). The Cariaco Basin record (Fig. 6.1) also showed reduced precipitation values between 8.3 and 7.8 cal kyr BP (Haug *et al.*, 2001). In the Colombian Llanos Orientales (Fig. 6.1), palynological evidence showed the existence of vegetation more open than today, suggesting lower moisture availability (Wymstra and Van der Hammen, 1966; Behling and Hooghiemstra, 1998; Berrío *et al.*, 2002a). Thus, it seems that a phase of reduced hydrological balance occurred over northern South America between these dates, probably due to a southward displacement of the Intertropical Convergence Zone (ITCZ) (Haug *et al.*, 2001).

In the El Paují record, the occurrence of local fires would have also contributed to the development of open savanna patches. The occurrence of local and regional fires has been documented in the Gran Sabana region since the Late Glacial and the early Holocene, and has been interpreted as a potential evidence for early human occupation (Rull, 2007, 2009; Montoya *et al*., 2011). The record studied here would support this hypothesis.

6.5.2. 7715 to 5040 cal yr BP

The high values of Urticales forest elements are typical of closed-canopy neotropical rainforests (Gosling *et al*., 2009), indicating a remarkable vegetation shift from open or mosaic vegetation to a densely forested landscape. The increasing trend of *Mougeotia* would suggest a weak, progressive increase in the P/E ratio, and the decrease in charcoal is indicative of a slight but progressive decline of local fires. The synergistic action of these two factors would have led to the observed vegetation change. However, this trend is significant only for the upper half of the zone. At the beginning of the zone, there was a charcoal peak concomitant with a decline of Poaceae. It could be proposed that fires acted on savanna vegetation thus allowing forest recovery. The wetter climate prevailing during the upper half likely favored forest persistence. Unfortunately, the unknown origin and ecological requirements of the NPP IBB-41 and IBB-42 do not help the interpretation, but their coincidence with forest expansion and densification would be useful to infer potential indication properties for these NPP. If fire incidence is linked to human activities, this time interval would have been characterized by a decrease in human pressure to forest favoring its recovery. Archaeology and paleoecology studies have widely reported the presence of early human settlements in nearby areas since the mid Holocene or earlier, despite the absence of cultivated plant evidence (e.g.: Saldarriaga and West, 1986; Gassón, 2002; de Toledo and Bush, 2007). At a regional level, paleoclimatic interpretations are contrasting. For example, conditions drier than today have been reported for several GS sequences (Montoya *et al*., 2009; Leal, 2010) and the Lake Valencia catchment (Bradbury *et al*., 1981; Leyden, 1985; Curtis *et al*., 1999). A progressive increase in precipitation has been reported in the Cariaco Basin coinciding with the Holocene Thermal Maximum, which occurred during this time interval (Haug *et al*., 2001). In Colombia, drier conditions were also reported for the Llanos Orientales (Behling and Hooghiemstra, 1998, 2000; Berrío *et al*., 2002a) and the Cauca Valley (Berrío *et al*., 2002b) (Fig. 6.1), as well as for the Amazonia (Mayle and Power, 2008). The El Paují record suggests a likely similar climate to PAU-I in the bottom part of the zone -drier than today-, despite the forest increment registered.

6.5.3. 5040 to 2690 cal yr BP

During this interval, there is a clear shift to more open vegetation after forest clearing. A climatic explanation of this vegetation shift is unlikely, as it occurs under wetter climatic conditions, as suggested by the maximum of algae remains. The increase in local fires, as manifested in the charcoal increase, is the more suitable interpretation. Therefore, savanna expansion would be due to forest burning, likely by humans. Once again, the NPP IBB-41 and IBB-42 follow the same trends than the Urticales-dominated forest, supporting their close relationship with this vegetation type. The same would be true for *Coniochaeta* cf. *ligniaria* and *Gelasinospora reticulispora*. The inferred wetter climate during this interval is supported by similar studies in closer regions (Rull, 1992; Montoya *et al*. 2009; Leal, 2010), which is also in agreement with regional trends indicating an increase in hydrological balance around 4000 cal yr BP (Marchant and Hooghiemstra, 2004), when the local maximum of *Mougeotia* is recorded in El Paují (Fig. 6.4).

6.5.4. 2690 to 1440 cal yr BP

The more conspicuous vegetation shift of the El Paují sequence took place during this interval. A dense forested landscape returned at the expense of grasses, but this time the forest was dominated by *Centrolobium* and other Fabaceae trees, whereas Urticales-dominated forests were either absent or far from the site. The savannas were strongly reduced in extension and they probably consisted of patches within a predominantly forested landscape. This strong vegetation shift coincides with drier climates and a dramatic decline in fire incidence. *Centrolobium* is a genus of deciduous trees (Allen and Allen 1981) typical of dry seasonal semideciduous forests of lowland Amazonia (Garcia *et al*., 2004; Toniato and de Oliveira-Filho, 2004; Ortuño *et al*., in press). *Centrolobium* species have the ability of regenerating from roots (Martini *et al*., 2008; Hayashi and Appezzato-da-Glória, 2009), becoming one of the more important invaders of the earlier phases of secondary forest regeneration after intense land use abandonment and/or fire (Gould *et al*., 2002; Park *et al*., 2005; Bertoncini and Rodrigues, 2008). Therefore, the more likely interpretation of PAU-IV is the rapid invasion of the site by *Centrolobium*-dominated dry forests after the sudden cessation of fires around 2700 cal yr BP. The increase registered in shrub taxa -frequent formation in dry secondary forests although not important individually- supports this interpretation. On the other hand, the synchronous appearance and further decline of IBB-43, point to a close relationship of this unknown NPP with *Centrolobium* and Fabaceae (others). A possibility is mycorrhizal symbioses, which are important in the nowadays Amazon forests, especially in forest regeneration stages where Fabaceae trees, including *Centrolobium*, are commonly dominant (Marques *et al*., 1997, 2003). This is a possibility to be confirmed with further studies. The whole landscape picture suggests the establishment of drier climates, favoring the development of secondary dry forests, and the abandonment of the site by humans. The slight *Cecropia* increase and the non-recovery of the Urticales-dominated rainforests -which require higher levels of moisture availability to develop- are consistent with such a scenario. Several studies from northern South American lowlands support the occurrence of regional drier climates since around 2800 cal yr BP (Bradbury *et al*., 1981; Curtis *et al*., 1999; Berrío *et al*., 2000, 2002a; Haug *et al*., 2001; Montoya *et al*., in prep.).

6.5.5. 1440 cal yr BP to present

During this time interval, forests retreated, and savanna vegetation expanded and dominated the landscape. Locally, present-day vegetation established in the El Paují peat bog, as indicated by the increase of *Brocchinia* and the appearance of *Stegolepis*. This vegetation shift coincides with an increased P/E ratio, which reached maximum values, as compared with former Holocene times. The establishment of savannas instead of forests in these climatic conditions would seem contradictory. Therefore, climate would not be the best explanation for the landscape shift. The dramatic increase in fire around 1400 cal yr BP would be the more likely driver for the observed savannization, suggesting the return of human populations to the site, but this time showing different landscape use practices. Indeed, whereas the middle Holocene fires were compatible with the occurrence of rainforests, during the last 1400 years forests seem to have been burnt until their almost eradication from the site. Fires have persisted through the whole interval, showing a second peak around 220 years ago (AD 1730), more 200 years after the European colonization (see below, Section 6.6). Regionally, the increase in human disturbance recorded in El Paují, leading to the present-day vegetation patterns, has been also documented. In other GS records, forest retraction and savanna expansion coincide with enhanced fire incidence and the local establishment of *morichales* around lakes and rivers (Rull, 1992, 1999; Montoya *et al*., 2009, in prep.; Leal, 2010).

The same patterns can be observed in the Colombian Llanos (Berrío *et al.*, 2000, 2002a; Behling and Hooghiemstra, 2001). It seems thus that human activities have been the major responsible for the shaping of current savanna landscapes in northern South America.

6.6. Discussion: human occupation and land-use practices

This section discusses the above results and interpretation of pollen data in terms of human occupation and landscape management, mainly in relation to fire practices. The consistent presence and abundance of charcoal, as fire proxy, during the whole record strongly suggests a maintained human occupation during the Holocene in the El Paují area. The continuous presence and abundance of some taxa indicator of secondary succession after human disturbance, notably *Cecropia* and psilate trilete spores, support this interpretation (Rull, 1999; Mayle and Power, 2008). Similar fire records were documented for the neighbor Guyana during the Holocene, linked to human activities (Hammond *et al.*, 2006). However, positive feedbacks between climate, humans and vegetation features (as the main fuel for fire) could have played a role. For example, the savanna expansion recorded at the base of the sequence (PAU-I, *ca.* 8250 to 7715 cal yr BP) occurred during a phase of regional dry climates (Mayle and Power, 2008), likely favoring fire occurrence.

It is noteworthy that, despite the maintained fire disturbance, rainforests experienced a remarkable expansion between 7715 and 5040 cal yr BP, likely favored by either fires developed in savannas vegetation or wetter climates, or both. The coexistence of wet climates, rainforests and fires would be explained by land-use practices similar to the observed nowadays in many neotropical forested landscapes, in which small forests spots (locally called *conucos*) are cleared and burnt for shifting agriculture (Figure 6.5). The absence of pollen from cultivated plants is not a problem, as it is typically absent in the whole Guayana region, even in modern *conuco* areas (Rull 2007, 2009; Leal, 2010). The subsequent rainforest reduction and savanna expansion recorded between about 5.0 and 2.7 cal kyr BP coincides with an increment in fire incidence, suggesting more intense forest burning either at a regional or at a local scale. Large charcoal particles, used as proxies for local fires, do not increase supporting the first possibility. After that, humans seem to have abandoned the study area more or less suddenly, as suggested by the abrupt decline of fire incidence around 2.7 cal kyr BP. The site was then colonized and inhabited by secondary dry forests until about 1.4 cal kyr BP, likely under drier climates and no any human pressure. Around these dates, humans returned though this time with a totally different land-use practices. Indeed, fire incidence increased and maintained in high values until the present, likely preventing forest re-expansion, despite the return of wetter climates. The situation is very similar to the nowadays Pemón practices of frequent and extensive fires affecting both savannas and forested areas.

Figure 6.5. Aerial view of shifting agriculture practices, showing an active *conuco* (top), and a newly opened one (bottom). Note the partially burnt fallen trees (Photo: V. Rull).

According to this interpretation, a remarkable shift in land-use habits occurred between the mid- and late-Holocene, separated by an interval of reduced or null human pressure between around 2.7 and 1.4 cal kyr BP. It is no clear if this indicates the presence of two different cultures or a shift in land-use practices within a single cultural group. The first hypothesis is favored by several lines of evidence. Based on anthropological evidence, the arrival of the present-day Pemón culture to the region has been proposed to have occurred very recently, around 300 years ago (Thomas, 1982; Colson, 1985). However, paleoecological indicators of the Pemón presence, namely the onset of modern fire regimes and the expansion of *Mauritia* palm stands in the GS, support an earlier colonization of this culture, at least since *ca.* 2000 years ago (Rull, 1998a; Montoya *et al.*, in prep.). On the other hand, the El Paují area, as mentioned above (Section 3), is located close to the biogeographical boundary between the open GS savannas and the Amazon rainforests (Fig. 6.1), which coincides with the limit between the GS Pemón and the Amazon Yanomami groups. The first show a marked preference for open landscapes, which is linked to the extensive use of fires, while the second live in forested habitats and practice shifting agriculture (Huber, 1995a). Therefore, early to mid Holocene landscapes and land use, as suggested by the El Paují record, are more consistent with the local presence of Yanomami-like groups, whereas the late Holocene scenario seems more prone for the Pemón culture. The absence of *Mauritia* palm stands along the whole time interval studied is noteworthy, as compared with other GS sequences. A possible explanation is that the dominant forested landscape is not as suitable as the open savannas for *morichal* development, but differences in human practices according to the dominant habitat cannot be excluded. This is an interesting and open research field.

The more recent paleoecological and fire trends from El Paují record would be related with European colonization. Indeed, a regional decline in indigenous population occurred around AD 1600, seems to have been caused by the consequences of the European contact (Bush and Silman, 2007). This would be reflected in the El Paují record by a significant charcoal minimum at AD 1630 (23 cm; 320 cal yr BP). The colonization of the Guayana region and its surroundings by the Europeans started in the 16th century, when several military expeditions from different countries (notably Spain, Great Britain and The Netherlands) competed with each other for the possession of the mythical *El Dorado*. Spanish conquerors and missionaries established in the 17th century and remained until the first half of the 18th century, when their activities were banned by the Venezuelan government (Huber, 1995a). The charcoal peak at AD 1730 coincides with these times and would be the reflection of burning by either the Spaniards just before their departure or a recovery of the indigenous population and fire practices after that.

