INVESTIGATING ENVIRONMENTAL (CLIMATE AND VEGETATION) CHANGE OF EASTERN AMAZONIA DURING PLEISTOCENE AND HOLOCENE USING MULTI-PROXY ANALYSIS

Dissertation
for the award of the degree
“Doctor of Philosophy” (Ph.D. Division of Mathematics and Natural Sciences)
of the Georg-August-Universität Göttingen

within the doctoral program Biodiversity and Ecology

submitted by
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from Tonekabon (Iran)
Göttingen, 2018

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Date of the oral examination: 10th January 2017

To my family

and

everybody who has taught me a single word

Contents

Acknowledgment

Studying in Göttingen, beyond learning pollen types, interpretation of pollen diagrams and statistical analysis, was an opportunity for me to meet and work with people from nearly 20 different nations. Here I learnt how to feed my ambition, develop my ideas (and partly my dreams), and manage my projects. More important I improved my ability of being patient (but not indolent) at work. All these were possible under supervision of a nice man whose calm, positive and hopeful face fascinated me and all my international colleagues to make our small family of palynologists in Göttingen. He has never forced me to follow him and instead let me to test my own crazy ideas. He has been always supportive and open minded about the projects I have proposed. A warm appreciation from me and my family to Prof. Dr. Hermann Behling.

The second person who has inspired me during my PhD and I really owe my successes to him as well is Dr. Thomas Giesecke. I appreciate his attempts to teach me how to think and look in a different way and also for introducing me the nice world of R (software). Special thanks to his occasional frank advice.

I am grateful for receiving the prestigious fund from Erasmus Mundus SALAM project that makes it possible for me to carry out my PhD in Germany. I also would like to thank the very nice coordinators of SALAM project both in Warsaw and Göttingen international office.

It was my pleasure to share the funny and enjoyable time I had in our department with my nice colleagues especially my best friend Dr. Jörg Christiansen. I received many helps from them and some of my ideas rose up when I talked or listen to them. Among my colleagues special thanks to Dr. Isabelle Matthias, Dr. Barbara Hermanowski, Dr. Jackson Martin Rodrigues and Paula Andrea Rodríguez Zorro who coauthored my manuscripts.

In my second manuscript that was a review on 19 years of palynological researches done by Prof. Behling and his colleagues, many people and funding institutes have contributed that I don't know them personally. I would like to express my gratitude to their great job that makes the base of my review.

The last but not the least, I will be grateful forever for all the encouragement from my family, specially my beloved one, Elmira Khansaritoreh for her constant love and support, and staying with me in all the difficult moment during the last decade. Of course the words are not capable to express my appreciation of her presence in my life.

Summary

This thesis contributes to better understanding of long-term vegetation history in eastern Amazonia and the possible role that climate, fire, soil and human may play to change the landscape. To achieve this aim, three new sediment records form eastern and southeastern Amazonia have been studied with a multi-proxy approach (pollen, charcoal, lithology, extractable Fe, remote sensing) and seven already published palynological records from other parts of tropical South America have been reviewed.

The first record named Curiaú (CUR) retrieved from a small swamp near the mouth of Amazon River. This 750 cm sediment core presents the first continuous record of vegetation change from the coastal savanna belt since the last 11600 cal yr BP. Occurrence of such savanna belt that cover the coastal area from British Guiana to northeastern Brazil cannot be explained by present-day climate. Therefore investigating the long-term environmental change in the area helps to find the origin of this unexpected savanna. Results indicate that the savanna has been always present since the beginning of the Holocene. However, the size and composition of the forest surrounding the study site experienced strong changes. The onset of Holocene was accompanied by a forest type composed primarily of the genus *Micropholis* (Sapotaceae) that has no modern analog and was more likely a relict of previously more extensive forest developed under cooler and moister Late Glacial conditions. This forest became locally extinct after 11,200 cal yr BP when an already existing grassy savanna with few scattered shrubs and trees replaced the forest. The savanna expansion occurred under a drier phase probably due to displacement of Intertropical Convergence Zone (ITCZ) to its northernmost position. Presence of pollen from mangrove trees of *Rhizophora* together with signals of swamp forest formation since the early Holocene and later (at ca. 10,000 cal yr BP), the *Mauritia* swamp development in the coastal depressions imply early Holocene sea level rise that caused rise of the ground water table. During the mid-Holocene between 8500 and 5600 cal yr BP gallery forest (composed mainly of Euphorbiaceae) and swamp forest succeeded the treeless savanna. This implies a wetter climatic condition probably due to collision of ITCZ and SACZ. The modern vegetation with continuous changes in the area of forest prevailed at ca. 5600 cal yr BP. This unstable condition might occur due to the intensification of ENSO that hampered the stability of the ecosystem during the last 5 millennia. Frequent charcoal particles especially during the early Holocene may imply that natural and/or anthropogenic fires might be the reason for occurrence of the savanna. However the synchrony of vegetation changes with the climate dynamics propose that climate is the main factor that maintain the coastal savanna belt.

A review on 8 palynological records (including CUR) from 5 different lowland ecosystems located in Amazonia and surroundings indicates that the predominance of forests with specific taxa composition as was recorded in CUR, might occur synchronously in the whole lowland tropical South America during the Late Glacial-Holocene Transition (LG-HT ≈ 13,000-10,000 cal yr BP). Because the palaeo-precipitation proxies from the Andes and the Amazon River Fan proposed that the LG-HT,

especially the Younger Dryas chronozone (YD, ca. 12,800-11500 cal yr BP) has been the driest period in the Amazon Basin, prevalence of such forest during the LG-HT is questionable. To explain this inconsistency between vegetation and climate, three different scenarios are propose based on the specific taxa composition and climatic condition of LG-HT.

The second sediment core called Vereda (VRD) was taken from a small swamp surrounded with fringe of *Mauritia*. This record reveals constant dominance of *Mauritia* around the swamp and occurrence of open savanna in surrounding area since 2500 cal yr BP. Because there is no significant correlation between fire frequency and the percentage of *Mauritia* neither in VRD nor in some other records from eastern Amazonia, the previous belief about the role of manmade fire in the late Holocene expansion of *Mauritia* is dubious. In order to further examine the relation between dynamics of *Mauritia*, fire frequency, ENSO intensity, history of human settlement and sea level changes a review on different records from tropical South America is required.

The third sediment core (Buriti (BRT)) was recovered from a forest hollow on the slopes around the plateau of Serra Sul dos Carajás located on southeastern Amazonia. This record shows constant dominance of forest elements on the slopes of the plateau since 6600 cal yr BP whereas the records from savanna on top of the plateau demonstrate the maximum signal of arboreal vegetation since 2500 cal yr BP. Because the site BRT is located in a short distance from modern forest borders and almost at the same elevation, it can be concluded that through a slow process lasted for ca. 4000 years forest borders shifted toward savanna horizontally. Therefore it can be proposed that some limiting factors might delay the forest expansion. Among different possible factors, natural or anthropogenic fires in the savanna and human hunting/gathering activities may play an important role by pushing back the forest borders. However the evidence suggests that this long period was more likely spent on the formation of sufficient soil layer that could support forest establishment.

In general the results of our studies clearly suggest that although the role of fire and human cannot be excluded, vegetation dynamics in eastern part of tropical South America is mainly derived by climatic and geological factors such as LG-HT specific climatic condition, sea level changes, shift in position of ITCZ and intensification of ENSO. Where the climatic conditions are equal, the different vegetation histories in adjacent ecosystems might be due to difference in soil properties.

In addition it has been realized that there are synchronous vegetation signals in the records from different location of tropical South America since the Late Glacial. The LG-HT expansion of a specific forest type, the early to mid-Holocene savanna expansion and the late Holocene forest expansion are the most important synchronous changes. The latter two changes are attributed to the shift in position of ITCZ due to the change in insolation according to Milankovitch cycles. Increase in population of *Mauritia* also shows some degrees of synchrony among different records that must be more investigated.

Acronyms

AMS: Accelerator Mass Spectrometry
BRT: Buriti
Cal yr BP: Calibrated year Before Present
where present is 1950 A. D.
CUR: Curiaú
ENSO: El Niño-Southern Oscillation
FCC: False Color Composite
ITCZ: Inter Tropical Convergence Zone
LDC: Lagoa da Cachoeira
LG-HT: Late Glacial-Holocene Transition
LGM: Last Glacial Maximum
m a. s. l. : meter above sea level
NDVI: Normalized Difference Vegetation Index
NTUAMS = National Taiwan University AMS laboratory.
OM: Organic Material
PC: Principal Component
PCA: Principal Component analysis
PDM: Pántano da Maurítia
SST: Sea-Surface Temperatures
SACZ: South Atlantic Convergence Zone
VRD: Vereda
YD: Younger Dryas

I. Introduction

The knowledge obtained from palynological research in Amazonia reveals that the Amazonian ecosystems and biodiversity were not constant during the late Quaternary. Some plants or plant communities those were dominant in the ancient time became extinct and others prevailed since the late Holocene. Forest-savanna boundary has been subjected to continuous changes since the Last Glacial Maximum (LGM). Forest expanded into the savanna during the wet periods and contracted when a dry climate condition prevailed.

Such marked changes in biodiversity and ecosystems under the upcoming climate change can directly affect human life. For example the carbon stored in the Amazonian trees and soil is much higher than that stored in savanna. Therefore tree death and savanna expansion caused by long term drought will release the carbon dioxide into the atmosphere and intensify the greenhouse effect. In this regard palaeoecological researches afford an efficient way to better understand and predict the future of Amazonia based on its climate and vegetation history.

Considering the vast expanse of the Amazonia, the available palaeoecological records are very few leading to a low resolution reconstruction of Amazonian environmental history. To emphasize the necessity of current study, the gaps in our knowledge of eastern Amazonian vegetation history is discussed here.

1. Gaps in palaeoecology of eastern Amazonia

Despite the huge extent of the region that is considered as eastern Amazonia, the number of palaeoecological studies is rare. Even where such records are available still there are large gaps of knowledge to be filled. In the following there are some examples of open questions that need to be addressed by palaeoecological studies.

- A belt of savanna occurs along the 2000 km coastal line of British Guiana, Surinam, French Guiana, and Brazil. The widest part of this belt is located in State of Amapá in Brazil but it also extents to Marajo Island and in part in the state of Pará. There is no record from this savanna in state of Amapá that shows its dynamics since the onset of the Holocene. The two sediment cores that have been already retrieved from coastal savanna of the State of Amapá (near Macapá) recorded the vegetation history of the area since mid-Holocene (Toledo & Bush 2007). Therefore the origin and long-term vegetation history of the coastal savanna belt on the northeast of South America is so far an open questions that needs still detailed high resolution records of a long time period to be answered.
- The studies from this long coastal area mainly focus on the sea level oscillations and mangrove dynamics (Cohen et al., 2012). Among these studies there are only two records from State of Pará

that cover the whole Holocene (Behling, 2001; Vedel et al., 2006). These records show signals of mangrove since the early Holocene implying that the early Holocene sea level rise has occurred faster than what has been claimed before. To obtain a better understanding of sea level changes along northern coast of South America more records are necessary from further northern part of the coastal belt.