6.7. Conclusions

The palynological study of El Paují peat record allowed reconstruction of the vegetation dynamics in the area since the early Holocene. The sequence has been characterized mainly by variations in forests (both rainforests and dry forests) and savanna extension since 8250 to 1440 cal yr BP, when the present vegetation established, under the wettest climates recorded during the whole interval. Thus, five main pollen zones have been registered: 1) savanna/rainforest mosaic (8250-7715 yr BP); 2) dense rainforests (7715-5040 yr BP); 3) savanna/rainforest mosaic (5040-2690 yr BP); 4) secondary dry forests (2690-1440 yr BP); and 5) peat bog in an open savanna landscape (1440 yr BP-present). Fire has been a common element during the whole sequence, and appears to have acted as a determinant driver in landscape shaping, though climate and the corresponding climate-vegetation-fire synergies should not be excluded. The frequency and magnitude of fires suggests human settlements near El Paují since the early Holocene. Variations in fire patterns and the corresponding vegetation responses suggest changing land-use regimes through time, including an interval of land abandonment in the late Holocene, around 2.7 cal kyr BP, which favored the development of a secondary dry forest instead of the recovery of former rainforests that had been dominant until the mid-Holocene. This has been interpreted as the result of a synergy between land abandonment by humans and drier climates. Around 1440 cal yr BP, a significant change in fire regime was recorded, likely as a consequence of the incoming of the modern Pemón culture, which replaced former human populations, which land-use practices were more linked to rainforests, like the present-day Yanomami Amazon groups. Therefore, the modern indigenous culture inhabiting El Paují area, and the Gran Sabana in general, could have arrived to the area around 1500 years ago, earlier that prior evidence suggest, but some 500 years later than in other Gran Sabana localities. In general, the observed ecological shifts in the El Paují area have been greatly affected by human activities since the early Holocene; hence, the role developed by humans in shaping the modern El Paují landscape has been crucial, with fire as the main driver. Further studies should hopefully provide more detail in the ecological development in this ecotonal area between the Gran Sabana and the Amazon rainforests, especially during the last millennia, when present-day cultures established.

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APPENDIX D

Descriptions of unknown NPP.

IBB-9: Ascospores ellipsoid one-celled, 21.8 - 33.4 x 13.0 - 17.0 µm; smooth wall or slights longitudinal sub-parallel striae over the entire spore-length, with two protruding apical pores. This morphotype could be related to Types 47 - 48 from SW Pacific Islands (Macphail and Stevenson, 2004) and/or Type UG-1187 described in East African lake sediments (Gelorini *et al*., 2011).

IBB-37: Fungal spores, two (three) septate, 17.1 - 25.8 x 11.8 - 16.5 µm; apical end rounded, and basal cell paled or hyaline and narrow. This morphotype could be related to Type 86 described for SW Pacific Islands (Macphail and Stevenson, 2004).

IBB-39: Ascospores slightly lemon-shaped, three-septate, 19.5 - 29.3 x 8.1 - 17.0 µm; constricted at the septum.

IBB-41: Fungal spores, 13.1 - 18.8 x 8.6 - 11.7 µm; wall with pronounced protuberances that confer it a highly irregular and variable aspect.

IBB-42: Globose microfossil of unknown origin, 112.4 - 153.2 x 62.3 - 100.7 µm. It presents a likely apical aperture or more easily breakable zone, more constricted than the main body (32.3 - 47.8 µm), and a basal end that can be presented as: (1) closed and rounded end with a likely inner hole; or (2) open end with two prominent terminations with rounded spines form. It appears frequently broken. Perhaps the basal zone differences represent the same morphotype before (close) and after (open) it breaks. This morphotype has been found in this sequence at high abundances in a zone (PAU-II, from 7715 to 5040 cal yr BP) where the water level did not show any significant change in the bottom part, but an increase in forest elements (Mainly Urticales) was recorded.

IBB-43: Ascospores fusiform, 12.3 - 21.3 x 6.3 - 10.2 µm; with two apical pores. This morphotype has been found in this sequence at high abundances in a zone (PAU-IV, from 2690 to 1440 cal yr BP) where it was recorded an abrupt increase of *Centrolobium* and other Fabaceae tree synchronous with the disappearance of fires.

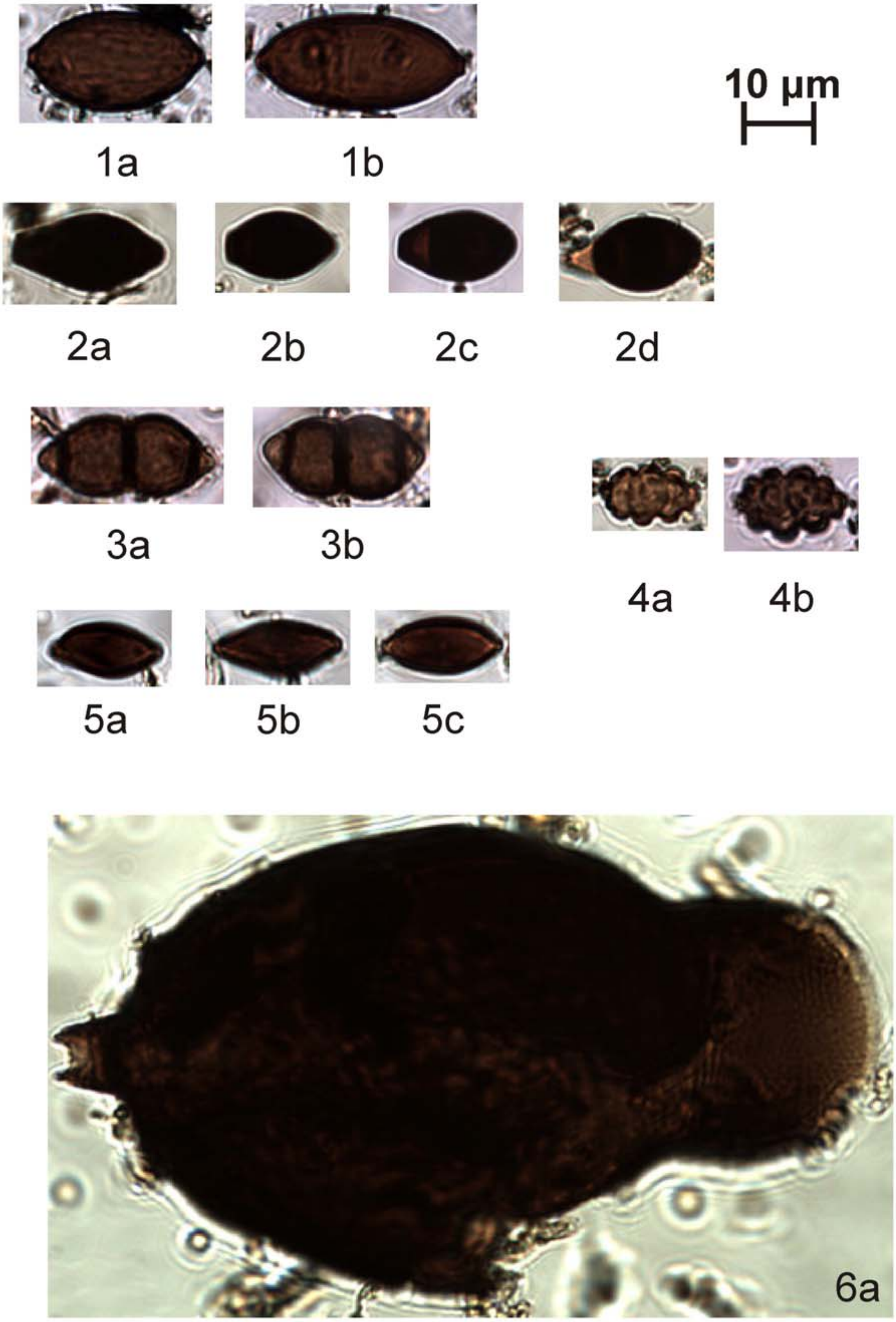

Plate IV. 1a-1b: IBB-9; 2a-2d: IBB-37; 3a-3b: IBB-39; 4a-4b: IBB-41; 5a-5c: IBB-43; 6a: IBB-42.

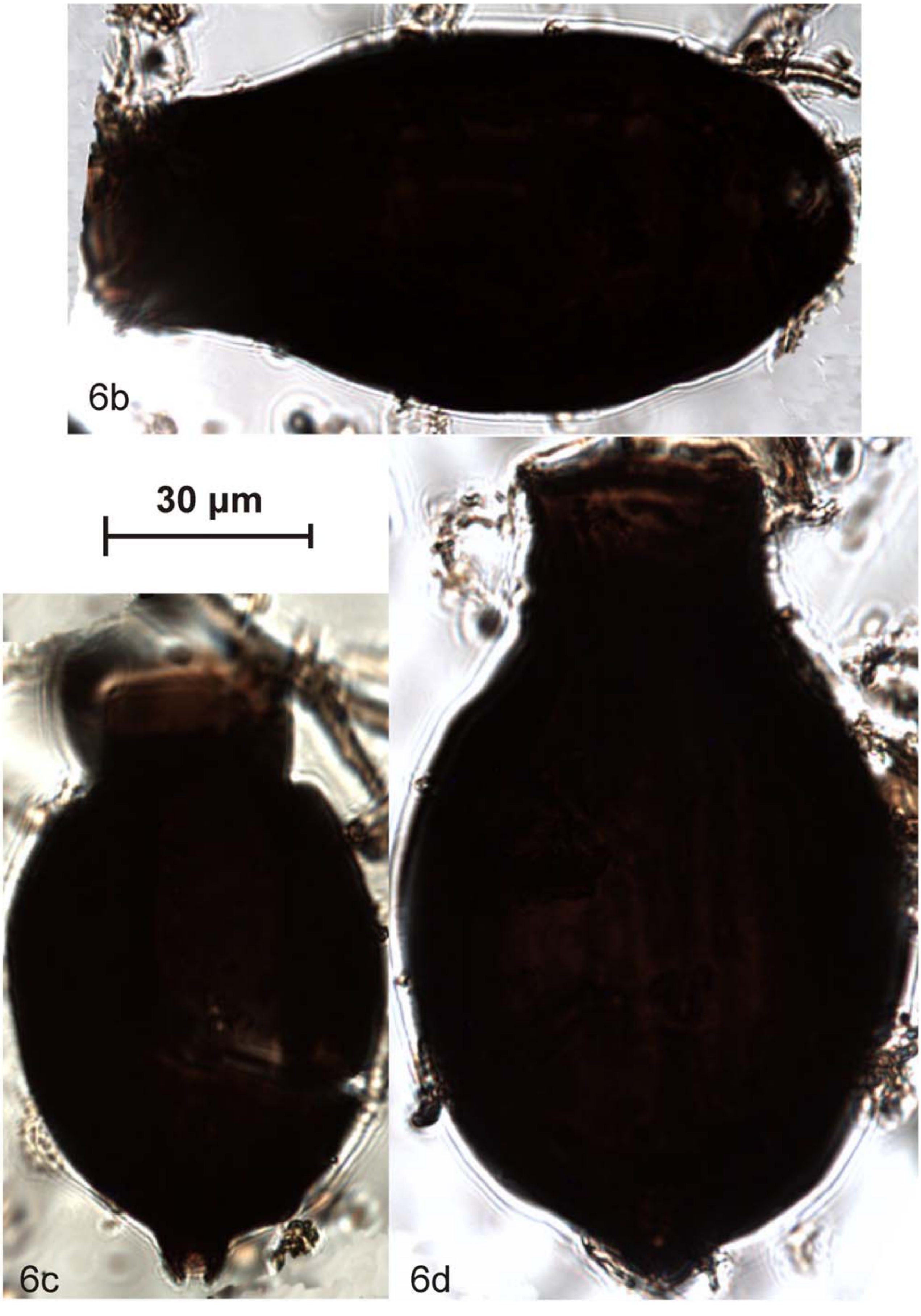

Plate V. 6b-6d: IBB-42.

CHAPTER 7:

Fire in the Gran Sabana (SE Venezuela): a paleoecological perspective.

Si quieres salvar a tu hijo del polio puedes
rezar o puedes vacunarlo... Aplica la ciencia.
Carl Sagan.

The contents of this chapter have been submitted as:
Montoya, E. & Rull, V. Submitted. *Fire in the Gran Sabana (SE Venezuela): a paleoecological perspective.* Quaternary Science Reviews.

ABSTRACT

Fires are among the most important risks for tropical ecosystems in a future climatic change scenario. Recently, paleoecological research has been addressed to discern the role played by fire in neotropical landscapes. However, given the magnitude of the study area, many studies are relegated to infer just local trends. Here we present the compilation of the paleo-fire records developed until now in southern Gran Sabana (SE Venezuela) with the aim to describe the fire regime of the area, as well as to infer the possible forcing factors implied. In this sense, southern Gran Sabana has been under fire perturbation since the Late Glacial, with the concomitant effects upon vegetation, and persisted during the Holocene. Around 2000 cal yr BP onwards, the fire regime highly increased promoting the expansion of pre-existing savannas, the decrease of forests and the appearance and establishment of *Mauritia* palm swamps. The continuous fire incidence registered for several thousands of years has likely promoted the supremacy of treeless savannas upon other vegetation types and the degradation to secondary landscapes. It has been postulated the anthropogenic nature of this continue high fire incidence, based on the available evidence. If so, it could be hypothesized that the timing arrival of Pemón, the present-day indigenous culture in the Gran Sabana, would be *ca.* 2000 cal yr BP onwards, contrary to the previously assumed recent settlement of 500 years ago. The implications of these ancient practices in the area are also discussed for present GS landscapes sustainability and future conservation strategies.

Keywords: Conservation; Fires; Gran Sabana; Indigenous populations; Microcharcoal; Paleoecology; Palynology; Venezuela.

7.1. Introduction

Fire is now recognized as a key factor in the Earth system, especially with respect to the global carbon cycle, atmospheric chemistry, and the regulation of terrestrial ecosystems and biodiversity (Power *et al*., 2008; Flannigan *et al*., 2009). The complexity of the relationships between the different forcing factors related to fire make understanding and predicting the behavior of fire a difficult task (Figure 7.1; Bowman *et al.*, 2009), although some accurate work has been done (e.g.: Hoffmann *et al.*, 2002). It is unquestioned that fire has played a significant role in determining present day vegetation (Hoffmann *et al*., 2002; Bond *et al*., 2005). The effect of fire on global vegetation distribution and occurrence has been highlighted by Bond *et al*. (2005), showing that e.g., in the total absence of fire, closed forests would double from 27% to 56% of vegetated landscapes.

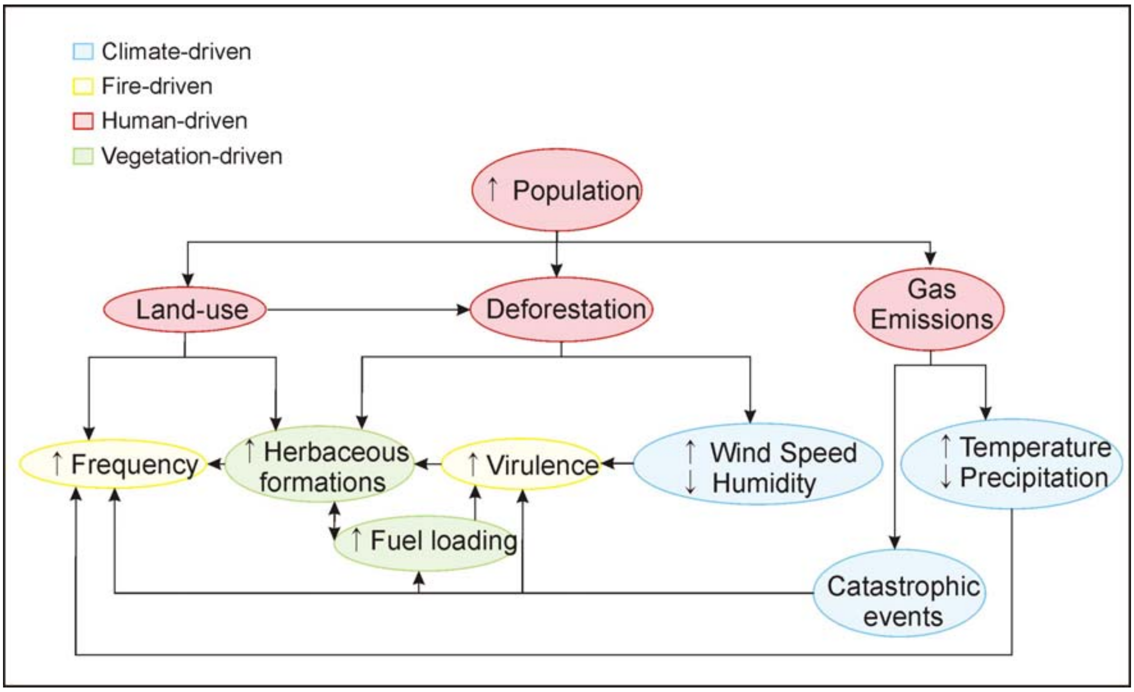

Figure 7.1. Schematic view of the main relationships between the major fire drivers. Information extracted from Hoffmann *et al.* (2002). ↑: Increase; ↓: Decrease.

These observations of present-day vegetation patterns and extent are especially true for tropical savannas (Bond *et al*., 2005), where the environmental conditions (mainly climate and soil properties) are in many cases suitable for the development of forests in the absence of fire. The Tropics have been highlighted as the region where the most fires occur on Earth (Cochrane, 2009). Savanna fires have been considered the largest source of natural pyrogenic emissions, showing the most fire activity of all major land cover types (Pereira, 2003). Although there have been some attempts to use satellite imagery to study them, several attributes of tropical fires greatly complicate such work (Pereira, 2003). In the Colombian Llanos, Romero-Ruiz *et al*. (2010) showed the high variability that fire incidence has in this region. Thus, the authors observed that, during an eight year period, variability in the studied area ranged from 33.5% of the area studied that never burned to an 18% that did it more than four times.

This high variability was mainly a result of differences in ecosystem type, land tenure, and rainfall, and it was observed that fires were more common in national parks and indigenous reserves than on ranches (Romero-Ruiz *et al*. 2010). For savannas from the State of Roraima, Brazil, a frequency of fire every 2.5 years in average was observed, with the major occurrence areas close to human settlements (Barbosa and Fearnside, 2005). That study also highlighted that between 70 and 80% of the burned areas did not register fire events the next year, but instead they were new fires produced in new zones, with the consequent ecosystem degradation that results.

Paleoecological studies are undoubtedly an important tool for obtaining information about past fire records and to thus try to establish a fire regime, useful for future predictions and fire prevention, if necessary (Whitlock and Larsen, 2001; Whitlock *et al*., 2010). Based on paleo-records, it was observed that global fire incidence has been increasing since the Last Glacial Maximum (LGM; *ca*. 21,000 cal yr BP) until the present (Power *et al*., 2008). This study also reflected the increase in spatial heterogeneity from 12,000 cal yr BP onward, probably caused by regional (direct or indirect) climate control, although the human role should not be ruled out. This is the case of the Neotropics, where a huge increase in fire frequency has been documented synchronous with human arrival, *ca.* 12.5 cal kyr BP onwards (Haberle and Ledru, 2001). Although, globally, fire has been mostly driven by climate until recent times (Marlon *et al.*, 2008), the situation in the Neotropics differs substantially due to the anthropogenic nature of most fire events (Shlisky *et al.*, 2009). Some paleoecological studies have shown evidence of fires related to human populations in NE Amazonia since at least 8000 cal yr BP (Hammond *et al*., 2006; Bush *et al.*, 2007). Moreover, although there is a general lack of paleo-fire records in the Neotropics, several studies have revealed the presence of paleo-fires in northern South America during the Holocene, probably related to a climate (mainly El Niño Southern Oscillation intensification and solar insolation) and human-driven synergism (Sanford *et al*., 1985; Hammond *et al*., 2006; Bush *et al*., 2008).

In this paper, we present a recompilation of the most recent paleoecological studies, including fire-regime records, conducted in a landscape that in the present-day is highly stressed by fire: the Gran Sabana (a mid-altitude plateau located in SE Venezuela). Paleoecology in this area has revealed several climatic variations, fire presence, and vegetation changes since the Early Holocene (Rull, 1992, 1999, 2007). Thus, the general trend in vegetation on the Gran Sabana is an increase of treeless savannas, a decline of forests, and the appearance and expansion of *morichales* (palm swamps of *Mauritia flexuosa*), which form the present landscape (Figure 7.2). The paleoecological analyses carried out suggested that climate and fires were the main forcing factors that favored this landscape in its current extent (Rull, 1992, 1999, 2007). Prior to the sequences reported here, only two records for Gran Sabana contain evidence of fire incidence, the Mapaurí and Urué sequences (Rull, 1999, 2007, 2009a). The aim of the present work is focused on the reconstruction of the long-term Gran Sabana fire regime. The detailed paleoecological reconstructions based on pollen analysis of the sequences presented here have been published elsewhere or are in progress (Montoya *et al*., 2009, 2011, in prep.a,b). Here, the emphasis is on fire history (based mainly on charcoal analysis), and the results are compared with previous fire records (namely Mapaurí and Urué sequences), with the aim of discerning a more regional overview of fire processes and their effect upon vegetation. The possible human occupation and the role developed are also discussed.

Figure 7.2. Image of present day Gran Sabana landscape with daily fires (Photo: V. Rull).

7.2. The Gran Sabana

The Gran Sabana (GS) is a region of about 18,000 km^2 located in SE Venezuela, between the Orinoco and Amazon basins (4º36' to 6º37'N and 61º4' to 74º2'W, Fig. 7.3). The GS geomorphology shows an undulated erosion surface developed on Precambrian Roraima quartzites and sandstones, which forms an *altiplano* slightly inclined to the south, ranging from about 750 to 1450 m elevation (Briceño and Schubert, 1990; Huber, 1995a). The climate has been described as submesothermic ombrophilous, with annual average temperatures of around 18 to 22ºC and precipitation values of 1600 - 2000 mm yr^{-1}, with a dry season (<60 mm/month) from December to March (Huber and Febres, 2000). With respect to vegetation, GS is a huge island of savanna within the normally forested Guayanan landscape. These savannas form wide, more or less continuous, treeless grasslands, but in some places they are intermingled with forests and shrublands, thus developing a typical forest-savanna mosaic (Huber, 1994a). The dominance of savanna vegetation in a climate apparently more suitable for the development of extensive rain forests (Huber, 1995a,b) has lead to several hypotheses basically centered on either natural climatic factors or anthropogenic fires as possible causes (see: Eden, 1974; Fölster, 1986; Rull, 1999, 2007; Fölster *et al*., 2001; Dezzeo *et al*., 2004a; Huber, 2006).

There is a visual differentiation between northern and southern GS vegetation, where the present study is focused (Huber and Febres, 2000). While in the northern GS the presence of shrubs and forest patches is common, in the south the savanna extension increases, relegating forests mainly to water courses or mountain slopes. Also in the southern GS there exists a special vegetation type, absent in the northern region, locally called *morichales* (Huber, 1994b). The *morichal* is a palm swamp developed in a wide alluvial plain and dominated by the Arecaceae *Mauritia flexuosa*. This vegetation type is especially common in the bottom of river valleys and flooded depressions, and it has been suggested that the absence of these communities in the northern GS is due to an altitudinal limit around 1000 m of distribution of this palm (Huber, 1994b, 1995b).

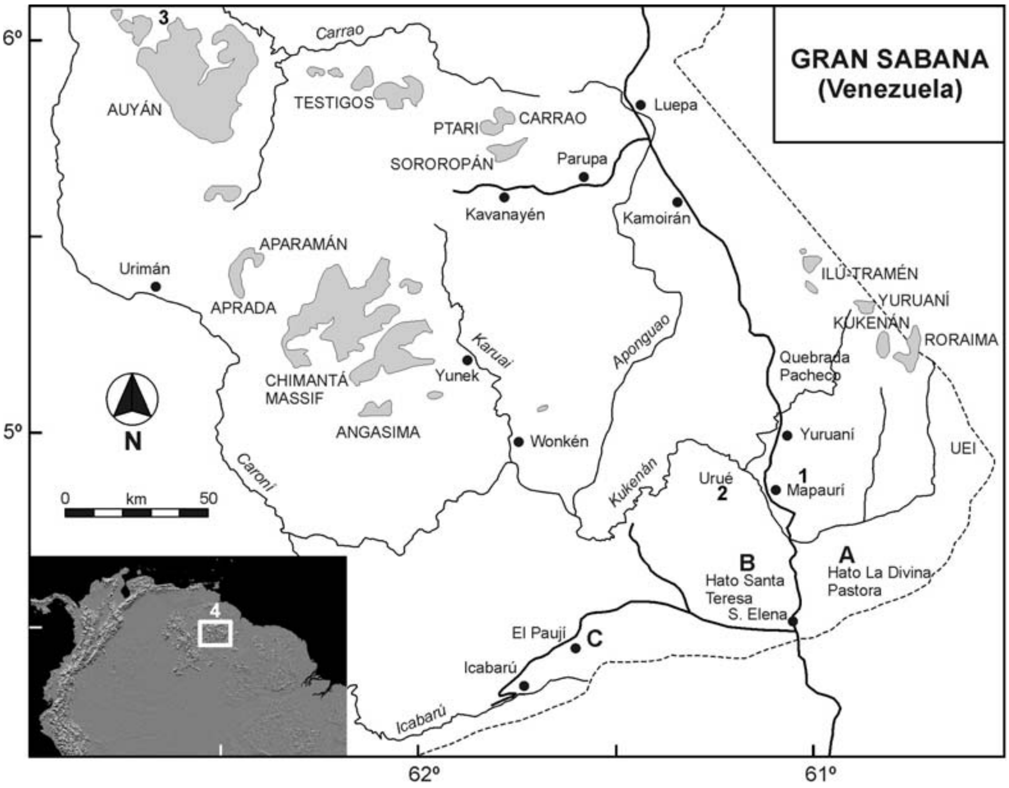

Figure 7.3. Location of the study area and its position within northern South America. (Radar image courtesy of NASA/JPL-Caltech). The coring sites are indicated by letters: A - Lake Chonita; B - Lake Encantada; and C - El Paují. Numbers indicate the sites with palaeoecological information mentioned in the text: 1 - Mapaurí (Gran Sabana); 2 - Urué (Gran Sabana); 3 - Canaima (Venezuela); and 4 - Tupuquen (Venezuela).

The GS region is presently the homeland of the Pemón indigenous group, from the Carib-speaking family. Today, they are sedentary, living in small villages, usually in open savannas. Though the GS population density is relatively low, the indigenous settlements have experienced an expansion since the arrival of modern-day European missions, and today more than 17,000 people live in GS (Medina *et al*., 2004). The date of arrival of the Pemón people to GS is still unknown. Based on anthropological evidence, it has been postulated that this culture settled in GS around 300 years ago, coming from the East (from the Rupununi savannas of Guyana; Thomas, 1982; Colson, 1985; Kingsbury, 1999), or around 500 - 600 years ago, migrating from the Rio Branco (Huber, 1995a). In either case, an early occupation cannot be dismissed. Indeed, there is some archaeological evidence consisting of pre-Hispanic remains (spearheads and bifacial worked knives), similar in style to others from about 9000 years old found in other Venezuelan localities (Gassón, 2002). Therefore, a definitive assessment is not yet possible.