- The savanna on the plateau of Serra Sul dos Carajás in southeastern Amazonia is well studied by four palaeoecological records (Absy et al., 1991; Hermanowski et al., 2014, 2012; Sifeddine et al., 2001). Nevertheless there is no record from forest on the slopes around the plateau. Realizing the dynamics of forest surrounding the savanna region is of especial importance to understand the long-term forest-savanna boundary shift.
- Reviews on the major trends of vegetation dynamics can contribute to our comprehension of synchronous vegetation changes in Amazonia and surrounding and therefore the large scale climatic events behind these changes. However still more high resolution and well dated records are required to find the differences in timing of significant vegetation changes between eastern and western regions of Amazonia. For example it is not investigated if the coastal savanna in Amapá state near the mouth of Amazon River experienced the same trend of savanna expansion during the early to mid-Holocene and forest expanded in this region during the late Holocene as it is recorded in savanna of Llanos Orientales (Behling and Hooghiemstra, 1999, 1998).

  Some reviews are available about topics such as the vegetation history of tropical South America since the Late Glacial (Mayle et al., 2004) and the increase in population of *Mauritia* palm during the late Holocene (Rull and Montoya, 2014). However these reviews need to be updated based on the new results obtained in the recent years or be rewritten from another point of view. For example it has not been so far discussed in detail that if the YD period has been the direst period since the Late Glacial (Maslin and Burns, 2000; Maslin et al., 2011), how has been the response of Amazon forests to this particular period of time. In addition the interpretation of pollen data from intervals like YD suffers from uncertainties about palaeoclimate data (van Breukelen et al., 2008).

2. Objectives of this thesis

This thesis use palynology, charcoal analysis, lithology and measurement of soil extractable Fe as well as remote sensing on three study sites in eastern Amazonian regions to address the following objectives and research questions:

I. The origin of coastal savanna belt and its dynamics during the Holocene.
    - Since when the savanna occurred in the landscape and when did the major changes in vegetation occur?
    - What is the role of climate (in particular ITCZ and SACZ), fire and human to form the modern landscape of coastal savanna belt?

- Is there any synchrony in vegetation changes between the records from eastern and other parts of Amazonia?

II. The sea level oscillations since the early Holocene and its effect on vegetation of South American northern coastal belt.

- Since when did the mangrove belt became established near the modern coastline?
- How did the sea level change affect the plant communities on the northern coast of South America?

III. The temporal and spatial extent and properties of the specific forest type that covered Amazonia during the transition from Late Glacial to Holocene.

- When and for how long did these forests occur in Amazonia?
- How was the taxa composition of these forests and under which condition did these forests occur?
- Can the environmental conditions of LG-HT give us an insight into the future of Amazonia under the upcoming climate changes?

IV. Forest-savanna boundary shifts in the plateau of Serra Sul dos Carajás since the mid-Holocene

- Did the forests on the slopes of the plateau exist since the mid-Holocene? Did these forests experienced marked changes during this period similar to what occurred in the savanna on the top of the plateau?
- When did the forest border started to shift toward the savanna? And what triggered this shift?
- How long does it take for the forest to reach its modern borders in the edaphic savanna and what were the limiting factors for forest expansion?

V. The population dynamics of *Mauritia* palms in eastern Amazonia and a review on its expansion in tropical South America.

- Was the expansion of *Mauritia* around wetlands of tropical South America limited to the late Holocene?
- Did the late Holocene expansion of *Mauritia* depend on manmade fire?

The chapters II to IV are the manuscripts prepared for submission in peer reviewed journals. The chapter II has been already published. Chapter V presents the first results and interpretation which are not complete yet.

The first and second objectives are discussed in chapter II that comprises of the results from pollen and charcoal analyses on the sediment core CUR. This record is the first high resolution and well dated continuous record from State of Amapá that affords a clear image of the Holocene vegetation history of the South American coastal savanna belt.

Chapter III is a review on the 8 palynological records (including the record CUR) from 5 different lowland ecosystems in Amazonia and surroundings and focuses on the objective number III. Also this chapter reviews the available palaeo-climatic studies from tropical South America.

Chapter IV compares the palynological results obtained from a new record called Buriti (BRT) from forest on the slopes around the plateau of Serra Sul dos Carajás with the palynological results from sites located in the savanna on top of the plateau. In this study that focuses on the objective number IV, remote sensing techniques and measurement of soil extractable Fe are used besides pollen and charcoal analyses.

Chapter V uses the palynological results of the record Vereda (VRD) together with the results from CUR to address the questions mentioned in objectives number V. The pollen and charcoal data from other sites in tropical South America will be reviewed in this chapter as well.

3. The study sites—an overview

The three sites studied here are located in northeastern (CUR and VRD) and southeastern (BRT) margins of Amazonia in Brazil (Fig. 1). The sites CUR and VRD are situated in coastal savanna near the city Macapá (capital of Amapá) close to the mouth of Amazon River. The site BRT is located in the forest around the plateau of Serra dos Carajás in State of Pará.

3.1 Climate

Figure 1 shows that all study sites are located in tropical savanna climate or type “Aw” based on the Köppen climate classification (Peel et al., 2007). However according to meteoroidal data from the city Macapá, sites which are located near the mouth of Amazon River (CUR and VRD) are mainly under influence of tropical monsoon climate or type “Am” in the Köppen system (Alvares et al., 2013). The rainfall in both study areas is mainly under influence of three atmospheric components (Fig. 1a):

1. Intertropical Convergence Zone (ITCZ): is a low-pressure belt where warm moist trade winds converge to form a zone of cloudiness and precipitation near the equator. ITCZ seasonally migrates toward the warmer hemisphere. During the austral summer, ITCZ cover nearly the whole tropical South America (Waliser and Jiang, 2014).
2. SACZ: The SACZ is defined as a northwest-southeast-oriented cloud band that is responsible for moisture transfer from the Amazon region to central and southeastern Brazil (Prado et al., 2013). Along the Equator rainfall made by SACZ is at minimum levels in December-February, while the wettest months are April and May (Waliser and Jiang, 2014).
3. ENSO: Is the main cause of inter-annual variability of the SACZ movement (Trenberth, 1997) and its warm phase or El Niño is responsible for rainfall decline during the wet season of northern South America (Marengo et al., 2012; Prado et al., 2013).

Besides these factors, precipitation in the southern Amazonia is also influenced by i) the associated moisture-bearing trade winds from the tropical Atlantic, ii) the evapotranspiration from the Amazon rainforest, and iii) the Amazon convection (Fu et al., 2001; Liebmann and Marengo, 2001; Marengo et al., 1993; Nobre and Srukla, 1996).

In general both regions (Carajás and coastal savanna) experience a seasonal climate comprising of a long wet season and a short dry season. The dry season in site BRT is longer (4 months) and mean annual precipitation is lower compared to CUR and VRD (3 months dry season). This difference implies the sensitivity of southern region of Amazonia to northern position of ITCZ during the dry season. The mean annual temperature in BRT (≈ 25 °C) is lower than the other two sites (≈ 27 °C).

Table 1. Summary of climate data for study areas in northeast and southeast Amazonia.

	Climate (Köppen Classification)	Wet season	Dry season	Mean annual temperature	Mean annual precipitation
East Amazonia*	tropical savanna climate (Aw) with close connection to tropical monsoon climate (Am)	Dec-Aug	Sep-Nov	27 °C	2500-3000 mm
Southeast Amazonia**	tropical savanna climate (Aw)	Nov–Jun	July-Oct	≈25 °C***	1900 mm

***** (IBGE 2002) , ****** (Sifeddine et al. 2001; Lopes et al. 2013), *** Mean annual temperature varies depending on the elevation**.**

3.2 Topography and soil

The sediment cores CUR and VRD are taken from a small swamp and lake, respectively. Both study sites are surrounded by *Mauritia* palm trees. Plenty of such swamps and lakes occur in the area in the meandering palaeo-channels. (Fig. 1b) These channels form a network among the hills that constitute the Pleistocene plain. This hilly plain is result of erosional and depositional processes due to sea-level changes and tectonic movements during the late Pleistocene and Holocene (Guimarães et al., 2013). As these low-laying channels are established only few meters higher than the sea level, small oscillation in water level of Atlantic Ocean and subsequently underground water table can affect the hydrology of the area.

The plateau of Serra dos Carajás (Fig. 1c) comprises of several hills ranging in elevation from 600 to 900 m a. s. l. and is developed upon a banded iron formation (Absy et al., 1991). The soil layer on top of the plateau is very shallow but a thicker soil horizon occurred on the slopes around the plateau (site BRT) and in the depressions. This gradient in soil depth is formed under erosional process that transports weathered material from top of the hills downward and cause a topographic inversion. There are several lakes and depressions on the plateau that are in different stages of filling by sediment (Absy et al., 1991; Hermanowski et al., 2014, 2012; Nunes et al., 2015; Sifeddine et al., 2001; Soubiès et al., 1991)**.** The lateritic substrate underlying the superficial soil horizon causes a series of restrictions to plant establishment, such as forming shallow and patchy infertile soils, high energy absorption from sunshine, raised temperatures, and soil poisoning (Meirelles et al. 1997). The topography and soil are discussed in detail in related chapters.

3.3 Vegetation

The typical vegetation around the *Mauritia* swamp where the study site CUR is located comprises of four different plant communities, which from the margin of the swamp up to the top of the surrounding hills are composed of i) *Mauritia flexuosa* and some stands of *Euterpe* that colonizes the central part of the gallery forest, ii) secondary forest taxa that constitute the outer zone of the gallery forest, iii) savanna with sparse *Byrsonima* shrubs that is positioned between gallery forest and the outer most zone which is iv) grass savanna on top of the hills dominated by Poaceae.

Around the lake where VRD is taken there is a monodominant population of *Mauritia* with a small contribution of gallery forest taxa similar to what occurred around the site CUR. More information on the vegetation of Amapá is available from Carvalho et al. (2006), Costa Neto (2004), Costa Neto et al. (2007) and Costa Neto and Silva (2004).

In the plateau of Serra dos Carajás four different vegetation units are separated according to the soil depth gradient whereby herbaceous *campo rupestre*, shrubby *campo rupestre*, *capão* forests and upland forests grow in shallower to the deeper soil respectively (Nunes et al., 2015). Herbaceous *campo rupestre* is an open vegetation covered by small shrubs. Shrubby *campo rupestre* is supported on more fragmented ironstone cap (canga) that provides a softer medium for root development. Vegetation is composed of a denser population of tall shrubs and herbaceous plants. *Capão* forests form isolated small islands of semi-deciduous forest within *campo rupestre* vegetation. Montane forests are dense ombrophilous forest established on the margin of plateau (Nunes et al., 2015).

4. Methodology

4.1 Fieldwork

Sediment cores CUR and VRD were taken by Hermann Behling and Marcelo Cohen in 2004 and BRT was taken by Hermann Behling and Marcondes Lima da Costa in 2005. All cores were retrieved using a Russian corer. Sediments were wrapped in cellophane film and placed in PVC tubes to prevent the drying. Cores were transported to Federal University of Pará (UFPA) in Belém, Brazil and stored in darkness at 4 °C.