Fire is a key component of the Pemón culture as they use it every day to burn vast areas of savannas, and occasionally forests (Kingsbury, 2001). The reasons for the extent and frequency of these fires include activities such as cooking, hunting, fire prevention, communication, magic, etc (Rodríguez, 2004; 2007). Surprisingly, land use practices, such as extensive agriculture or cattle raising, typical of other cultures strongly linked to fire, are not characteristic of the Pemón culture (Rodríguez, 2004).
The large number of fires today in GS (between 5000 and 10,000 fires per year [Gómez *et al*., 2000]) is essentially human-made, which has resulted in a debate related to the sustainability of the present landscape and the possible factors that led to its development (Rodríguez, 2004; Dezzeo *et al*., 2004b; Rull, 2009b).

With respect to conservation issues, it seems logical to postulate that fire is a key factor to take into account, due to the intensive and extensive fires that currently occur. Since 1981, the government of the region (through the regional hydro-electric company, called EDELCA) has developed several actions focused mainly on fire suppression (EDELCA, 2004). However, the low effectiveness obtained (about 13% of fires are controlled and extinguished) has called the utility of these expensive measures into question (Sletto, 2008; Bilbao *et al.*, 2010). This low success rate is mainly due to (*i*) the large extension of the area susceptible to fires; (*ii*) the high number of daily fires; (*iii*) a bias in fire control measures focused only in specific locations; and (*iv*) the anthropogenic character of fires, which make any kind of prevention measures difficult (Rodríguez, 2007; Bilbao *et al.*, 2010).

7.3. Coring Sites and Methods

The cores studied belong to the southern GS region. Two cores, Lake Chonita and the Lake Encantada peat bog, are located within treeless savannas, whereas the third core (El Paují peat bog) is located on the boundary between treeless GS savannas and Amazonian rainforests. These localities are close to Santa Elena de Uairén at 910 m elevation (Fig. 7.3), with annual precipitation of about 1700 mm, and a moderate dry season from December to March (Huber, 1995a).

7.3.1. Lake Chonita

The study site (4º39’N - 61º0’W, 884 m elevation) is located within a private farm called “Hato Divina Pastora” (Fig. 7.3). The lake is within a treeless savanna landscape, surrounded by scattered *morichal* patches. The core studied (PATAM1 B07; 4.67 m long) was obtained in the deepest part of the lake (3.13 m water depth), using a modified Livingstone squared-rod piston core (Wright *et al.*, 1984). This record contains the last 15.3 cal kyr BP. The Late Glacial vegetation history has already been published (Montoya *et al.*, 2011), and the study of the Holocene section is now in progress.

7.3.2. Lake Encantada

The study site (4º42’N - 61º4’W; 867 m elevation) is located within a private farm called “Hato Santa Teresa” (Fig. 7.3). The lake is surrounded by extended treeless savanna, which at the shores is transformed into a peat bog with some scattered *Mauritia flexuosa* individuals. The sequence studied (PATAM4 D07; 3.92 m long) was extracted with a Russian core (Jowsey, 1966) from one of these peat bogs at the shore. This record accounts for the last 7500 cal years BP, and the main vegetation trends, at a millennial time scale, are already available (Montoya *et al.*, 2009).

7.3.3. El Paují

The last sequence of the present study (4º28’N - 61º35’W, 865 m elevation) is located near the El Paují indigenous community, in the most southern part of the GS region, and close to the Brazilian border (Fig. 7.3). The peat bog is situated on a slight slope and is near to different forest types. The peat bog is formed by *Brocchinia* (Bromeliaceae) and surrounded by *Orectanthe* and *Xyris* (Xyridaceae) as the main vegetation. The landscape is formed by an open herbaceous vegetation type on both sides of the road from Santa Elena to Icabarú within a forested zone. The core studied (PATAM5 A07; 2.19 m long) was obtained in the deepest part of the peat bog, using a Russian core (Jowsey, 1966). This core records the past 8250 cal years BP, and a palynological study of it is in progress (Montoya *et al.*, in prep.b).

Samples for radiocarbon dating were measured at the AMS Radiocarbon Laboratory of the University of California and Beta Analytic Inc. Samples for pollen and microcharcoal analyses were processed using standard palynological techniques slightly modified according to the sediment characteristics (Rull *et al.*, 2010) after spiking *Lycopodium* tablets (Lake Encantada: batch 124961, average 12,542 ± 2081 spores per tablet; Lake Chonita and El Paují: batch 177745, average 18,584 ± 1853 spores per tablet). The slides were mounted in silicone oil without sealing. Diagrams were plotted with *PSIMPOLL 4.26*, using a time scale derived from an age-depth model based on radiocarbon dating, developed with the *clam.R* statistical package (Blaauw, 2010). The zonations were performed by Optimal Splitting by Information Content (OSIC), and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Charcoal counts were based on size classes following Rull (1999), where three main groups are defined:

- Type I: (smaller microcharcoal particles: 5 - 100 µm): used as proxy for mostly regional fires because of their easy dispersion by wind and/or water.
- Type II: (larger microcharcoal particles: > 100 µm): used as proxy for local fires.
- Type III: (largest microcharcoal particles: > 500 µm): used as proxy for high virulence local fire events. Used only for peat bog sequences (Lake Encantada and Paují). Due to the low concentrations presented, only presence/absence data were recorded (Figs. 7.5 and 7.6).

7.4. Results and Interpretation

7.4.1. Late Glacial/Early Holocene transition

The Late Glacial record of Lake Chonita shows the presence of fires since the Younger Dryas (YD; 12.7 - 11.7 cal kyr BP). Smaller charcoal particles - interpreted as regional fire proxies - were present from the beginning of the zone, as well as psilate trilete spores, indicative of early successional stages after fire in GS (Rull, 1999), which showed a very pronounced increasing trend (Figure 7.4). The increase in regional fires and the beginning of local fires (indicated by the presence of larger charcoal particles) coincided with a dramatic vegetation replacement, dated at the end of the zone (around 11.7 cal kyr BP), coinciding with the end of YD (Fig. 7.4). The frequency reached since the first evidence of fires remained until the top of the sequence, even when an increase in water level was recorded in the Early Holocene (Montoya *et al.*, 2011). The nature of the increments of these fires could be climatic, anthropogenic, or both (Montoya *et al.*, 2011).

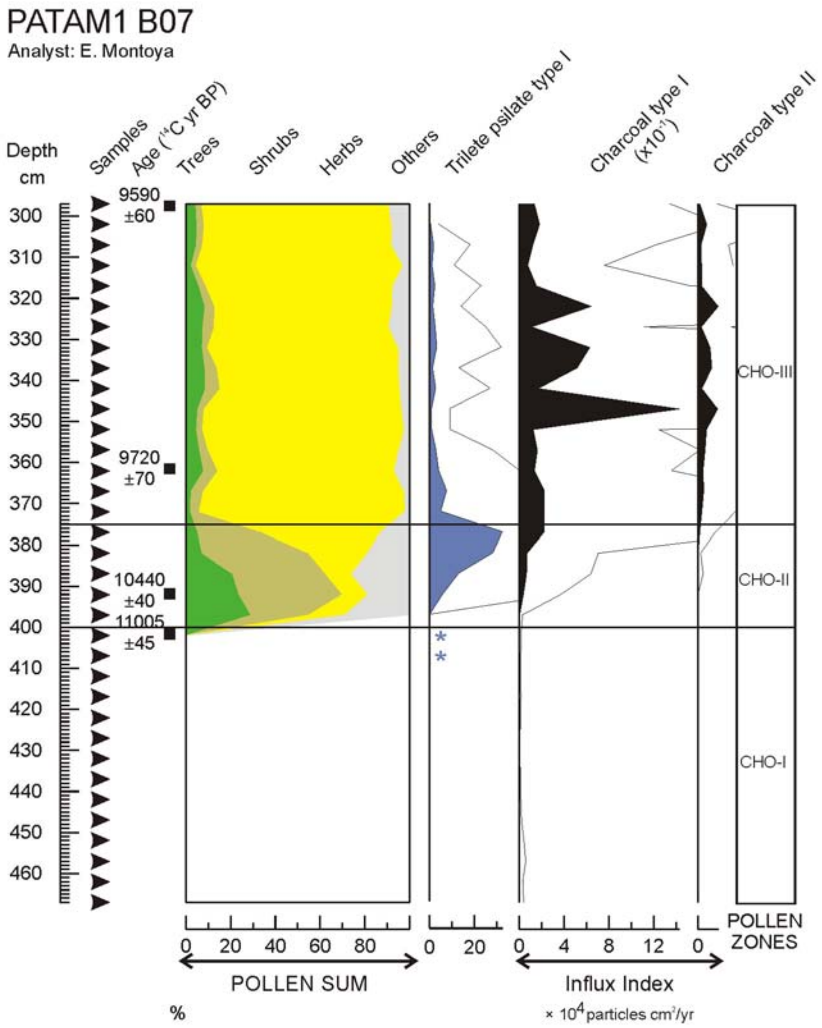

Figure 7.4. Summary diagram of Late Glacial interval at Lake Chonita, with charcoal record and the related proxies. Solid lines represent x10 exaggeration.

7.4.2. Holocene

The two peat bog sequences (Lake Encantada and El Paují) reported the main trends of vegetation during the Holocene, spanning from 8 cal kyr BP until the present day. Both sequences are characterized by the presence of fires since the onset of the records. Local fires were registered at the beginning in low abundance. At Lake Encantada, regional fires were characterized by a continuous presence without marked changes prior to 2470 cal yr BP, excepting two peaks that differed in their vegetation response (Figure 7.5). After the first fire peak, an increase in shrubs was recorded, whereas the second one did not correspond to any clear shift in vegetation. The El Paují record was marked by an oscillating trend until 5040 cal yr BP, with a slight decreasing tendency in the upper part (Figure 7.6). Around 7715 cal yr BP, a sudden increase in forest elements was recorded, synchronous with a peak in regional fires and a decline of Poaceae, probably the consequence of savanna fires. From 5040 to 2690 cal yr BP, the location was marked by an increasing trend of fires, which promoted a decrease in forest extension. The beginning of the Late Holocene in these two sequences differed substantially. From 2470 to 1220 cal yr BP, Lake Encantada was marked by an increasing trend in regional and local fires with respect to the former zone (SM-I; Fig. 7.5), which ended with an abrupt peak in regional fires.

The vegetation during this interval was characterized by a decrease in forest elements and the appearance of *Mauritia,* though in low abundances (Fig. 7.5). In the El Paují sequence, however, the same interval (from 2690 to 1440 cal yr BP) was characterized by a decline in the fire regime, both in regional and local fires (Fig. 7.6). The decline of fires was paralleled by a drop in the former existing rainforest (Urticales-dominated), which initiated a decreasing trend in the previous zone, and the rapid appearance of a secondary dry forest (Fabaceae-dominated), likely favored by the existence of dry climates (Montoya *et al*., in prep.b). The Late Holocene section of Lake Chonita has been studied in higher resolution elsewhere (Montoya *et al*., in prep.a). Regional fires were present since the beginning of the interval analyzed *ca.* 3.6 cal kyr BP and were characterized by a slightly increasing trend, whereas local fires appeared around 2.2 cal kyr BP (Figure 7.7).

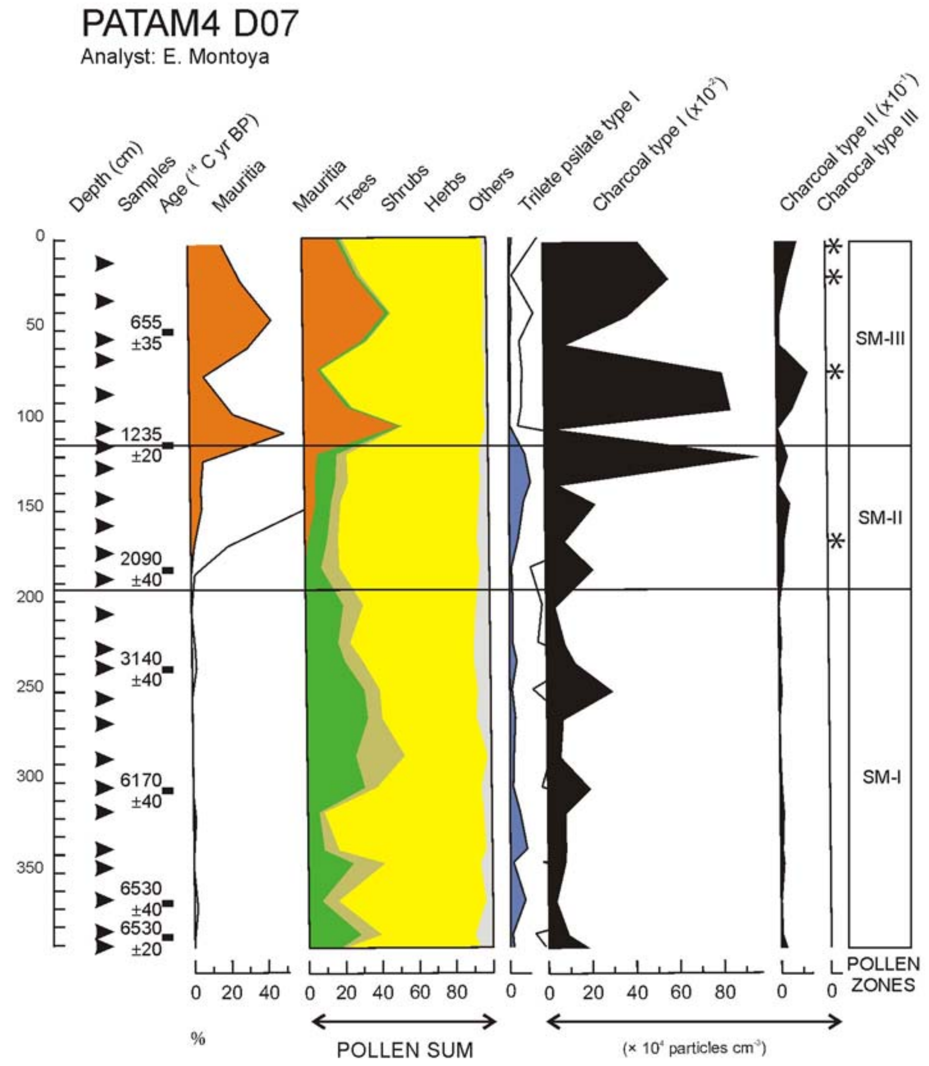

Figure 7.5. Summary diagram of Lake Encantada peat bog, with charcoal record and the related proxies. Solid lines represent x10 exaggeration.

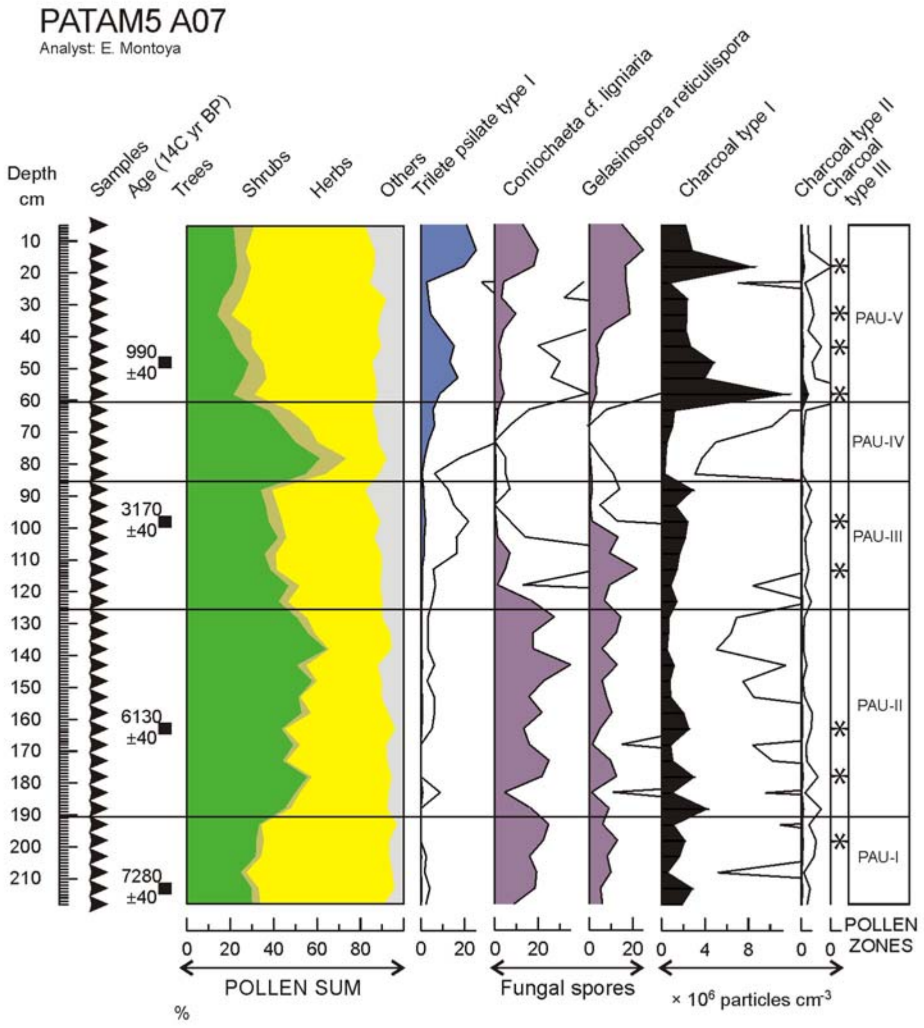

Figure 7.6. Summary diagram of El Paují peat bog, with charcoal record and the related proxies. Solid lines represent x10 exaggeration.

7.4.3. Last two millennia

The last two millennia of the Lake Encantada and El Paují sequences showed the same trend and were marked by a dramatic increase in charcoal percentages (Figs. 7.5 and 7.6). At Lake Encantada, there was a pronounced increase of *Mauritia* synchronous with the fire increase, which almost completely replaced the forest (Fig. 7.5). This landscape, a treeless savanna with *morichales*, has remained until the present day. Also at El Paují, an abrupt increase in fire incidence can be noted, and this has been maintained until the present, which likely promoted the expansion of grasslands. Therefore, the current landscape of Lake Encantada and El Paují was established around 1220 and 1440 cal yr BP, respectively. With respect to Lake Chonita, the beginning of local fires (*ca.* 2.2 cal kyr BP) was synchronous with a dramatic increase in regional fires and a vegetation shift. This sequence was characterized by savannas with nearby forests that were suddenly replaced by a savanna with *morichales*, the present-day landscape, once local fires started (Fig. 7.7).

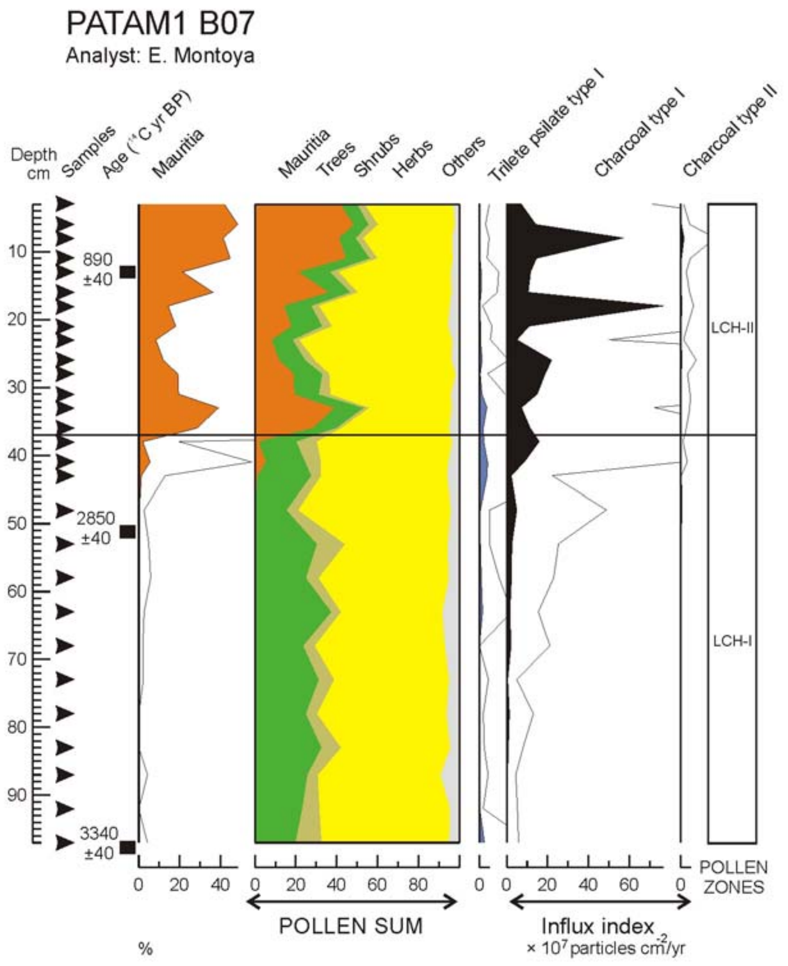

Figure 7.7. Summary diagram of last millennia at Lake Chonita, with charcoal record and the related proxies. Solid lines represent x10 exaggeration.

7.5. Discussion

The present results show that GS has suffered high fire incidence at least since the Late Pleistocene, and especially during the last two millennia. The main effect of these fires, in some cases probably coupled with climatic variations and other factors like the edaphic conditions (Montoya *et al*., 2009), has been a continuous impoverishment of the landscape diversity. A comparison with other GS sequences containing fire regimes will be made in this section, and the implications these results have for different disciplines will be elucidated.

7.5.1. Comparison with other GS fire records

The time interval analyzed in previous GS studies containing fire regime in the Mapaurí record is since the Early Holocene (Rull, 2007, 2009a), and the Urué sequence spans the last two millennia (Rull, 1999).

In the Mapaurí sequence (Figure 7.3), Rull (2007) observed an abrupt vegetation replacement from a cloud forest to the establishment of a treeless savanna during the Early Holocene. The Mapaurí vegetation shift was recorded at the same time as the presence of regional fires (Rull, 2009a). With regard to climatic conditions, it was postulated the migration of the former forest to higher altitudes due to an increase of 2 - 3 ºC in average temperatures (Rull, 2007). In this way, along with Lake Chonita, the paleoecological studies of the two unique sequences containing Late Glacial/Early Holocene intervals have shown that the GS landscape was probably a mosaic between forests, shrubs, and savannas, without the current dominance of this last vegetation type. Climate seems to have been the main forcing factor involved in the observed changes, but fires, which locally appeared during this interval in Lake Chonita, possibly also played a role.

The Urué sequence (Fig. 7.3) was marked by a high fire incidence around 1.7 cal kyr BP that triggered a secondary succession. This perturbation event also promoted a significant forest reduction and the expansion of savannas with *morichales* (Rull, 1999). In Mapaurí, Rull (2009a) also documented an increase in both regional and local fires in the upper part of the sequence that has been maintained until the present. However, the lack of additional radiocarbon dates prevents accurate determination of the onset of the interval neither the onset of fires increase. Other sequences studied in GS (Divina Pastora and Santa Teresa; Rull, 1992) also showed an abrupt appearance of *morichales* during the last millennia that were interpreted as result of mainly climatic conditions. Unfortunately, these two records did not contain charcoal analysis, so the presence and influence of fires upon vegetation, if they existed, cannot be taken into account.

Altogether, the results obtained so far regarding the fire regime of GS suggest that forests were present in variable extension during the Early and Mid-Holocene, and changed their range according to mainly climatic conditions, fires, or a synergy between them. In the Late Holocene, however, forests showed a dramatic decrease in all sequences, likely the result of the continuous and high fire incidence. Given the evidence reported, all sequences studied containing the last millennia highlighted the important role of fire in shaping the modern-day landscape in GS, likely accompanied by climate-driven effects that played a minor role. Moreover, this interval has been characterized in all records by an increase in treeless savannas and, except for the Mapaurí and El Paují sequences, the establishment of *morichales*.

7.5.2. Implications for human occupancy

The continuous frequency reached in all sequences once fires started, even during intervals where wet conditions (unfavorable for wildfires) were reported (Montoya *et al*., 2009, 2011, in prep.a,b), indicates that human activity can likely be implicated as a key component. In paleoecological records of the Neotropics, it has been suggested that the occurrence of high fire incidence can be interpreted as a proxy for human settlements even in the absence of other land use signals, such as cultivated plants (de Toledo and Bush, 2007; Bush *et al*., 2007). Moreover, recent GS studies about modern pollen depositional rates have highlighted the absence of cultivated plant signals in this region, including locations where agriculture was developing, so the direct human impact in pollen records can easily go unnoticed (Rull 2007, 2009a; Leal, 2010). In this sense, the onset of fires in the Lake Chonita catchment around 12.4 cal kyr BP might be evidence of postglacial human occupation in the region, being among the oldest fire events registered so far in northern South America (Colinvaux *et al*., 1997; Behling, 2001).

There are some archaeological studies that documented the presence of stone tools of unknown radiocarbon age in nearby locations (Tupuquen and Canaima, Fig. 7.3) that were interpreted as evidence of Early Holocene cultures, who probably lit fires in open savannas for hunting (Navarrete, 2008; Rostain, 2008; Heckenberger and Neves, 2009). The presence of savannas at Lake Chonita from 11.7 cal kyr BP onwards coeval with the occurrence of local fires supports this hypothesis.