4.2 Laboratory work

After the fieldworks the CUR that is a 7.5 m sediment core was subsampled in Brazil and the subsamples were taken to Department of Palynology and Climate Dynamics, in University of Göttingen, Germany. VRD and BRT were transported to Göttingen as complete sediment cores and were subsampled there. Prior to subsampling, the cores were photographed and the lithology of the cores was described based on their physical attributes (color, grain size, plant remains). From each section of the cores with different lithological properties one 0.5 cm^3 test subsample was taken. These test subsamples give an idea about the pollen concentration in the sediment and the amount of the sediment needed for the next steps. The interval of subsampling was decided after the ages for the bottom of the cores were determined. After counting the pollen content of the first set of subsamples, in VRD few additional subsamples were taken from intervals between the previous subsampling points.

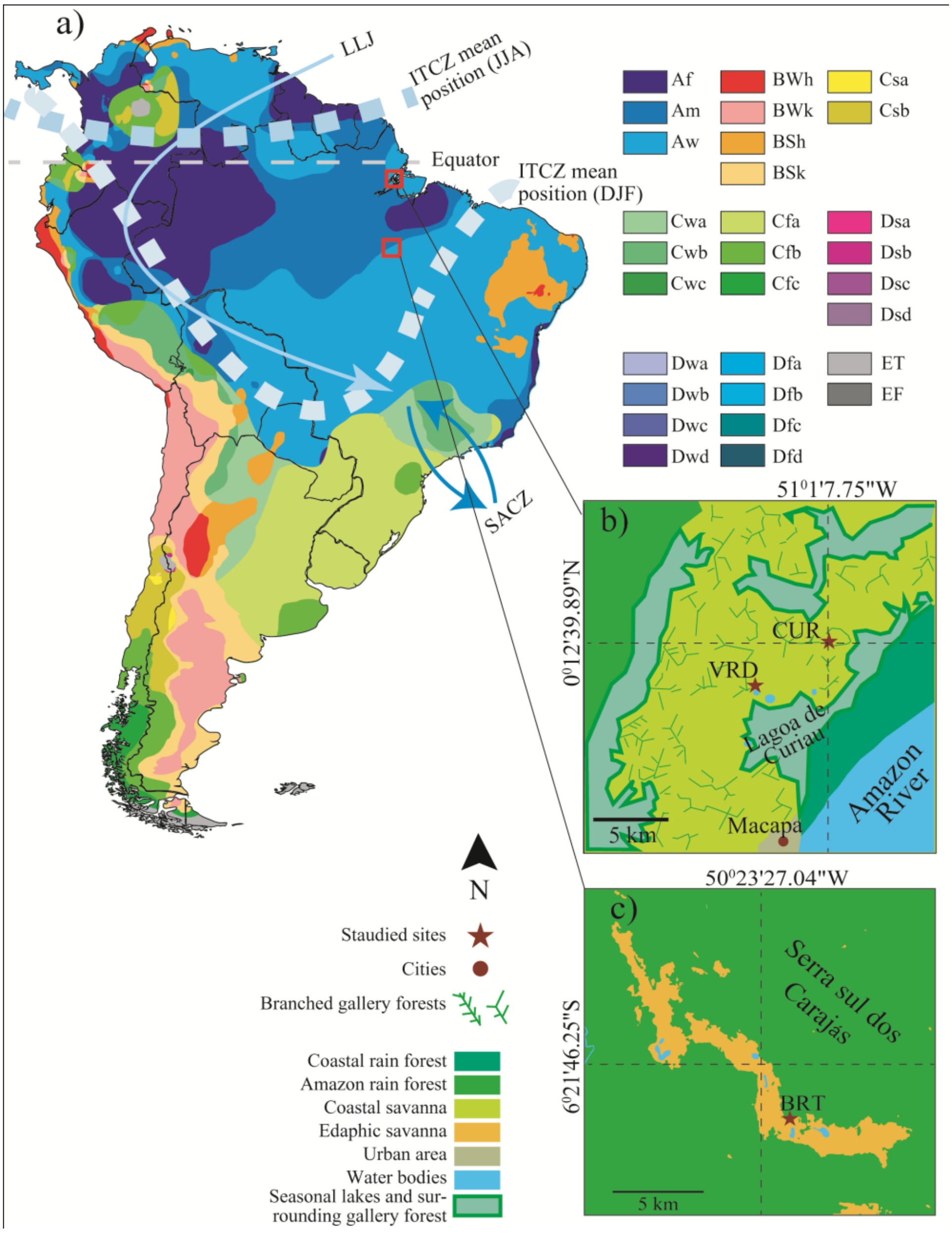

Fig. 1. Map showing the study areas. (a) Climate of South America according to Köppen Climate Classification besides the main air circulation systems. (b) The coastal savanna near mouth of

Amazon River and the location of study sites CUR and VRD. (c) The plateau of Serra dos Carajás and the location of the study site BRT.

4.2.1 Slide preparation for pollen and charcoal

At the first steps the subsamples were added to 5 ml of a solution composed of *Lycopodium* tablets dissolved in hydrochloric acid (HCl) 10%. Each tablet contains 20848 ± 1546 spores of *Lycopodium clavatum* that can be easily identified under the microscope. The counted number of this exotic marker against counted number of pollen grains is used for calculation of pollen concentration (Stockmarr, 1971). The number of tablets used per subsample varied based on the volume of the subsample and the preliminary estimation of pollen content (via test subsamples) in the lithological section where the subsample is taken. HCl is used to dissolve the Calcium Carbonate in the tablets and in the subsamples (where available). The mixture of HCl, sediment and tablet is sieved using a 150 micron mesh. Then 5 ml hydrofluoric acid (HF) is applied to subsamples in order to dissolve minerals. Subsamples stay overnight in this step. In the next step subsamples are dehydrated with acetic acid to be treated by a mixture of one unit concentrated Sulfuric acid and 9 units Acetic Anhydride for 5 minutes in warm water 50 °C. The acetolysis remove cellulose (intine) from the pollen surface so that the ornamentation on exine can be better observed under the light microscope. In order not to damage small pollen grains, the acetolysis step is slightly modified compared to the original method by Faegri and Iversen (1989) that use a hot water bath (90 °C) for 10 minutes. After acetolysis and washing with distilled water, the product is mounted on slides together with glycerin gelatin to be used for light microscopy.

4.2.2 Radiocarbon dating and age-depth modeling

In total 21 samples were radiocarbon dated using Accelerator Mass Spectrometry (AMS) to provide chronologies for the records (Table 2). The calibration of dates was implemented in R using different methods. For the record CUR, method Clam 2.2 (Blaauw, 2010) and Northern Hemisphere terrestrial calibration curve IntCal13 (Reimer, 2013) were used. The age-depth model of VRD and BRT were plotted in Bacon 2.2 (Blaauw and Christeny, 2011) using IntCal13 and SHCal13 (Hogg et al., 2013) respectively. In chapter III, in order to avoid errors caused by application of different calibration methods, the calibration and age-depth modeling were redone for all 8 palynological records using appropriate calibration curves depending on the position of the records (Northern/Southern Hemisphere). In this chapter Oxcal (Bronk Ramsey, 2001) is used because it offers the possibility of extracting the age probability distribution for each depth. Then the probability distributions for desired depths are plotted together in R to make a sum of probabilities that show the temporal extent of a specific event. For the detailed methodology of age-depth modeling please see chapter II-IV.

4.3 Pollen and spore counting

The pollen counting and identification were done under the light microscopy. For the records CUR and VRD counting continued up to at least 300 terrestrial grains. But for BRT, besides the criterion of 300 terrestrial grains, counting is continued to also reach the number of 100 *Lycopodium* spores (marker). These measures are adopted to reduce the error in our dataset. However sometimes due to the very low pollen concentration in subsamples, a lower number of grains were counted. The identification of pollen types was carried out using literature (Roubik and Moreno, 1991; Colinvaux et al., 1999; Carreira and Barth, 2003) and pollen reference collection available at the Department of Palynology and Climate Dynamics, University of Göttingen. In total 93 pollen and 10 spore types were distinguished, mostly to family and genus and rarely to species level. A relatively high amount of pollen types remained unknown.

4.4 Data analysis, interpretation and presentation

The data produced from pollen counting is presented as percentage, concentration and influx diagrams. These three values are calculated via the following equations:

> Percentage of pollen type X = (number of counted pollen type X / total sum of terrestrial pollen) x100
>
> Concentration of pollen type X (grains/cm^3) = (number of counted pollen type X x number of spores in each *Lycopodium* tablet x number of tablets) / (number of counted *Lycopodium* spore x sample volume)
>
> Influx of pollen type X (grains/cm^2/year) = Concentration of pollen type X (grains/cm^3) x Accumulation rate (cm of sediment/year) for the depth that subsample is taken from

Accumulation rate can be obtained either from output .txt file from Clam (if Clam is used) that is automatically named "core name_interpolated_ages.txt" or via the equation below:

> Accumulation rate = (depth N_2 - depth N_1) / (interpolated weighted mean age of depth N_2 - interpolated weighted mean age of depth N_1)

These calculations are done in Excel and the results are plotted in TILIA and TILIAGRAPH, version 2 (http://www.ncdc.noaa.gov/paleo/tiliafaq.html) as X axis where the depth and age scale constitute the Y axis. For charcoal the number of particles, concentration and influx and for extractable Fe the concentration (mg/l) are plotted. In chapter III, the percentage and influx diagrams as well as climate data are plotted in R.

Ecological grouping of the identified pollen taxa is done according to the online plant species list in Brazil (http://floradobrasil.jbrj.gov.br) and floristic studies in the area (Cleef and da Silva, 2008;

Marchant et al., 2002; Nunes et al., 2015, 2009; Silva et al., 1996). The zonation of pollen diagrams is carried out using CONISS either in TILIA (Grimm, 1987) or in R.

The Principle Component Analysis (PCA) is done in R using packages Vegan (Oksanen et al., 2016), Cluster (Maechler et al., 2015), Analogue (Simpson 2015) and Rioja (Juggins 2015).

Table 2. Details of samples sent to AMS ^{14}C laboratory and the results of dating.

Sediment core	AMS Lab ID	Depth (cm)	Material	^{14}C dates	Weighted mean calibrated date (cal yr BP)
CUR	NTUAMS-580	50	**Data not available**	1606±10	1481
	NTUAMS-581	100	**Data not available**	2994±16	3205
	NTUAMS-582	150	**Data not available**	4162±26	4707
	NTUAMS-345	200	**Data not available**	5092±28	5828
	NTUAMS-583	300	**Data not available**	6471±30	7377
	NTUAMS-346	400	**Data not available**	9268±40	10431
	CUR-500	500	**Data not available**	8711±57	9685
	NTUAMS-723	550	**Data not available**	9165±38	10328
	NTUAMS-347	600	**Data not available**	10160±50	11831
	CUR-700	700	**Data not available**	9610±67	10948
	NTUAMS-724	745	**Data not available**	9873±164	11433
VRD	NTUAMS-1168	34	Wood	438±1	485
	NTUAMS-1773	47	Plant remains	1612±8	1425
	NTUAMS-1449	58	Wood	2352±21	2355
	NTUAMS-1169	75	Wood	1542±6	1446
	NTUAMS-1774	77	Plant remains	2378±18	2465
BRT	NTUAMS-1771	33	Organic material	1295±6	1240
	NTUAMS-1166	53	Charcoal	2745±16	2782
	NTUAMS-1167	53	Organic material	4320±26	4898
	NTUAMS-2019	80-82	Bulk sediment	5270±20	5949
	NTUAMS-1772	83	Plant remains	814±5	722

4.5 Remote sensing

Remote sensing of Landsat 8 images is done in Arc GIS for desktop 10.2 to produce maps. In particular remote sensing is used in chapter IV to find the relation between vegetation, elevation and ferruginous soil. For this purpose, cloud free Landsat 8 / OLI satellite images captured in May and August 2013 were used. To correct the effect of different sun angles in different seasons, radiometric calibration (top of atmosphere reflectance) is done on the images. Normalized Difference Vegetation Index (NDVI) was calculated to quantify vegetation differences throughout the landscape and to measure the seasonal change in vegetation cover. The values for elevation are calculated based on Aster Global Digital Elevation Model (GDEM) with 30 meters horizontal and vertical resolution.