On the other hand, the anthropogenic impact on GS can be clearly observed during the Late Holocene. The present-day indigenous culture in GS (Pemón) is characterized by living in open grasslands landscapes, with fire being a daily present element. For instance, besides the huge variety of cultural reasons already mentioned (Section 7.2), the ignition of savanna fires during their trips and migrations is a common practice in this culture (Huber, 1995a). It could be assumed therefore that a shift in the GS fire regime should be registered coeval with the arrival of this indigenous group, as the pronounced increase in fire of the last two millennia recorded in all sequences. This hypothesis is consistent with the lack of evidence of regional drier climates, which would favor fires, and the abrupt *Mauritia* appearance and establishment, which could be an indicator of human presence (Behling and Hooghiemstra, 2000). To date, this palm has often been related with a warm and wet climate in paleoecological interpretations (Rull, 1992; Behling and Hooghiemstra, 1999; Berrío *et al.*, 2000). In GS, its pyrophilous nature has also been postulated due to the observed synchrony between fire increase and *Mauritia* appearance (Figs. 7.5 and 7.7) (Montoya *et al.*, 2009, in prep.a). However, the socio-economical importance of this palm for indigenous cultures has not been sufficiently considered in the paleoecological literature. *Mauritia flexuosa* is commonly known as *moriche*, *buriti*, or *tree of life,* among others (Haynes and McLaughlin, 2000). This last name is refers to the utility of the palm for many present-day indigenous cultures, who obtain not just food resources from it but also housing materials and materials for other relevant activities (Henderson *et al.*, 1995; Gomez-Beloz, 2002). In some archaeological studies, it has also been proposed that ancient cultures used the palm intensively (e.g.: Heckenberger and Neves, 2009), as is the case on Marajó Island. The mystery of the Marajó culture lies in the uncertainty of how a highly complex culture with a large population could have survived in unfavorable environmental conditions (e.g.: very low agricultural potential). In that case, Meggers (2001) proposed that the sustainability of the Marajó culture was based on starch extraction from *M. flexuosa*, due to the similarities found between modern-day artifacts from nearby cultures that use the palm with those obtained on the island. In GS, soils are also characterized by nutrient deficiencies and progressive degradation after fire, resulting in a low agricultural efficiency (Dezzeo *et al.*, 2004a). Therefore, the simultaneous appearance of *Mauritia* and increase of fires in GS might be due to intentional planting or semi-domestication of the palm for human use.

Another potential signal of early human settlement in GS is provided at the El Paují record. The development of vegetation succession pattern, inferred climate and fire regime along the sequence pointed to human occupation at the location from the Early Holocene. The fire incidence sometimes appears contradictory with the inferred climate, increasing in wet intervals and decreasing during drier climate periods, bolstering the interpretation of humans as the main driver for this fire occurrence. Additionally, it was postulated that the fire regime and vegetation shifts documented during PAU-IV (from 2690 to 1440 cal yr BP; Fig. 7.6) were likely driven by a synchrony between land abandonment and dry climate.

This sequence is located near the current boundary between the Yanomami and Pemón groups and was tentatively interpreted as the existence of two different cultures at the site: (1) the first one present until 2690 cal yr BP, characterized by living in forested areas, with burnings attributed mainly to shifting cultivation (Yanomami-like culture); and (2) the second one present in the area from 1440 cal yr BP onwards, marked by the intensive practice of fires without an active land use, as the Pemón indigenous group does today (Montoya *et al.*, in prep.b).

Hence, GS appears to have been occupied at least since the Late Holocene, especially during the last two millennia by the Pemón culture. For the first time in the region this assumption is based on empirical data, and the timing of arrival proposed is much earlier -around 1500 years- than previously thought (Thomas, 1982; Colson, 1985; Huber, 1995a). Despite the scarce knowledge regarding early human populations in the region, some archaeological studies carried out in neighboring areas would agree with this hypothesis. For instance, Heckenberger and Neves (2009) postulated a north-south migration to tropical uplands and lowlands of Carib-speaking cultures (like Pemón) around 2500 - 2000 yr BP. On the other hand, an increase in population density has been suggested *ca.* AD 600 in Guianas, due to the arrival of new cultures coming from the Orinoco delta and the Apure-Orinoco confluence to the zone (Rostain, 2008). In this sense, the maintained increased fire regime recorded in GS characteristic of the last millennia could be interpreted as permanent presence in the region. However, sporadic or intermittent human settlements could have existed before, given the evidence of earlier fire events (Rostain, 2008).

7.5.3. Implication for conservation: landscape management and local vs. global protection figures.

Given the evidence discussed, the present day GS likely reflects a landscape intensively fire-managed during the Holocene, and especially during the last two millennia, rather than being the result of the response to only natural environmental conditions. However, the human activities have not been homogeneous throughout the GS. The sequences obtained within GS savannas (Lakes Chonita and Encantada) were characterized by continuous fire incidence with minor variations, until the regime dramatically increased during last two millennia. At El Paují, the establishment of a secondary dry forest registered in PAU-IV highlights that, although fire appears to be determinant regarding the establishment of current GS landscapes, the succession processes have likely been driven through time by a synergism between several factors. Besides climate, which also appeared as a main forcing factor in the general paleoecological analyses (Montoya *et al.*, 2009, 2011, in prep.a,b), the previously mentioned GS edaphic conditions were also probably involved (Fölster and Dezzeo, 1994; Dezzeo *et al.*, 2004a). Other evidence of the importance of edaphic conditions is the absence of *morichales* in Mapaurí and El Pauji records, which could be due to the lack of some soil or landscape features required by this vegetation type (such as the presence of permanent water-saturated soils or the existence of open landscapes, in terms of available free space, for the palm establishment). Therefore, it can be postulated that the managed landscape of southern GS is the result of the interplay between climate, edaphic conditions and anthropogenic impact.

Currently, a high fire incidence is maintained, so taking into account the paleoecological information provided, the already existing conservation polices carried out in GS deserve special attention. In addition to the already mentioned regional conservation strategies performed by the hydro-electric company for its own interests, GS is located within the Canaima National Park, a UNESCO Biosphere Reserve and World Heritage Site (Huber, 1995c; http://whc.unesco.org/en/list/701).

However, EDELCA strategies are focused only where potential economically profitable locations (gallery forests close to main river courses exploited by the company) can be under fire risk. This policy is therefore a reflection of the company economic interests rather than a conservation strategy for the region itself. Overall, the lack of connection between local practices and broader-scale conservation issues reveals a likely incoherence (Rull, 2009a).

Here, two main aspects come to light: 1) the contradiction of allowing a high fire use in a protected region that has showed a large history of fire perturbation and concomitant vegetation responses, even more so when this high fire incidence is not produced currently for indigenous economical land uses (like agricultural or cattle-raising lifestyle); and 2) the futility of global conservation policies without the agreement of local inhabitants.

The fire history presented here for southern GS provides key information concerning effects on vegetation in the long-term and should be taken into account to develop and address adequate environmental policies for the region. For instance, Bilbao *et al*. (2009, 2010) proposed, as an alternative conservation strategy, the development of the patch mosaic burning method (PMB) to maintain or even increase the GS biodiversity, due to the ancient culture of fire use in the region. However, this initiative should be carefully studied, as it is not a valid method for all ecosystems (Parr and Andersen, 2006), especially given the contrary effect caused in GS ecosystems in the long-term. The results presented here support the view of GS fires as an important impact for landscapes rather than a helpful tool. In this sense, the approach of PMB in GS could seem to be more focused on the maintenance of the indigenous, fire-prone culture, rather than be a measure for nature conservation itself.

A key point that should also be taken into account to acquire a more accurate view of the problem (and possible solutions) is the current relationship between indigenous and non-indigenous people in the region. Several authors have documented that fire use carried out by some indigenous cultures differs substantially depending on their remoteness with non-indigenous people and fire-fighter relationships, which primarily are reflected in cultural practices (Nepstad *et al*., 2006; Rodríguez, 2007; Sletto, 2009). The assistance provided by missions, the change from nomadic to sedentary communities, and the uncontrolled growth of communities, have altered the life-style of the Pemón and have promoted the unsustainability of ancient practices (Kingsbury, 2001, 2003; Dezzeo *et al*., 2004b). Moreover, the presence of fire-fighters in the region is perceived by the Pemón as a threat to their culture and therefore is not well received. In some Pemón sectors, fire use has changed sometimes to a habit rather than maintaining a specific purpose. In this sense, it has even been declared by some Pemón that one of the reasons for burning savannas is to irritate EDELCA and make the fire-fighters "work and get wet" (Rodríguez, 2007). It appears obvious that these practices are extremely harmful for GS ecosystems and by extension for GS inhabitants, even more if their survival as an indigenous culture is partially based on natural resources (namely from the forest). Undoubtedly, to succeed, future conservation strategies in GS should improve in terms of communication and positive interaction with the local population and monitoring (also from extra-local authorities) the compliance with established regulations.

To summarize, the southern GS vegetation trends and fire regime have revealed several shifts regarding climatic and anthropogenic factors. The present results highlight: (1) the importance of long-term studies for present and future management and conservation strategies; and (2) the complex relationship between all forcing factors implicated in shaping the current GS landscape. However, these observed landscape patterns should not be interpreted as tendencies for the whole region. New studies should be aimed to improve the knowledge about past and present-day GS landscape dynamics, as well as for future sustainability under climate change scenarios.

Paleoecological approaches based on new complementary proxies such as macrocharcoal analysis (oriented to establish high resolution local fire regimes), or expanding the study area and/or nearby locations (e.g.: developing more studies, especially in northern GS where until recently there was research conducted; see Leal, 2010) are highly recommended, as well as the usefulness of multi-disciplinary research.

7.6. Conclusions

The paleo-fire records developed until now in the southern GS have been interpreted together to obtain a regional view of the fire regime of the study area. Fire occurrence has been observed since the Late Glacial and throughout the Holocene. During the Late Holocene, around the last two millennia onwards the fire incidence abruptly increased in all sequences analyzed, and this high frequency has been maintained through to the present. The recorded fire regime in the area suggests that the present-day southern GS landscape is the result of a land highly managed and altered by humans, rather than a product just of climate variations. The evidence presented here supports the hypothesis of early human occupation since the postglacial period in the region and surroundings. The anthropogenic impact in GS through fire use has likely promoted the expansion of savannas, the decline of forests and shrublands, and the appearance of *morichales*. Contrary to savannas, which existed prior to increasing fire incidence, the *Mauritia* stands were completely absent in the zone and appeared synchronously with the increased fire frequency recorded during the last millennia. This synchrony between *Mauritia* and fires around 2000 cal yr BP may be indicative of the arrival of the Pemón to GS. This is supported by the continuous high fire regime during this period to the present and by the high palm usefulness for humans, especially in areas with unfavorable soils for agriculture, like GS. Other evidence of pre-Columbian settlements was found in the El Paují record, where the presence of two cultures with different fire and land uses is postulated. All the records showed that the present-day GS landscape results from a secondary succession process after fire perturbation. For this reason, it has been proposed that the fire-prevention strategies currently developed in GS are necessary but insufficient, and they should be supplemented with positive interactions with local inhabitants, as well as extra-local agency monitoring tools.

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CHAPTER 8:

Discussion.

> *La Tierra es un lugar más bello para nuestros ojos que cualquiera*
> *que conozcamos. Pero esa belleza ha sido esculpida por el cambio:*
> *el cambio suave, casi imperceptible, y el cambio repentino y violento.*
> *En el Cosmos no hay lugar que esté a salvo del cambio.*
> Carl Sagan.

In this section, a general discussion of all of the results obtained in producing the present thesis, together with former paleoecological analyses carried out in southern Gran Sabana will be presented. Given the time range provided by the sequences analyzed (Figure 8.1), the discussion will be divided into three main temporal periods. The research carried out to date in the study area will be used in an attempt to provide a regional view, rather than a local view, which has been the usual focus in previous studies. Finally, possible future directions for paleoecological research in the Gran Sabana will be also proposed.

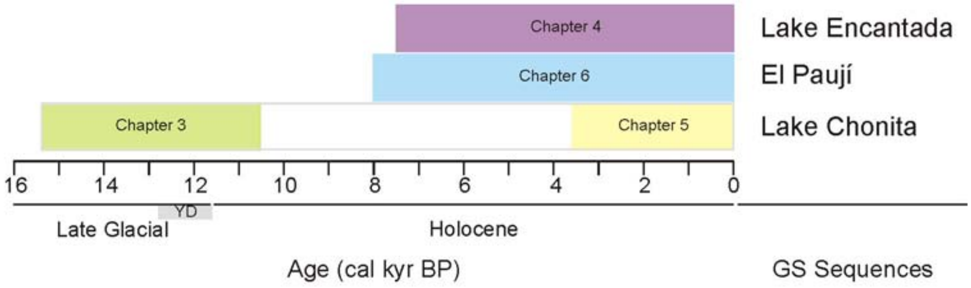

Figure 8.1. Time range of the southern GS sequences analyzed in the present work.

8.1. General paleoenvironmental history of southern Gran Sabana from the Late Glacial to the present

The paleoecological reconstructions of the sequences collected in this study have provided some key information about GS vegetation dynamics since the Late Glacial period. For instance, it has been documented that the main drivers of GS landscapes have been climate and fire, in agreement with the findings of former studies, sometimes enhanced by synergistic effects between them. However, these forcing factors have not played the same role along the temporal scale studied, displaying different importance in specific intervals. In this sense, from the Late Glacial period until the Mid-Holocene, vegetation changes have mainly been the consequence of climatic variations, mostly hydrological balance but also temperature, in almost all sequences, despite the occurrence of and interaction with fire (except for El Paují record, Chapter 6). In contrast, from the Late Holocene onwards, fire has appeared as the main driver of the recorded vegetation changes, with climate playing a minor role. The implications that these results have for southern Gran Sabana paleoecology, as well as for other related disciplines, will be discussed in pertinent time interval sections and in Section 8.1.4.

8.1.1. Late Glacial/Early Holocene transition

The Late Glacial section of Lake Chonita (Chapter 3) has been subdivided into three paleoecological intervals coeval with the northern Hemisphere Oldest Dryas-Bølling/Allerød (OD/BA), YD, and Early Holocene Warming (EHW). This sequence has shown the occurrence of shrubland as a dominant vegetation type, rather than the currently prevalent savanna (Chapter 5), coeval with the YD interval. Replacement by a treeless savanna approximately 11.7 cal kyr BP was produced parallel with the initiation of local fires at this location (Chapter 3, Figure 3.3). The likely migration of the shrubland to higher elevations suggests an increase in average temperatures of aroud 0.7 ºC - 1.5ºC at the beginning of the Holocene. The synchrony of all of these events is interpreted as suggesting a climatic origin of the vegetation shift. Maintenance of the savanna once it appeared, even when an interval of increased hydrological balance was recorded, was probably due to the occurrence of local fires at the location. This evidence is in agreement with the other existing GS sequence spanning the Early Holocene interval (the Mapaurí record), which showed a similar event. In this sequence, the Early Holocene interval was characterized by vegetation replacement of a *Catostemma*-dominated cloud forest by treeless savannas and has been interpreted as an increase in average temperatures of approximately 2ºC - 3ºC (Rull, 2007). Local fires appeared in this location after the savanna was established, although an incidence of regional fires since the beginning of the interval analyzed has been documented (Rull 2007; Rull 2009). These two sequences reveal that climate was possibly determinant in an Early Holocene expansion of treeless savannas in GS, likely related to an increase in temperature. Fire seems to have also played a role in Chonita vegetation shifts, whereas the existence of regional fires in Mapaurí has been interpreted as savannas burning in surrounding areas (Rull, 2009). Moreover, the onset of regional fires at Lake Chonita catchment was documented at approximately 12.4 cal kyr BP, being among the oldest fire events recorded until now for northern South America. The oldest fire onset registered thus far for northern South America corresponds to the Lake Curuça record (Brazil) and was dated to approximately 12.9 - 12.5 cal kyr BP (Behling, 2001). Another ancient fire event is registered at Lake Surucucho (Ecuador) around the Pleistocene/Holocene boundary (Colinvaux *et al*., 1997) (for more information, see Pinter *et al*. [2011]). Although the occurrence of these fires at Lake Chonita can be explained as a result of the postulated increase in average temperatures, an anthropogenic origin should not be ruled out (Rull 2009). Indeed, several archaeological studies in nearby locations (Tupuquén and Canaima, Chapter 7, Fig. 7.3) have documented the existence of stone tools that were interpreted as early indigenous cultures (defined as inland small mammal hunters) *ca.* 11,000 BC (estimated age from unknown dating methodology), who probably lit fires in open savannas for hunting (Navarrete, 2008; Rostain, 2008; Heckenberger and Neves, 2009). Thus, it could be postulated that the presence of these fires might be due to a synergistic effect of climate and early human presence.

The joint interpretation of these two sequences suggests that the scenario related to the Late Glacial/Early Holocene transition in GS is likely to consist of a complex mosaic between forests, shrubs, and savannas, in contrast to the current dominance of the last of these vegetation types (Figure 8.2). The Late Glacial section of Lake Chonita has allowed paleoclimatic inferences for the intervals to be established for the first time in the region regarding the Pleistocene: i) the occurrence of very dry conditions during OD/BA; ii) a dry and probably cold phase coeval with YD; and iii) wetter and warmer conditions than YD during EHW. The Early Holocene savanna expansion recorded in both sequences (Chonita and Mapaurí) appears to be closely related to climatic conditions, with the development of fires also playing an important role, at least in the further persistence of savannas. Moreover, the Late Pleistocene age of the sediments found at Lake Chonita contradicts the hypothesis of extended aridity in Guayana prior 8.0 ^{14}C kyr BP (Schubert and Fritz 1985; Schubert *et al*. 1986).

8.1.2. Early and Mid-Holocene

The Holocene sequences of Lake Encantada and El Paují have revealed the main vegetation tendencies of the last 8 cal kyr BP (Chapters 4 and 6). Although these are characterized by different locations and dominant vegetation types in the landscape (Chapter 1: Study Area), both sequences present some general similarities (Figure 8.2), such as the continuous presence of fires throughout the entire sequences, with local fires being documented in a low abundance initially. During the Early Holocene, the vegetation was mainly characterized by an open landscape somewhat similar to that of today, but with greater abundances of trees and/or shrubs than the current landscape, with savanna with shrubs being present at Lake Encantada prior to 7.45 cal kyr BP (Chapter 4, Fig. 4.3) and a savanna/forest mosaic existing until 7.71 cal kyr BP at El Paují (Chapter 6, Fig. 6.3).

The Mid-Holocene interval was marked by an increment in forest elements (Urticales-dominated), likely promoted by an increase in water balance, with some variations being observed between sequences. At Lake Encantada, the forest extension was larger or closer than today from 7.45 to 2.47 cal kyr BP and reached its maximum extent at around 4 cal kyr BP (Chapter 4, Fig. 4.3), although the prevalent vegetation type continued to be savanna. From 7.71 to 5.04 cal kyr BP, the El Paují record was marked by an increase in forest, which was probably initially caused by burning of the savanna. Subsequently, an increase in the extent of savanna was recorded until 2.69 cal kyr BP, resulting in a savanna/forest mosaic landscape interpreted as being caused by an increment of fires related to the forest (Chapter 6, Fig. 6.3).

The main vegetation trends of two Mid-Holocene records from southern GS have been determined by Rull (1992) and are characterized, as in the Lake Encantada record, by the continuous presence of treeless savannas, with some variations in the composition of taxa (Fig. 8.2). From 5.4 to 4.1 cal kyr BP in Divina Pastora (DP) and from 5.1 to 3.9 cal kyr BP in Santa Teresa (ST), the landscape was marked by a treeless savanna with larger or closer forests than today. Subsequently, (from 4.1 to 2.7 cal kyr BP in DP and from 3.9 to 2.7 cal kyr BP in ST), a decline in the extent of forest was recorded, probably caused by a decrease in the hydrological balance.

The interpretation of all these sequences together allows some important inferences to be made regarding Holocene GS vegetation dynamics (Figure 8.2). For instance, the two sequences where the fire regime was analyzed (Lake Encantada and El Paují) showed a continuous occurrence of fires from the beginning of the records. However, forest expansions and retractions appear to have mainly responded to climatic variations during the Early and Mid-Holocene in all sequences. The El Paují record differs slightly, with the development of fires also playing an important role regarding vegetation dynamics during these intervals. Therefore, a likely synergy between climate and fire is proposed as the main forcing factor related to Early and Mid-Holocene GS landscape dynamics.

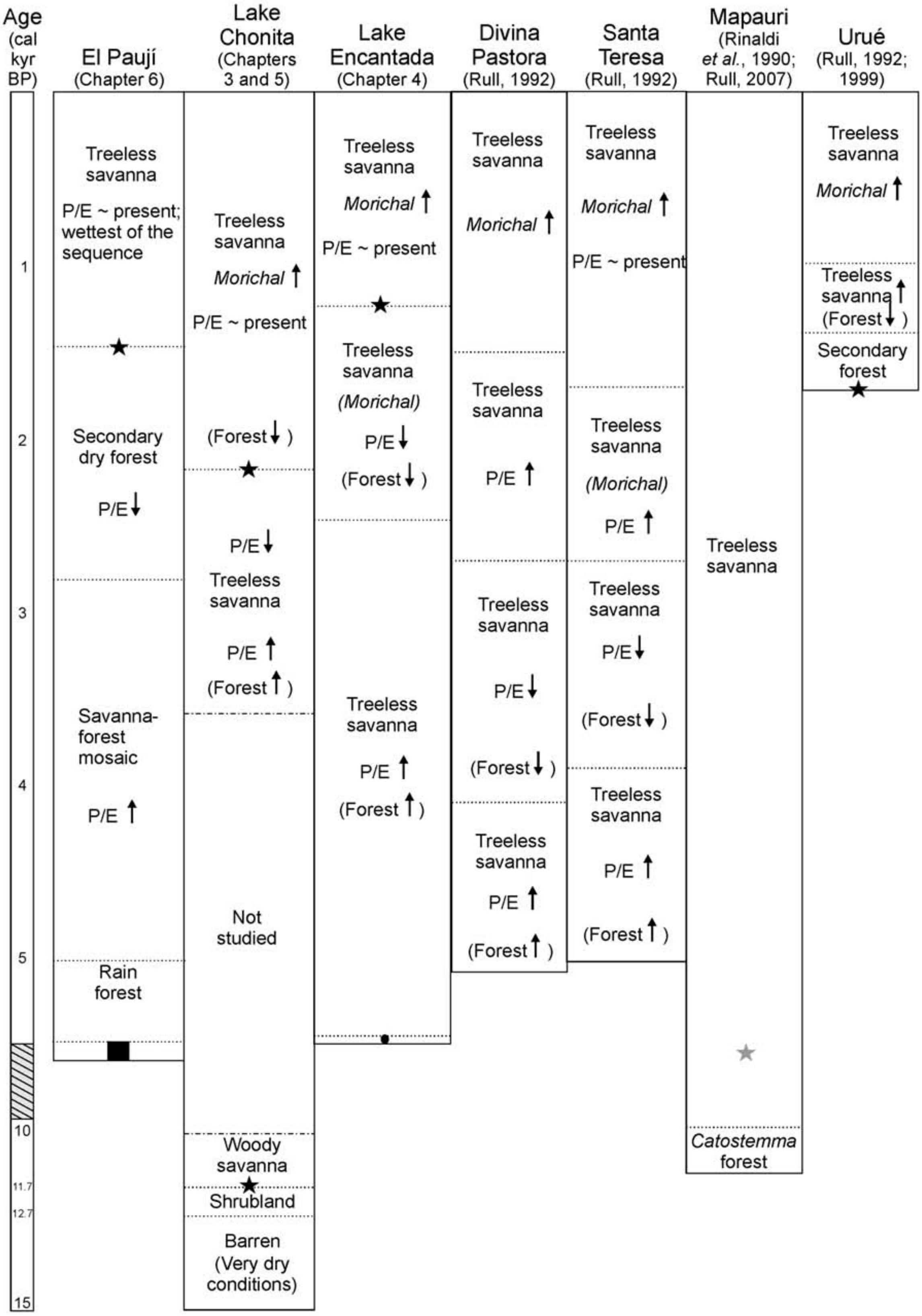

Figure 8.2. Summary paleoecological interpretation with the main results of the present thesis and those from previous analysis of southern GS. Black stars mark the onset of high local fires, grey star indicates fires of unknown age but interpreted as Early Holocene. ↑ = high or increase; ↓ = low or decrease; ■ = savanna/forest mosaic, with ↓ P/E; • = shrubby savanna, with ↑ P/E. Data of records not studied in this thesis were obtained from Rinaldi *et al*. (1990) and Rull (1991, 1999, 2007, 2009).

8.1.3. Late Holocene

The establishment of modern-day GS landscapes in the three sequences analyzed here (Lakes Encantada and Chonita, and El Paují) occurred during the Late Holocene (Chapters 4 to 6). The beginning of the Late Holocene was characterized by a decline in aquatic elements, suggesting a decrease of the water balance that promoted different scenarios in these three sequences (Chapters 4, 5, and 6, Figures 4.4, 5.4, and 6.4, respectively). Thus, from 2.47 to 1.22 cal kyr BP, Lake Encantada was marked by a remarkable decrease in forest elements and an increase in the extent of savanna. *Mauritia* appeared for first time in the record, although in low abundance (Chapter 4, Fig. 4.3). However, the El Paují record showed the appearance of a (Fabaceae-dominated) secondary dry forest during the same interval (from 2.69 to 1.44 cal kyr BP) (Chapter 6, Fig. 6.3). The dissimilarity of these two landscapes (Lake Encantada and El Paují) during the same interval and under likely similar climatic conditions suggested that another factor must have acted as the main driver of these differences. In this case, while the fire regime showed an increasing trend in Lake Encantada, the El Paují record documented the cessation of fires, which allowed expansion of secondary dry forest. At Lake Chonita, wetter conditions were recorded prior to 2.8 cal kyr BP in a treeless savanna landscape with a close or larger forest extent than is seen at present, where this prevailed until 2.18 cal kyr BP (Chapter 5, Figs. 5.3 and 5.4). Regarding the DP and ST records, the P/E likely increased from 2.7 to 1.5 cal kyr BP and from 2.7 to 1.7 cal kyr BP, respectively, but without the recovery of former forest extensions. Instead, *Mauritia* appeared in both locations, but in low abundance (Rull, 1992).