The Sabins color composite (Sabins, 1999) is produced using spectral band ratios red/SWIR1 (4/6) and red/blue (4/2) and SWIR1/SWIR2 (6/7) combined in red, green and blue channels respectively. The produced map reflects the ferruginous soil in orange, red and magenta. The vegetation is shown in shiny green. Information obtained through several fieldworks can confirm the authenticity of the produced maps. The relation between vegetation distribution, ferruginous soil and elevation was examined by means of correlation matrix between NDVI, band ratio 4/2 and Aster DEM.

References

Absy, M.L., Cleef, A., Fournier, M., Martin, L., Servant, M., Sifeddine, A., Ferreira da Silva, M., Soubiès, F., Suguio, K., Turcq, B., Van der Hammen, T., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le Sud-Est de l'Amazonie au cours des 60 000 dernières années : première comparaison avec d'autres régions tropicales. Comptes Rendus l'Académie des Sci. 2 Mécanique. 312, 673–678.

Alizadeh, K., Cohen, M., Behling, H., 2015. Origin and dynamics of the northern South American coastal savanna belt during the Holocene – the role of climate, sea-level, fire and humans. Quat. Sci. Rev. 122, 51–62. doi:10.1016/j.quascirev.2015.05.009

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. K??ppen's climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. doi:10.1127/0941-2948/2013/0507

Behling, H., 2001. Late Quaternary enviornmental changes in the Lagoa da Curuça region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. Veg. Hist. Archaeobot. 10, 175–183. doi:10.1007/PL00006929

Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. J. Paleolimnol. 21, 461–476. doi:10.1023/A:1008051720473

Behling, H., Hooghiemstra, H., 1998. Late quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 139, 251–267. doi:10.1016/S0031-0182(97)00139-9

Blaauw, M., 2010. Methods and code for "classical" age-modelling of radiocarbon sequences. Quat. Geochronol. 5, 512–518. doi:10.1016/j.quageo.2010.01.002

Blaauw, M., Christeny, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. doi:10.1214/11-BA618

Bronk Ramsey, C., 2001. Development of the radiocarbon calibration program. Radiocarbon 43, 355–363. doi:papers2://publication/uuid/5B399323-3576-4144-BF98-497069142583

Cleef, A.M., da Silva, M.F.F., 2008. Plant communities of the Serra Dos Carajás (Pará), Brazil. Bol. Mus. Para. E. Goeldi. sér. Bot. 10, 269–281.

Cohen, M.C.L., Pessenda, L.C.R., Behling, H., de Fátima Rossetti, D., França, M.C., Guimarães, J.T.F., Friaes, Y., Smith, C.B., 2012. Holocene palaeoenvironmental history of the Amazonian mangrove belt. Quat. Sci. Rev. 55, 50–58. doi:10.1016/j.quascirev.2012.08.019

De Toledo, M.B., Bush, M.B., 2007. A mid-Holocene environmental change in Amazonian savannas. J. Biogeogr. 34, 1313–1326. doi:10.1111/j.1365-2699.2006.01606.x

Fu, R., Dickinson, R., Chen, M., Wang, H., 2001. How do tropical sea surface temperatures influence the seasonal distribution of precipitation in the equatorial Amazon? J. Clim. 4003–4026. doi:10.1175/1520-0442(2001)014<4003:HDTSST>2.0.CO;2

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35. doi:10.1016/0098-3004(87)90022-7

Guimarães, J.T.F., Cohen, M.C.L., França, M.C., Pessenda, L.C.R., de Jesus Souza, E., Nogueira, A.C.R., Alves, R., 2013. Recent effects of tidal and hydro-meteorological changes on coastal plains near the mouth of the Amazon River. Earth Surf. Process. Landforms 38, n/a–n/a. doi:10.1002/esp.3396

Guimaraes, J.T.F., Cohen, M.C.L., Pessenda, L.C.R., Franca, M.C., Smith, C.B., Nogueira, a. C.R., 2012. Mid- and late-Holocene sedimentary process and palaeovegetation changes near the mouth of the Amazon River. The Holocene 22, 359–370. doi:10.1177/0959683611423693

Hermanowski, B., Da Costa, M.L., Behling, H., 2014. Possible linkages of palaeofires in southeast Amazonia to a changing climate since the Last Glacial Maximum. Veg. Hist. Archaeobot. 24, 279–292. doi:10.1007/s00334-014-0472-0

Hermanowski, B., da Costa, M.L., Behling, H., 2012. Environmental changes in southeastern Amazonia during the last 25,000yr revealed from a paleoecological record. Quat. Res. 77, 138–148. doi:10.1016/j.yqres.2011.10.009

Hogg, A., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., Turney, C.S.M., Zimmerman, S.R., 2013. SHCal13 Southern Hemisphere Calibration, 0–50,000 Years cal BP. Radiocarbon 55, 1889–1903. doi:10.2458/azu_js_rc.55.16783

Juggins, S. (2015) rioja: Analysis of Quaternary Science Data, R package version (0.9-9). (http://cran.r-project.org/package=rioja)

Liebmann, B., Marengo, J.A., 2001. Interannual variability of the rainy season and rainfall in the Brazilian Amazon Basin. J. Clim. 14, 4308–4318. doi:10.1175/1520-0442(2001)014<4308:IVOTRS>2.0.CO;2

Lopes, M.N.G., De Souza, E.B., Ferreira, D.B. da S., 2013. Climatologia Regional Da Precipitação No Estado Do Pará. Rev. Bras. Climatol. 12, 84–102.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2015. Cluster Analysis Basics and Extensions. R package version 2.0.1. CRAN.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-Garćia, S., Hooghiemstra, H., Ledru, M.P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev. Palaeobot. Palynol. 121, 1–75. doi:10.1016/S0034-6667(02)00082-9

Marengo, J.A., Druyan, L.M., Hastenrath, S., 1993. Observational and modelling studies of Amazonia interannual climate variability. Clim. Change 23, 267–286. doi:10.1007/BF01091619

Marengo, J.A., Liebmann, B., Grimm, A.M., Misra, V., Silva Dias, P.L., Cavalcanti, I.F.A., Carvalho, L.M. V, Berbery, E.H., Ambrizzi, T., Vera, C.S., Saulo, A.C., Nogues-Paegle, J., Zipser, E., Seth, A., Alves, L.M., 2012. Recent developments on the South American monsoon system. Int. J. Climatol. doi:10.1002/joc.2254

Maslin, M. a, Burns, S.J., 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. Science 290, 2285–2287. doi:10.1126/science.290.5500.2285

Maslin, M.A., Ettwein, V.J., Wilson, K.E., Guilderson, T.P., Burns, S.J., Leng, M.J., 2011. Dynamic boundary-monsoon intensity hypothesis: Evidence from the deglacial Amazon River discharge record. Quat. Sci. Rev. 30, 3823–3833. doi:10.1016/j.quascirev.2011.10.007

Mayle, F.E., Beerling, D.J., Gosling, W.D., Bush, M.B., 2004. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 359, 499–514. doi:10.1098/rstb.2003.1434

Nobre, P., Srukla, J., 1996. Variations of Sea Surface Temperature, Wind Stress, and Rainfall over the Tropical Atlantic and South America. J. Clim. doi:10.1175/1520-0442(1996)009<2464:VOSSTW>2.0.CO;2

Nunes, J.A., 2009. Florística, estrutura e relações solo-vegetação em gradiente fitofisionômico sobre canga, na Serra Sul, FLONA de Carajás - Pará.

Nunes, J.A., Schaefer, C.E.G.R., Júnior, W.G.F., Neri, A. V., Correa, G.R., Enright, N.J., 2015. Soil-vegetation relationships on a banded ironstone “island”, Carajás Plateau, Brazilian Eastern

Amazonia. An. Acad. Bras. Cienc. 87, 2097–2110. doi:10.1590/0001-376520152014-0106

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., O'Hara, R., 2016. Vegan: community ecology package. R Packag. 2.3-3. doi:10.4135/9781412971874.n145

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Ko¨ppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644. doi:citeulike-article-id:8144782

Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. t., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. Science (80-.). 323, 1344–1347. doi:10.1126/science.1164033

Prado, L.F., Wainer, I., Chiessi, C.M., Ledru, M.P., Turcq, B., 2013. A mid-Holocene climate reconstruction for eastern South America. Clim. Past 9, 2117–2133. doi:10.5194/cp-9-2117-2013

Reimer, P., 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. Radiocarbon 55, 1869–1887. doi:10.2458/azu_js_rc.55.16947

Rull, V., Montoya, E., 2014. Mauritia flexuosa palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. Quat. Sci. Rev. 99, 17–33. doi:10.1016/j.quascirev.2014.06.007

Sabins, F.F., 1999. Remote sensing for mineral exploration. Ore Geol Rev 14, 157–183.

Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubiès, F., Cordeiro, R.C., Suguio, K., 2001. Variations of the Amazonian rainforest environment: A sedimentological record covering 30,000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 168, 221–235. doi:10.1016/S0031-0182(00)00256-X

Simpson, G.L. and Oksanen, J. 2016. analogue: Analogue matching and Modern Analogue Technique transfer function models. (R package version 0.17-0). (http://cran.r-project.org/package=analogue).

Silva, M., Secco, R., Lobo, M., 1996. Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. Acta Amaz. 26, 17–44. doi:10.1590/1809-43921996261044

Soubiès, F., Suguio, K., Martin, L., 1991. The Quaternary lacustrine deposits of the Serra dos Carajás (State of Pará, Brazil): ages and other preliminary results. Bol. IG-USP. 223–243.

T., M.S., E.A., D.M., A.C., D.S., 1997. Potential desiccation tolerant vascular plants from Southeastern Brazil. Polish J. Environ. Stud. 06.

Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. The Holocene 13, 499–505. doi:10.1191/0959683603hl615rp

Trenberth, K.E., 1997. The Definition of El Niño. Bull. Am. Meteorol. Soc. 78, 2771–2777. doi:10.1175/1520-0477(1997)078<2771:TDOENO>2.0.CO;2

van Breukelen, M.R., Vonhof, H.B., Hellstrom, J.C., Wester, W.C.G., Kroon, D., 2008. Fossil dripwater in stalagmites reveals Holocene temperature and rainfall variation in Amazonia. Earth Planet. Sci. Lett. 275, 54–60. doi:10.1016/j.epsl.2008.07.060

Vedel, V., Behling, H., Cohen, M., Lara, R., 2006. Holocene mangrove dynamics and sea-level changes in northern Brazil, inferences from the Taperebal core in northeastern Pará State. Veg. Hist. Archaeobot. 15, 115–123. doi:10.1007/s00334-005-0023-9

Wanner, H., Beer, J., Butikofer, J., Crowley, T., Cubasch, U., Fluckiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J., 2008. Mid- to Late Holocene climate change: an overview. Quat. Sci. Rev. 27, 1791–1828. doi:10.1016/j.quascirev.2008.06.013

II. Origin and dynamics of the northern South American coastal savanna belt during the Holocene – the role of climate, sea-level, fire and humans

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Published in *Quaternary Science Reviews (2015) 122: 51–62*
http://dx.doi.org/10.1016/j.quascirev.2015.05.009

Abstract

Occurrence of a coastal savanna belt expanding from British Guiana to northeastern Brazil cannot be explained by present-day climate. Using pollen and charcoal analyses on an 11,6000 years old sediment core from a coastal depression in the savanna belt near the mouth of the Amazon River we investigated the paleoenvironmental history to shed light on this question. Results indicate that small areas of savanna accompanied by a forest type composed primarily by the genus *Micropholis* (Sapotaceae) that has no modern analog existed at the beginning of the Holocene. After 11,200 cal yr BP, savanna with scattered shrubs replaced the forest. At this time swamp forest developed in the depressions and it was replaced by *Mauritia* swamp at ca. 10,000 cal yr BP. Between 8,500 and 5,600 cal yr BP gallery forest (composed mainly of Euphorbiaceae) and swamp forest succeeded the treeless savanna. The modern vegetation with alternating area of gallery forest established after 5,600 cal yr BP. We suggest that the early Holocene forest is a relict of previously more extensive forest under cooler and moister late glacial conditions. The early Holocene savanna expansion indicates a drier phase probably related to the shift of the Intertropical Convergence Zone (ITCZ) towards its northernmost position. The mid-Holocene forest expansion is probably a result of the combined influence of ITCZ and SACZ. The ecosystem variability during the last 5,600 years, formed perhaps under influence of intensified ENSO condition. High charcoal concentrations, especially during the early Holocene, indicate that natural and/or anthropogenic fires may have maintained the savanna. However, our results propose that climate change is the main driving factor for the formation of the coastal savanna in this region. Our results also show that the early Holocene sea level rise established mangroves near the study site until 7,500 cal yr BP and promoted swamp formation in depressions, but did not influence the savanna vegetation.

Keywords: Holocene, pollen and charcoal analyses, Amazon rainforest, gallery forest, savanna, mangrove, vegetation change, human impact, climate change, ITCZ and SACZ shift, ENSO

1. Introduction

Present-day savannas occupy approximately 16.1 million km^2, or 11.5% of the global landmass. The proportion of trees and grasses in savannas is related to climate and land use practice. In addition, extensive biomass burning during the dry season plays an important role to inhibit tree growth (Murphy, 2012; Scholes and Hall, 1997). Considering the large difference between above ground carbon storage capacity of treeless grasslands (2 tons C/ha) and woodland savannas (30 tons C/ha), besides the huge amount of CO_2 that may be emitted to atmosphere by biomass burning of savannas (estimated at 0.5–4.2 Gt C per year globally) (Grace et al., 2006), plans for CO_2 management need to consider climatic/anthropogenic influences which trigger change from savanna with arboreal taxa (cerradão) to treeless grasslands (campo limpo).

A narrow strip of savanna known as “coastal savanna belt” in northern South America is found along the coast of British Guiana, Surinam, French Guiana, and in State of Amapá, Marajo Island and in part in the state of Pará. This discontinuous belt about 2,000 km long is disrupted locally by other types of coastal vegetation (Fig. 1a). Based on the meteorological data (NOAA), annual precipitation in the coastal savanna belt is in a range similar to most of Amazon regions (between 1,750 and 3,500 mm) (Nimer, 1989; Snow, 1976; Weischet, 1996). Therefore instead of savanna, prevalence of Amazon rainforest is expected. Because of its considerable area the occurrence and dynamics of coastal savanna belt have a substantial effect on the regional carbon budget.

Several palaeo-environmental studies using pollen and charcoal analyses have previously been carried out to investigate the vegetation history of the coastal area in northern South America. Although these studies are mainly focused on mangrove development, useful information can be obtained regarding savanna/forest/mangrove interaction. Records from Guyana (Van der Hammen, 1963), Suriname (Wijmstra, 1971) and French Guiana (Tissot and Marius, 1992) show expansion of savanna (and shoreline regression) during the full glacial periods and mangrove development (and sea level transgression) during the interglacial period. Swamp savanna with dominance of Poaceae and Cyperaceae was present during the last c. 5700 years in the coastal regions of Guyana, Suriname, and French Guiana (Behling and Hooghiemstra, 2001). In Amapá State lacustrine littoral records from lakes Tapera and Marcio (Toledo and Bush, 2007) also demonstrate changes in vegetation from closed forests with swamp taxa to open flooded savanna at c. 4750 cal yr BP. In the pollen record of Lago Arari, on Marajó Island in the mouth of the Amazon River in northeastern Pará there is a marked change from the more or less close to open swamp savanna and forest at ca. 7,400 cal yr BP (Absy, 1985). Another study from Lake Arari investigated four sediment cores, which reveal replacement of mangrove by herbaceous vegetation at 2,300 cal yr BP and an expansion of herbs during the last 1,000 years (Smith et al., 2012). In the Southern Hemispheric part of the coastal savanna belt, in Lago Crispim (Behling and Costa, 2001), Lagoa da Curuça (Behling, 2001) and Lagoa do Caco (Ledru 2001; Pessenda et al., 2005) Holocene started with predominance of arboreal taxa which with different timing (due to different latitudinal position) gradually became accompanied by swamp trees and finally replaced by open vegetation.

In addition to being interesting for palaeoenvironmental research, lands on the eastern Amazonia on the Amazon River bank or near the river mouth host many archeological surveys. Late Pleistocene paleo-indian camp side at Monte Alegre in the eastern Brazilian Amazon documents presence of ecologically adapted foragers with presumably limited big-game hunting habit (Roosevelt et al., 1996). In another study on Marajo Island, Roosevelt and her colleagues (1991) found that mound builders have occupied the alluvial floodplains of the Lower Amazon from 400-1300 A.D.

This work presents the analysis of a 750 cm-long sediment core taken from a key area of the coastal savanna belt near the mouth of the Amazon River, which forms an ecotone between Amazon rainforest and coastal vegetation. In order to test different hypotheses concerning probable driving forces for the development of this savanna belt, such as sea level change, climate, fire, human and edaphic factors, a continuous pollen and charcoal record was analyzed and compared with other results from northern South America.

2. Study area

The core named Curiaú (CUR), was collected from a small *Mauritia* swamp 15 m in diameter (00°12'30.3" N, 51°01'12.1" W, 5 m a.s.l) located 16 km north of the city Macapá in the south of the State of Amapá near the mouth of Amazon River (Fig. 1b). The studied swamp is surrounded by small hills which have an elevation up to 22 m a.s.l.

2.1 Regional geomorphology

During the late Pleistocene and Holocene, sea-level changes together with tectonic movements resulted in alternation of erosional and depositional processes, which shaped a hilly terrain (relief) along the coast of Amapá (Lima et al., 1991). These reliefs are broad low elevation hills (mean height is 20 m a.s.l.), formed by water erosion of old colluvial clayey terraces which constitutes Pleistocene plain. On the eastern side of this plain, the sediments deposited during the Holocene cover the Amazon River bank and on its western side, Amapá hills are established on crystalline basement rocks. This Mesoarchean-Devonian Crystalline basement rocks continue to constitute the base of the Pleistocene terraces as well (Souza, 2010).

2.2 Hydrology

Depressions between reliefs on Pleistocene terraceae form a network of meandering inundated palaeo-channels and shallow lakes. The largest water body of this kind is an isolated lake called Lago do Curiaú that covers area of 150 km^2 including some small lakes such as Tapera and Marcio which may dry out almost completely in the dry season (Toledo and Bush, 2007). Meandering ramified branches of these lakes expand in the area and at the end produce low-order drainage channels on the Pleistocene plains (Guimarães, 2013). The studied swamp lies at the end of one of these channels connected to a lake, which is located 3 km distant from the site. This lake has accumulated fluvial-lacustrine sediments during the Holocene, and is only 3-4 meters above the sea level.

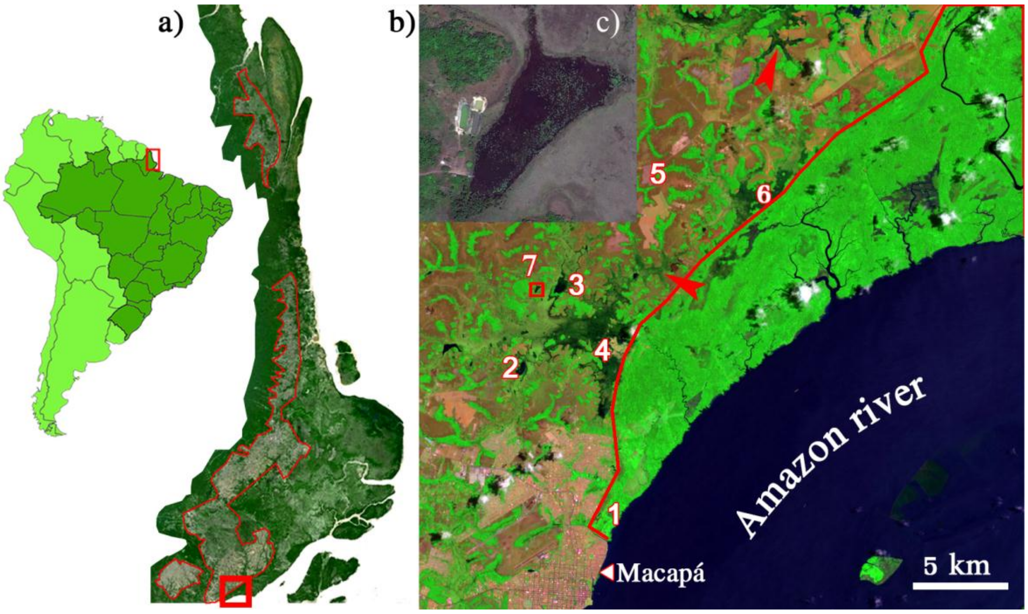

Figure 1. Study area. (a) Amapá coastal belt. Red line shows approximate borders of the savanna compartment. (b) False color map of the study area produced from Landsat 8. Red arrows show palaeo-channels. 1 = site Macapá (Guimarães et al., 2012), 2 and 3 = lakes Tapera and Marcio respectively (Toledo and Bush, 2007), 4 = Lake Curiaú, 5 = site CUR and 6 = lake connected to CUR swamp by a palaeo-channel. The area bordered in red is Holocene deposited sediment of river bank (Guimarães, 2013).

2.3 Geobotany

Four different plant communities cover today the study area, which from margin of the swamp up to the top of the hills are composed of i) *Mauritia flexuosa* and some stands of *Euterpe* that colonizes the highest central part of the gallery forest, ii) secondary forest taxa that constitute the outer zone of the gallery forest, iii) savanna with a sparse *Byrsonima* shrubs that is situated between gallery forest and the outer most zone which is iv) grassy savanna on top of the hills dominated by Poaceae. The mentioned secondary forest is mainly represented by Euphorbiaceae and few members in the families of Melastomataceae, Combretaceae, Anacardiaceae and the genous *Sloanea*.