The last two millennia of the three sequences analyzed in this work were characterized by an expansion of treeless savanna, a decrease in forest and a high fire incidence, which resulted in the establishment of the current landscape (Fig. 8.2). The forest reduction that began in the former interval at Lake Encantada continued until its almost complete disappearance (Chapter 4, Fig. 4.3), parallel with the emergence of the present-day *morichal* community approximately 1.22 cal kyr BP. At El Paují, the increase in fire occurrence recorded from 1.44 cal kyr BP onwards likely favored the expansion and persistence of savanna (Chapter 6, Fig. 6.3). Therefore, based on these results, it can be proposed that the modern day landscape and fire regime of the Lake Encantada and El Paují locations were established approximately 1220 and 1440 years ago, respectively. At lake Chonita, a vegetation change was documented approximately 2.18 cal kyr BP, manifested by a decline in forest (though not as dramatic as in the Lake Encantada record), the sudden appearance of *Mauritia*, and the establishment of a treeless savanna with *morichales*. Despite some variations in abundance, this landscape has persisted until today (Chapter 5, Fig. 5.3). The last two millennia were also characterized by establishment of the present-day landscape, a treeless savanna with *morichales*, in DP and ST at approximately 1.5 and 1.7 cal kyr BP, respectively (Rull, 1992). All of these results are also in agreement with the findings of a study on the last millennia performed at a nearby location, the Urué record (Rull, 1999). This record was characterized at the beginning of the sequence by a closer gallery forest than is seen today, prior to an increase in local fires *ca.* 1.7 cal kyr BP. This perturbation event likely promoted reduction of the forest extent and favored a concomitant secondary succession that culminated in the establishment of a treeless savanna with *morichales*, the present-day landscape (Fig. 8.2). Thus, sequences in which the presence of both charcoal and *Mauritia* pollen have been reported show the synchronous occurrence of increases in local fires and *morichal* establishment (Chapters 4 and 6, Figs. 4.3 and 6.3; Rull, 1999).

Therefore, the records containing the Late Holocene interval studied to date in GS agree, showing the appearance and establishment of the present fire regime and landscape since around the last two millennia onwards (Figure 8.2). It has been suggested that the influence of fires has played a major role in the development of these present-day GS ecosystems. Paleoecological studies of Colombian lowlands also highlight the last millennia as a period marked by increased human impact (e.g., Berrío *et al.*, 2002). However, the establishment of *morichales* in these sequences was reported at around the Mid-Holocene, earlier than in GS (Chapter 5). Despite the similarity regarding general trends for all GS sequences, there is a time lag between DP and ST and other records analyzed. Dating uncertainties in the first studies derived from the use of large quantities of bulk sediment for dating (using conventional radiocarbon methods instead of AMS techniques) and the few dates available for a sound age-depth models should not be dismissed.

8.1.4. *Mauritia* biogeography and indigenous arrival to the Gran Sabana

In addition to the inferences obtained regarding southern GS landscape trends, the paleoecological interpretation of the different sequences studied during this work and their comparison with former studies (Figure 8.2) allow some suggestions to be made regarding other disciplines, such as biogeography and archaeology. As has been noted, the recorded vegetation changes appear to be mainly driven by climate variations and fire. However, other factors, such as edaphic conditions, should not be ruled out. For instance, the nutrient poverty characteristic of GS soils and the progressive degradation of these soils after fire could be determinant in allowing succession processes to occur following perturbations (Fölster *et al.*, 2001; Dezzeo *et al*. 2004; Dezzeo and Chacón, 2005), thus acting in synergy with climatic factors and fire (Chapter 4). A possible explanation regarding the interaction between these three factors might be that either climate or fires (or both) could trigger a disturbance effect on vegetation, and edaphic conditions would play a role in the further recovery of landscape cover. For example, the El Paují record showed the appearance of a secondary dry forest that was interpreted as probably being facilitated by a sudden interruption of fires, rather than recovery of the former rainforest (Chapter 6). Moreover, the absence of *Mauritia* communities in the Mapaurí and El Paují sequences could be due to the absence of certain soil or landscape features required by this vegetation type (such as the presence of permanent water-saturated soils or the existence of open landscapes, in terms of available free space, for the establishment of these palms).

The appearance of *Mauritia* in GS has been documented as abrupt and restricted to the last 2000 years in all the GS sequences studied to date (excepting the already mentioned Mapaurí and El Paují records). Although the preference of these palms for wet conditions cannot be dismissed (Berrío *et al*. 2000), other factors have probably been involved in their establishment in GS, as was suggested in Chapter 5. The difference observed between the arrival and establishment of *morichales* in Colombian Llanos and southern GS (Chapter 5, Fig. 5.6) would support the presence of forcing factors in addition to climatic conditions and would indirectly support the hypothesis postulated by Rull (1998) regarding the postglacial expansion of *Mauritia*. This hypothesis argues that the range of *morichales* could have been expanding since the Last Glacial Maximum, favored by both climate and fire (Rull, 1998). If Rull is correct, biogeographical barriers could cause the gap between these two regions, such as 1) the altitudinal range of northern GS, which lies above the upper altitudinal limit of *Mauritia* and/or 2) the isolation of GS in terms of the disruption of adequate landscapes (open grasslands with water-saturated soils) for its establishment. On the other hand, the parallel appearance of *Mauritia* stands and local fires in all sequences where both proxies were analyzed indicates a close relationship between fires and *morichales* in southern GS (Chapter 5, Fig. 5.5).

Therefore, in Chapter 4 it was proposed the likely pyrophilous nature of *Mauritia*, in terms of its colonization being facilitated by the clearing resulted from the forest reduction promoted by fire.

In addition to the establishment of *morichal*, the abrupt increase in fires during the last two millennia in all records analyzed in this thesis also deserves special attention. This coeval increased frequency is unlikely to have been due to a regional dryness (favoring fire occurrence and/or expansion), as this was documented in the wettest interval of the entire sequence in some records, such as El Paují (Chapter 6). Thus, an anthropogenic nature of these fires seems to be more plausible, as was suggested in Chapter 7, and this appears even more likely if the highly fire-prone culture of the current GS indigenous inhabitants is taken into account. A probable explanation for this increased fire regime spreading throughout southern GS is that it coincided with the arrival of the Pemón people to the region. This assumption is supported by archaeological evidence reporting a north-south migration of Carib-speaking cultures (such as the Pemón) approximately 2500-2000 yr BP to tropical uplands and lowlands (Heckenberger and Neves, 2009). Important evidence of the Holocene human presence in the region has been provided by this work, specifically in the El Paují record (Chapter 6), in which the existence of two different cultures with an interval of land abandonment between them was suggested. These two cultures likely differed in their practices and lifestyle: i) the first settlement (prior to 2.69 cal kyr BP) probably lived within forested areas and carried out forest burnings mainly addressed to shifting cultivation, as is currently done by Yanomami indigenous people in neighboring areas; whereas ii) the second group (from 1.44 cal kyr BP to the present) is characterized by a high and maintained fire incidence that has promoted the expansion of open landscapes, which is characteristic of the current Pemón lifestyle. An earlier human occupation of GS than was previously thought would also have implications for *Mauritia* communities, given the extensive use of this palm by indigenous people (Chapter 7). Thus, the establishment of *morichal* in GS appears to have likely occurred through a synergy between biogeographical, climatic and anthropogenic factors. Taking into account all of the information provided herein, the current state of southern GS would reflect a long-term managed landscape shaped by indigenous people according to their needs, which has resulted in an increase in the extent of savanna with the arrival of the Pemón people.

In summary, considering all the evidence presented here (those obtained both in the course of this thesis and from previous analyses), the southern GS can be interpreted as an ecosystem that has mainly responded to climatic conditions and fire regime variations, representing a heavily managed landscape, at least during the last two millennia. Although the influence of climate, as well as positive feedbacks among climate, fire and edaphic conditions, should be taken into account, fire has been highlighted as a major factor responsible for the establishment and further persistence of the modern-day GS landscape. Therefore, although its influence on different vegetation types has varied, the role of fire in the appearance and establishment of *morichales* has been crucial in GS. The final result of the interaction of all of these factors (climate, vegetation, edaphic conditions, and humans) has been a decrease of GS landscape diversity, manifested mainly in the general decline of the extent of forests, the expansion of treeless savannas, and the appearance and establishment of *morichales*. The resilience of GS landscapes should be evaluated for developing management strategies given the large number of fires currently being caused by indigenous people in a World Heritage Site (particularly taking into account the effects of fire on vegetation observed in the long-term) and the consequences that ongoing and future climatic change scenarios could have in this region.

8.2. Future work

The multi-proxy approach implemented during the course of this thesis and its complementation with information from other disciplines has been crucial for acquiring a long-term view of GS ecosystem processes as accurate as possible. Therefore, the use of independent and complementary proxies is encouraged for further paleoecological research, in addition to combining these with data from related disciplines (e.g., edaphology, biogeography, archaeology, etc.), especially in poorly studied areas, such as the Neotropics. Moreover, the incorporation of new techniques and improvement of those that are already in use, for example, in modern-day GS vegetation studies including both plant and pollen identification, is highly recommended.

Given the results presented here, performing paleoecological analysis of additional GS sequences of Pleistocene age would be very helpful to support or refute the hypothesis proposed regarding a different extent of vegetation types prior the Early Holocene. Within the paleoecological approach, the study of nearby and poorly studied or unstudied areas would offer a more regional view of the ecological processes that have occurred in GS. Locations such as the northern GS, which have been uncharacterized from a paleoecological point of view until recently (Leal, 2010), might provide new insights regarding the landscape evolution of the region.

In addition to climate and other drivers, fire has been and remains an important disturbance factor in GS, as was highlighted in Chapter 7. The long-term fire regime reconstruction of these sequences through charcoal, pteridophyte spores and NPP analyses revealed important characteristics of past and present GS ecosystems and should be incorporated into conservation policies for the region. This kind of study is encouraged for further paleo- and neoecological research.

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CHAPTER 9:

Conclusions.

Estos son mis principios, si no les gustan tengo otros.
Groucho Marx.

The main conclusions of this work, based on the preceding chapters, are listed below and grouped according to the principal objectives put forth in Chapter 1.

9.1. An increase in useful proxies and adjustment of laboratory techniques for neotropical sediments.

- Pteridophyte spore and NPP identification, as well as charcoal analysis, have provided useful and complementary information regarding neotropical paleoecology, allowing independent inferences to be made regarding past ecological dynamics.

- A multidisciplinary approach, both within and outside paleoecology, has been essential for understanding GS landscape dynamics.

9.2. Reconstruction of southern Gran Sabana plant communities since the Late Glacial period to the present.

- The GS landscape has suffered several vegetation shifts since the Late Glacial period. During the Late Glacial/Early Holocene transition (LG/EH), the southern GS landscape seems to have comprised a mixture of forests, shrublands, and grasslands, without the characteristic present-day dominance of treeless savannas. The appearance and establishment of the current GS ecosystems has been documented from the last two millennia onwards.

- Climate and fires have acted as major drivers with respect to GS landscape dynamics, although other factors, such as edaphic conditions, probably also influenced succession processes. Regarding the main forcing factors, climate played a major role since the Late Glacial period until the Mid-Holocene, influencing processes such as the savanna expansion occurred in the Early Holocene and the forest extent variations during the Holocene. However, fire has been crucial since the Late Holocene in shaping the present-day GS landscape, decreasing the forest coverage and allowing the appearance and expansion of *morichales*, as well as favoring persistence and expansion of savanna during the Holocene.

9.3. Compilation of paleoecological research carried out in Gran Sabana thus far.

- The Lake Chonita record has allowed documentation of the susceptibility of neotropical midlands to widespread rapid climatic events, such as the YD cold reversal, especially with respect to the increase in temperatures registered subsequently during the onset of the Early Holocene, which was manifested in this record by a dramatic vegetation shift.

- The joint interpretation of all southern GS sequences studied to date has provided indications of some general regional climatic trends. An increase in temperatures (a warm and wet phase) during the LG/EH, a likely dry interval from 8 to 5 cal kyr BP, and a wetter phase during the Mid-Holocene centered around 4 cal kyr BP have been documented.

- The present results have assisted in the validation or rejection of former hypotheses concerning GS ecosystem dynamics: i) the Late Pleistocene age of the Lake Chonita sequence has refuted the assumption regarding extended aridity prior to the Holocene; and ii) the appearance of *Mauritia* in GS over last two millennia has supported the hypothesis of a post-glacial expansion of this palm.

- The features associated with the *morichal* appearance in GS have revealed that the establishment of *Mauritia* in the region is probably the result of an interaction between biogeography (post-glacial expansion), climate (humid conditions), and humans (fire). Moreover, the parallel appearance of *Mauritia* stands and the increase in local fires has suggested a pyrophilous nature for this taxon in terms of its rapid colonization of burned areas if adequate climatic conditions for this palm exist.

9.4. Study of the Gran Sabana fire regime and inferences about human settlements.

- The general and dramatic increment of fire activity from 2000 cal yr BP onwards registered in the analyzed sequences has indicated this date as the probably time of the Pemón arrival to the region, in contrast to former assumptions suggesting the last few centuries.

- The paleoecological data presented here have revealed key aspects concerning human occupation in GS. First, the existence of fires at the Lake Chonita catchment *ca.* 12.4 cal kyr BP has led to a hypothesis regarding a human presence, at least intermittently, around the region since the LG/EH. The El Paují record has provided clear evidence of Holocene human settlements that differed in their practices from those currently living in the region. Finally, the last millennia has been characterized by an increased human impact, with the GS landscape being heavily managed by indigenous people (Pemón) according to their needs, which has resulted in savanna expansion.

- The main effect of the fire activity in GS observed in the long-term has been decreased landscape diversity (manifested by the decline in extent of forests and savanna expansion), rather than appearing to represent a sustainable measure for ecosystem management, as has been proposed by other authors. Thus, there is a need for successful conservation strategies in GS given ongoing and future climatic change and the existing high-intensity fire regime in the region. Overall, the evidence provided in this study has highlighted the complex relationship between all drivers implicated in past, present, and future GS ecosystem trends.

They may take our lives,
but they'll never take our freedom!
William Wallace; Braveheart.