About 30 km distance from the study site, *terra firme* rainforest grows on the Amapá hills. Therefore the site is located in a key area of savanna-forest boundary. Also a complex of wetlands and denser secondary forest with patches of grasslands covers the 5 km wide area on the river bank. This vegetation is established on extensive north-south trending Holocene terraces composed of sand and clay representing fluvial-marine deposits along the bank of Amazon River (Guimarães, 2013). More information on the vegetation of Amapá is available from Carvalho et al. (2006), Costa Neto (2004), Costa Neto et al. (2007), Costa Neto and Silva (2004) and Thomaz et al. (2004).

2.4 Climate

The climate of the study area is tropical humid with 2500 - 3000 mm annual rainfall with the wet season between December and August and three dry months (September, October, November) (IBGE - UNIT OF STATE AMAPÁ, 2002). Based on Köppen-Geiger classification (Peel et al., 2007), the area is located in the tropical savanna climate (Aw) with close connection to tropical monsoon climate (Am). The temperature fluctuates between 23-32 ^{o}C with a mean annual of 27 ^{o}C (IBGE, 2002).

Modern precipitation regime over the study area is mainly under influence of three atmospheric phenomena:

1. Intertropical convergence zone (ITCZ): is a low-pressure belt where warm moist trade winds converge to form a zone of cloudiness and precipitation near the equator, which seasonally migrates toward the warmer hemisphere. During the austral summer over South America, the rainy season encompasses nearly the entire tropical area of the South American continent that lead to a latitudinally and longitudinally broad ITCZ (Waliser and Jiang, 2014).
2. SACZ: The SACZ is defined as a northwest–southeast-oriented cloud band that is responsible for moisture transfer from the Amazon region to central and southeastern Brazil (Prado et al., 2013). Along the Equator rainfall made by SACZ is at a near-minimum in December-February, while the wettest season occurs in April and May (Waliser and Jiang, 2014).
3. ENSO: Is the main cause of inter-annual variability of the SACZ movement (Trenberth et al., 1997) and its warm phase or El Niño is responsible for rainfall decline during the wet season of northern South America (Marengo et al., 2012; Prado et al., 2013).

3. Material and methods

The core CUR was taken from a *Mauritia* swamp in November 2004 using a Russian Corer and was transported to the Federal University of Pará and stored in a refrigerator after subsampling.

3.1 Radiocarbon dating and age-depth model

Based on changes in lithology of the core, eleven samples of sedimentary organic matter (2-3 g each) were selected for radiocarbon dating (Table 1). Dating was carried out in the Radiocarbon Laboratory at Erlangen/Nürnberg University, Germany and the Department of Geosciences, National Taiwan University by an accelerator mass spectrometer (AMS). The age-depth model was plotted by Clam 2.2 (Blaauw, 2010) package in R studio version 3.0.1, (2013) using Northern Hemisphere terrestrial calibration curve IntCal13 from Reimer et al. (2013). The Gaussian distribution was used to calibrate dates and linear interpolation between neighboring levels was applied to construct the age-depth model for the core.

Table 1. C^{14} Radiocarbon and calibrated dates plus accumulation rate based on age depth model. Asterisk show dates that are considered as outliers.

AMS Lab ID	Depth	14C yr BP	Age (cal yr BP)			Accumulation Rate (cm/year)
			Min	Median	Max	
NTUAMS-580	50	1606±10	1421	1481	1540	0.029
NTUAMS-581	100	2994±16	3084	3205	3226	0.032
NTUAMS-582	150	4162±26	4585	4707	4821	0.044
NTUAMS-345	200	5092±28	5754	5828	5909	0.064
NTUAMS-583	300	6471±30	7324	7377	7431	0.086
NTUAMS-346	400*	9268±40	10,296	10,431	10,567	-
CUR-500	500	8711±57	9553	9685	9885	0.078
NTUAMS-723	550	9165±38	10,243	10,328	10,466	0.241
NTUAMS-347	600*	10,160±50	11,614	11,831	12,048	-
CUR-700	700	9610±67	10,731	10,948	11,173	0.092
NTUAMS-724	745	9873±164	10,952	11,433	11,964	0.092

3.2 Pollen and micro-charcoal analysis

Seventy-six subsamples (1 cm³) were taken at about 10 cm intervals along the core and were prepared using standard pollen analytical methods (Faegri and Iversen, 1989) including application of 70% HF treatment. Exotic marker *Lycopodium clavatum* spores were added (Stockmarr, 1971) for pollen concentration and influx calculations. A minimum of 300 terrestrial pollen grains were counted in each sample to calculate pollen percentages. Spores and pollen of aquatic taxa were excluded from the total sum. Between 750 and 730 cm core depth (three samples), only 100 pollen grains were counted due to the low pollen concentration. The micro-charcoal particles were counted on the pollen slides. To reconstruct the fire history, concentration of the number of charcoal fragments, which are highly correlated with area of charcoal fragments, was used (Tinner and Hu, 2003). Pollen identification was done according to literature (Roubik and Moreno, 1991; Colinvaux et al., 1999; Carreira and Barth, 2003) and the pollen reference collection in Department of Palynology and Climate Dynamics, University of Göttingen. Pollen grains were categorized into 7 groups as follows: Palms, swamp forest trees, forest-gallery forest trees, savanna shrubs, savanna herbs, mangrove and pteridophyta. This classification was done mainly based on studies by Guimarães et al. (2012), Behling and Hooghiemstra (2000) and Marchant et al. (2002), Guilherme et al. (2013). Software packages TILIA and TILIAGRAPH were used to plot pollen diagrams and charcoal data. The pollen diagrams were statistically subdivided into pollen assemblage zones using CONISS for a square-root transformation of the percentage data, followed by stratigraphically constrained cluster analysis (Grimm, 1987).

3.3. Statistical analysis

Principal Component Analysis (PCA) was implemented in R studio using Vegan package version 2.0-10, after square root transformation of the data (Oksanen, 2013). For this purpose, the lower most four subsamples, which contain mainly *Micropholis* (Sapotaceae) pollen, were excluded, because this taxon constituted a single-species-dominant forest with little contribution of other taxa. The other subsamples were divided into two groups, one containing subsamples with mangrove pollen and the other with subsamples from the upper Holocene when mangrove became locally absent, and gallery forests expanded. This approach was adopted in order to achieve a better ordination.

4. Results

4.1. Stratigraphy and chronology

In the sediment core CUR two major types of deposits are recognizable: The bottom of the core (750-700 cm) contains grey sandy sediments with small amounts of organic material. Between 700 and 0 cm the sediment is composed of dark grey material with a high organic content. In the uppermost 30 cm some bioturbation might occur. In general, from the base to the top of the core accumulation rate decreased. However, between 700 and 550 cm accumulation rate is three times the rate in the upper part of the record that shows a strong change in the sedimentation regime (Fig. 2).

Based on the linear interpolation between radiocarbon dates of 700 and 745 cm (Table 1), the deposition started at ca. 11,500 cal yr BP. Radiocarbon dates at 600 and 400 cm core depth were excluded from the age-depth model because they show ages older than the dates from the deeper parts of the record.

Based on the visual inspection of the pollen assemblages and according to cluster analysis the core is divided into 5 zones and 2 subzones (Fig. 3).

Zone CUR-I (750–720 cm, 11,500-11,230 cal yr BP): This zone is marked by a high amount of *Micropholis* (Sapotaceae) pollen (mean=71%, maximum (max) 88% at 735 cm). The second most frequent pollen type is Poaceae, which constitutes 17% of pollen content on average with a maximum of 40% at 740 cm. Contribution of *Mauritia*, *Symphonia*, *Ilex, Curatella, Protium, Rhyzophora* and Myrtaceae pollen is low. A specific fungal spore is observed only in these subsamples.

In this zone the pollen concentration and influx have the lowest values of the whole record. Also charcoal concentrations and influx show relatively low values.

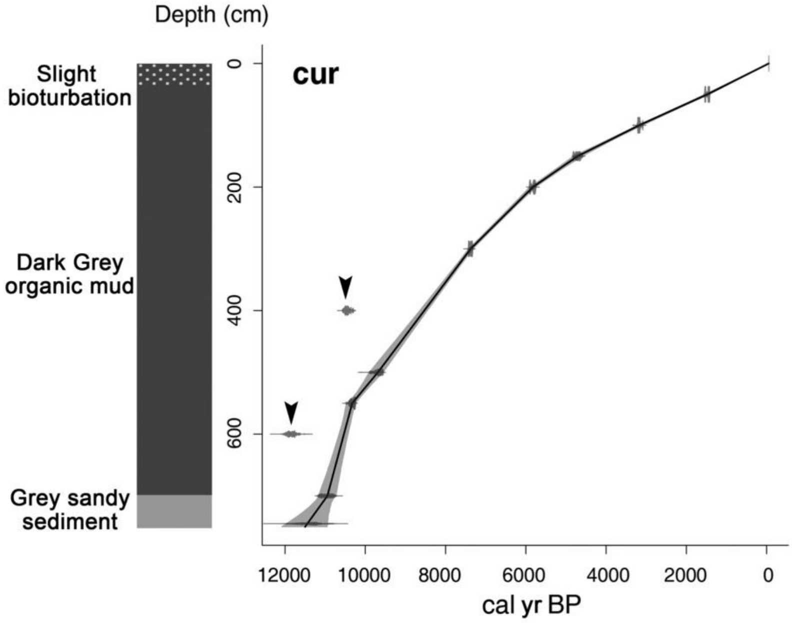

Figure 2. Stratigraphy and age-depth model of the core Curiaú (CUR). Arrows show outlier dates (400 and 600 cm).

4.2 Pollen and charcoal analysis

Zone CUR-II (720–530 cm, 11,230-10,000 cal yr BP): This zone is characterized by herbs (Poaceae, mean=56%, max=82%). *Spermacoce* occurs with high values at the beginning of the zone (48%). The second important group is the swamp forest trees *Symphonia* (mean=9%, max=57% at 675 cm), *Ilex* (max=34% at 575 cm) and *Virola (max at 575 cm).* Palms are rare at the beginning of the zone. *Mauritia* pollen presents an increasing trend from 0% in the lower part of the zone to 24% at 555 cm core depth. The contribution of savanna shrubs is low, but *Curatella* pollen is present at the beginning of the zone (max=28%). A maximum of *Casearia* pollen (60%) is found at 535 cm. *Rhizophora* pollen shows an increasing trend and reaches 9% at 555 cm.

Concentration of swamp forest trees is higher than concentration of other groups of this zone and the highest along the whole core. Charcoal has also high concentration.

Zone CUR-III (530–310 cm, 10,000-7500 cal yr BP): This zone is divided into two subzones CUR-IIIa and CUR-IIIb.

The CUR-IIIa (530-400 cm, 10,000-8500 cal yr BP) is characterized by high values of palm and savanna herbs pollen. Pollen percentages of Poaceae reaches 69% at 495 cm and percentage of *Mauritia* shows 56% at 455 and 465 cm. Contributions of *Byrsonima*, *Curatella* and Combretaceae/Melastomataceae are low. Pollen of *Rhizophora* has a decreasing trend from 12% in the beginning to nearly 0% in the upper part of this subzone.

Pollen concentration of palms is very high and their influx reaches the highest value in the middle part of this subzone. Pollen concentrations of mangrove, savanna herbs and charcoal are higher compared to zone CUR-II.

CUR-IIIb (400-310 cm, 8500-7500 cal yr BP) reveals a decreasing trend in pollen percentage of palms, from 19% to almost 0% for *Mauritia*. Pollen of forest-gallery forest trees, mainly represented by Euphorbiaceae (mean=4%, max=17%), *Sloanea* (only in this zone with mean= 5%, max= 12%) and Combretaceae/Melastomataceae (mean=8%, max=16%) show moderate values. Pollen of the savanna shrub *Curatella* (mean= 4%, max= 11%) and *Byrsonima* (mean=3.12%, max= 8%) also contribute with substantial percentages. CUR-IIIb is the youngest zone with notable amounts of *Rhizophora* pollen (mean= 4%, max= 9%).

Concentration and influx values of forest-gallery forest trees, savanna herbs, savanna shrubs and mangrove in this zone are markedly higher compared to CUR-IIIa. Charcoal concentrations in CUR-III are similar to CUR-II, but charcoal influx is higher in CUR-II.

Zone CUR-IV (310–190 cm, 7500-5600 cal yr BP): This zone is characterized by a marked rise in pollen of forest-gallery forest trees and the decrease in pollen of savanna herbs. Euphorbiaceae (mean=30%, max=67%) represent highest values. *Mabea* pollen occurs only in this zone. Although percentages of Combretaceae/Melastomataceae decrease in CUR-IV compared to CUR-III, pollen of Anacardiaceae, Fabaceae, Myrtaceae, *Bombax, Protium, Banara* are present with high percentages. Pollen of Moraceae is present in low values. Poaceae occurs with the lowest values along the core (Mean=17.5%, Min=5.3% in 225 cm). Cyperaceae contributes with low percentages. *Mauritia* has lower values (Mean=10%, Max=23.8%) in this zone than in CUR-IIIa. Pollen of other Arecaceae and swamp forest trees increase in CUR-IV. Percentages of *Symphonia* have a maximum of 20% (mean=3.7%) and pollen of *Ilex, Virola* and Humiriaceae are also present. Pollen of *Curatella* decreases from 22% to 0%, in contrast, *Byrsonima* show the highest values (mean=6%, max=14%). *Rhizophora* occurs with 5% only in one sample (285 cm) and then becomes absent for the rest of the core. A trilete spore occurs only in three subsamples (225-245 cm) with very high amounts (max=219 spores against 300 counted terrestrial pollen grains at 235 cm).

Pollen concentration and influx of forest-gallery forest trees reach the maximum in this zone, while savanna herbs showing a marked decrease in these values. Pollen concentration and influx of savanna shrubs is almost similar to CUR-IIIb but those of swamp forest trees increased. Charcoal concentration and specially influx decreased.

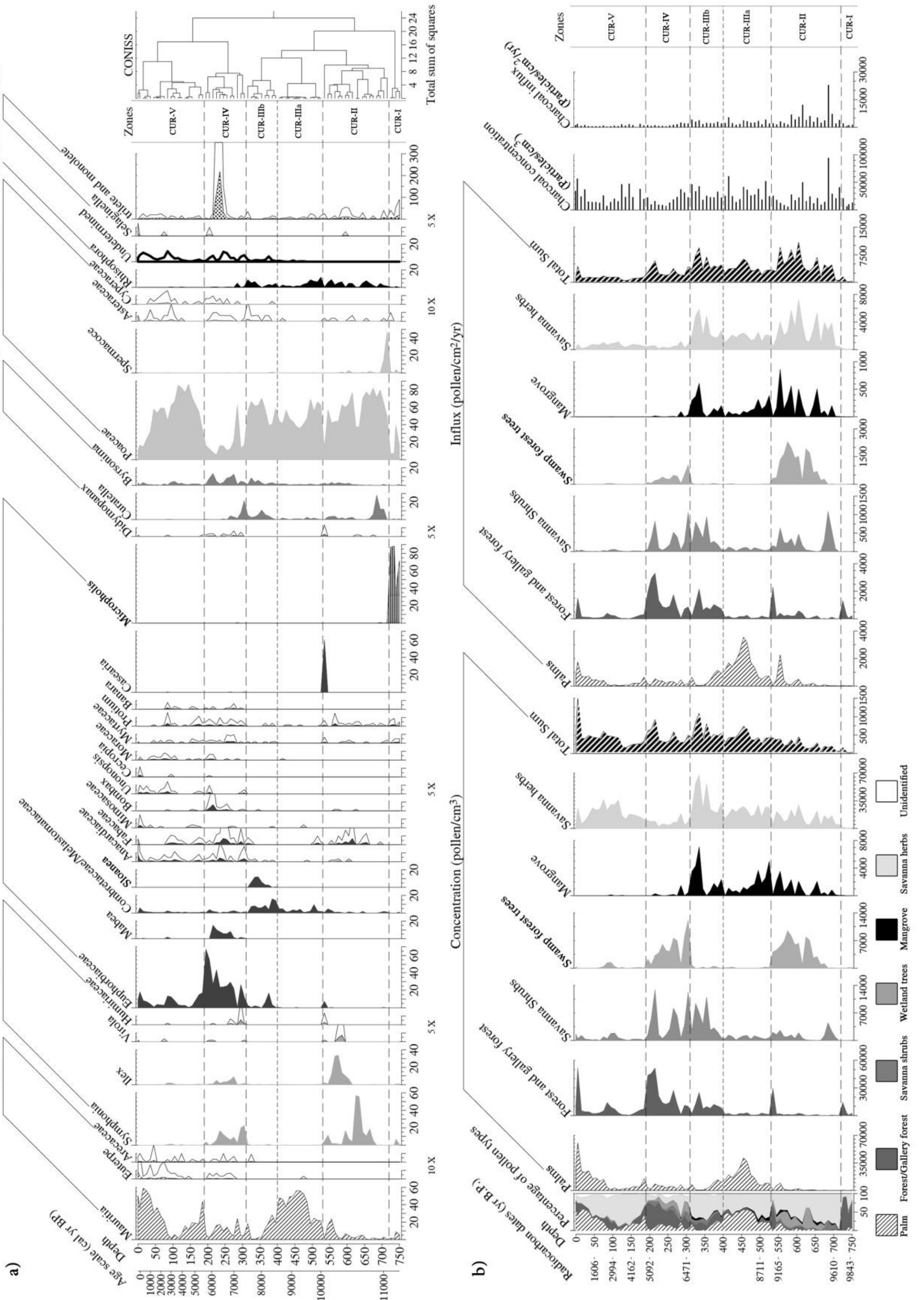

Figure 3. pollen diagram of the core CUR. (a) Pollen percentage diagram and zonning by CONISS. (b) Pollen sum, concentration and influx of each ecological group and concentration and influx of charcoal

Zone CUR-V (190–0 cm, 5600 cal yr BP to present): This zone is characterized by marked fluctuations in palms and savanna herbs and an oscillation in pollen of forest-gallery forest tree pollen. Pollen of *Mauritia* first decreases from 44% at 185 cm to 1% at 95 cm core depth and then again reaches a maximum value of 59% at 15 cm. Pollen of *Euterpe* and other Arecaceae have their highest percentages in this zone. Poaceae occurs with 33% at 185 cm and reaches a maximum of 86% at 145 cm, and then decrease to 11% at the surface. Cyperaceae shows its highest values in this zone.
Euphorbiaceae shows two ascending trends with maximum values of 14% at 85 cm and 18% at 5 cm. Pollen of Combretaceae/Melastomataceae, Anacardiaceae, Mimosaceae, *Unonopsis* contribute with low percentages, but they increase at the uppermost part of this zone. Pollen of Fabaceae, Moraceae, Myrtaceae, *Cecropia*, *Banara*, *Protium* are represented with trace amounts.

Pollen concentration and influx of palms and forest-gallery forest trees increase in the upper part of this zone. Savanna herbs have the highest pollen concentration among all groups. Charcoal influx decrease to the lowest value compared to the whole record.

4.3 Principle Component Analysis (PCA)

In the first PCA (Fig. 4a) which contains 12 taxa and 47 subsamples (72-26) for the period between 11,120 and 6680 cal yr BP, the first and second axes account for 33.5% and 26% of the variance. This PCA is compatible with taxa grouping in the pollen diagram and clearly shows 4 groups of 6 vegetation types as demonstrated in the pollen diagram. Representatives of savanna shrubs and mangrove were not strongly present in the dataset so that they could form an independent dimension in the PCA.

The second PCA (Fig. 4b) which contains 19 taxa and 26 subsamples (1-26) covers the period between 6,680 cal yr BP to present. The first and second axes account for 51.1% and 26.7% of the variance.

5. Palaeoenvironmental reconstruction

5.1 Beginning of the Holocene (Zone CUR-I, 11,500-11,200 cal yr BP)

The pollen assemblages of this period indicate a landscape occupied by a mono-specific arboreal community composed of *Micropholis* and mixed with sparse trees of *Protium* and Myrtaceae family, which probably grew in the depressions. Small patches of savanna probably covered the top of the hills in the Pleistocene plains. Today *Micropholis* is found mainly both in the lowland and upland rainforests of South America (Lorenzi, 1992, 1998). Therefore it can be concluded that the formation of such this forest required enough moisture availability. However, this moisture supply might not be in the form of sufficient rainfall, because rain could cause accumulation of water in depressions between hills and facilitates formation of swamp forest or gallery forest similar to modern vegetation, whereas the low content of organic material and lack of the pollen from swamp forest or gallery forest in the sediment imply absence of such this water dependent vegetation. Probably, *Micropholis* was a relict of a forest that existed during the late glacial, when higher moisture was available under colder conditions (Behling and Hooghiemstra, 1998). Because of the proximity to the sea and colder climate, perhaps the region obtained humidity from wind blowing from Atlantic Ocean. In addition, co-occurrence of a specific fungal spore with pollen grains of this *Micropholis* forest in the lowest subsamples suggests presence of collaboration between mycorrhizal network and a mono-dominant tropical forest (McGuire, 2007). Mycorrhizal network may transfer water and minerals to *Micropholis* roots in the dry and poor soil condition. This scenario may better explain the abrupt replacement of *Micropholis* population by a herbaceous savanna composed of Poaceae and *Spermacoce* at ca. 11,200 cal yr BP. Because a mono-dominant population can survive only under specific circumstances (Peh et al., 2011) and is very sensitive to environmental changes. The increased pollen percentage of *Spermacoce* a herb of open vegetation with regular disturbance (Marchant et al., 2002) in two subsamples after the extinction of *Micropholis* (between 11,200 and 11,000 cal yr BP) may support this assumption. Progressive warming and drier conditions during the early Holocene would have been unfavorable for survival of *Micropholis*.

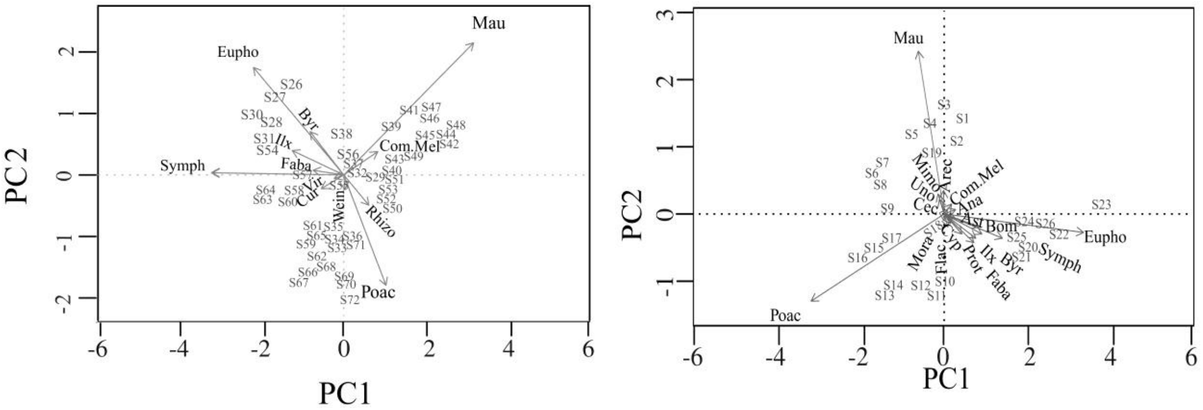

Figure 4. Principle Component Analysis of the core CUR. (a) PCA1, (b) PCA2. Ana: Anacardiaceae, Arec: Arecaceae, Ast: Asteraceae, Bom: *Bombax*, Byr: *Byrsonima*, Cec: *Cecropia*, Cyp: Cyperaceae, Com.Mel: Combretaceae-Melastomataceae, Cur: *Curatella*, Eupho: Euphorbiaceae, Faba: Fabaceae, Flac: Flacurtiaceae, Ilx: Ilex, Mau: Mauritia, Mimo: Mimisaceae, Mora: Moraceae, Poac: Poaceae, Prot: *Protium*, Rhizo: *Rhizophora*, Symph: *Symphonia*, Vir: *Virola*, Uno: Unonopsis, Wein: *Weinmannia*.

5.2 Early Holocene (Zones CUR-II and CUR-IIIa, 11,200-8500 cal yr BP)

Savanna with variable tree density and arboreal composition was the dominant ecosystem in the study area during this period. *Curatella* and *Byrsonima,* which were dominant at the beginning of this phase, were replaced by Combretaceae/Melastomataceae after a treeless phase. This succession indicates a transition from dry early Holocene (11,200 to 10,000 cal yr BP) to slightly wetter condition (10,000 to 8500 cal yr BP). Interesting for this period is the development of *Rhizophora* mangroves relatively close to the study site. This was coupled with development of swamp forest (*Symphonia*, *Ilex* and *Virola*) in palaeo-channels which later (ca. 10,000 cal yr BP) was replaced by a

Mauritia swamp. Both changes imply a fast sea level rise at the early Holocene that caused incursion of brackish water into palaeo-lakes (mangrove formation) and inundation of or higher groundwater levels in palaeo-channels and depressions (swamp forest development). Consequently due to the higher water level and high sedimentation rates, palaeo-channels were drowned and swamps developed in the depressions. This provided a suitable environment for the *Mauritia* swamp formation. The difference between *Mauritia* and swamp forest trees (*Symphonia*, *Ilex* and *Virola*) is evident from the PCA1.

5.3 Mid-Holocene (Zone CUR-IIIb and CUR-IV, 8500-5600 cal yr BP)

At ca. 8500 cal yr BP arboreal taxa (Combretaceae/Melastomataceae and *Sloanea*) expanded and reached maximum expansion between 7500 and 5600 cal yr BP with the dominance of Euphorbiaceae, *Mabea* and with lower occurrence of Fabaceae, Anacardiaceae and *Bombax*. The area of savanna herbs became smaller and treeless savanna was replaced by a savanna with a denser arboreal stands (*Byrsonima* and *Curatella*). Also a marked decrease of *Mauritia* and increase of taxa that represent the swamp ecosystem, such as *Ilex*, *Virola* and *Symphonia* imply a higher rain water input that changed the *Mauritia* swamp in favor of swamp forest, suggesting a wetter mid-Holocene. In addition, low charcoal concentration and influx recorded during this period can also confirm lower fire frequency under a wetter climate.

5.4. Mid- to late Holocene (CUR-V, 5,600 cal yr BP to present)

Despite the two episodes between 3300 and 2300 cal yr BP and the last 1000 years, which were characterized by more abundant arboreal taxa (similar to arboreal composition during the mid-Holocene wet phase), periods between 5600-3300 and 2300-1000 cal yr BP were dry phases dominated by a savanna with few shrubs on the upper part of the hills and *Mauritia* swamp in the depressions. These oscillations signify that during the last 5600 years, the studied site experienced unstable climate conditions in which arboreal taxa could not reach the maximum density of forest as during the mid-Holocene (8500-5600 cal yr BP). Also high charcoal concentration indicates the high fire frequency perhaps due to the longer dry seasons during the late Holocene.

6. Discussion

This study reveals that during the last 11,500 years, savanna was an integral part of the landscape in the Amapá coastal region. However, it expanded after the extinction of the specific arboreal vegetation, which covered the area at the beginning of the Holocene (>11,500-11,200 cal yr BP). During the early Holocene (11200-8500 cal yr BP) savanna was dominant and occurred on the elevated areas of the hills in the Pleistocene plain and forest swamp established along palaeo-channels. At ca. 10,000 cal yr BP, the swamp forest was replaced by *Mauritia* swamp and mangrove expanded in the palaeo-channels. Throughout the mid-Holocene (8500-5600 cal yr BP) gallery forest expanded and replaced the savanna. The mid- to late Holocene (after 5600 cal yr BP) was characterized by fluctuation between savanna and gallery forest, and also between swamp forest and *Mauritia* palm swamp. The mangrove vegetation is absent during the late Holocene.

To address the question of how the coastal savanna belt formed and how vegetation changes (mentioned above) occurred during the Holocene, the factors that may control the savanna dynamics need to be discussed. Possible factors are land-sea hydrologic interactions, climate, soil and geomorphologic attributes, fire and the human influence.

6.1 Land-sea hydrologic interaction

To reconstruct land-sea hydrologic interactions the following circumstances need to be considered:

1. The early Holocene sea level rise: Little is known about Atlantic sea level changes near the mouth of the Amazon river at ca. 10,000 cal yr B.P. Due to diverse coastal settings and tectonic activity, studies on sea level rise along the coastal zone of the western Atlantic Ocean show large differences ranging from ca. 40 m in Barbados (Faribanks, 1989) to only ca. 3 m below the current sea level in southeastern coast of Brazil, state of Rio de Janeiro (Castro et al., 2014) around 10,000 yr B.P. Palynological studies from both CUR and Lagoa da Curuça (Behling, 1996) which are located on two sides of the Amazon delta confirm the result from Rio de Janeiro. These records show a small amount (10-12%) of pollen of wind pollinated mangrove tree *Rhizophora* between ca. 10,300-10,000 cal yr BP. Since the uppermost (modern) part of Lagoa da Curuça record has approximately the same amount of *Rhizophora* pollen (around 15%) which comes from the nearest tidal river located at 1.7 km distance, it can be concluded that the mangroves existed in a distance of 2-3 km distant from these two sites during the early Holocene.
2. Oscillations in discharge of the Amazon River during the Holocene: According to Cohen et al. (2012), the coastal zone of the study site (core CUR) is part of the wetland system dominated by *várzea* and swamp vegetation, mainly characterized by palm trees, such as *Mauritia* and is under influence of the Amazon River. However, during the early to mid-Holocene, the studied coastal zone was influenced by marine tidal waters due to both sea level rise and low river discharge resulting from increased aridity during the early Holocene that in turn caused increased tidal water salinity. During the late Holocene, near the Amazon River a marked increase in fluvial influence fragmented the mangrove belt. In consequence, mangrove was replaced by *Várzea* vegetation. The increase of river freshwater discharge during the late Holocene, caused also a decrease of tidal water salinity for parts of the Amapá coastline.
3. The relative low elevation of the studied swamp (and the whole Pleistocene terrace) during the early Holocene, when Holocene deposited sediments were not accumulated yet.
4. The widespread network of palaeo-channels and palaeo-lakes in the area.

Based on these above mentioned circumstances it can be concluded that the early Holocene rapid sea level rise, together with the low water discharge of Amazon River and the absence of Holocene deposited sediments on the river banks facilitated the incursion of brackish water into palaeo-lakes and formation of mangrove. Consequently due to the sea level rise the water table rose along the network of palaeo-channels which favored the development of *várzea* and swamp forest vegetation. Later (after 10,000 cal yr BP), some channels were abandoned perhaps because of high sedimentation rate between 11,000 and 10,000 cal yr BP and channel shifting, which resulted in meander cutoff and channel-belt avulsion (Toonen et al., 2012). The abandonment of channels favored the development of shallow water bodies in the depressions. These lacustrine environments were suitable to the expansion of the *Mauritia* palm swamps. Noteworthy is that the formation of *Mauritia* swamps, *Várzea* and *Igapó* forests is wide-spread in the Amazon Basin, such as Rio Curua (Behling and Costa, 2000) and Lago Calado (Behling et al., 2001) due to the sea level rise that affect the water table during the early Holocene.

After 7000 cal yr BP, higher precipitation in Amazonia caused higher input of fresh water, sediment deposition on the river bank and the isolation of palaeo-lakes (Cohen et al., 2012). These changes decreased the salinity of palaeo-lakes and triggered the local extinction of mangrove. In the PCA 1, the 180º angle between direction of *Rhizophora* and Euphorbiaceae confirms the negative relation between Euphorbiaceae (as indicator of more precipitation) and mangrove.

In summary, land-sea hydrologic interaction changed the vegetation composition in palaeo-channels. However, the high occurrence of Poaceae between 11,200-8,500 cal yr BP indicates that the sea level rise could not affect the savanna on top of the reliefs.

6.2 Climate

6.2.1 Relict of the late glacial vegetation in the coastal area of Amapá

Similar to *Micropholis* in our study, unknown arboreal communities composed of different cold adapted taxa such as *Podocarpus*, Ericaceae, *Humiria* and/or higher amount of *Ilex, Hedyosmum, Myrsine (Rapanea)* are found from late glacial period until ca. 11,600-11,300 cal yr BP in different regions of Amazonia such as Lagoa da Curuça in Pará State (Behling, 1996), hill of six lakes in western part of Amazon rainforest (Bush et al., 2004; Colinvaux et al., 1996) and Laguna Sardinas in savannas of the Llanos Orientales of Colombia (Behling and Hooghiemstra, 1998). These arboreal communities became locally extinct or contracted after 11,300 cal yr BP. Since in the modern Neotropics, *Podocarpus* is largely restricted to temperate humid upper mountain forests of the Andes or Guyana Highlands, the presence of this genus and other cold adapted taxa indicate cooling over lowland Amazonia (e.g. Behling, 1996; Colinvaux et al., 1996). More concentration of fog and higher moisture levels under colder conditions (Behling, 2001; Behling and Hooghiemstra, 1998) or precipitation that was not less than required amount for arboreal vegetation (Colinvaux et al., 1996) promoted the formation of these specific forests. Beside this specific arboreal communities, presence of minor amounts of Poaceae pollen imply existence of small savanna patches at least since the onset of the Holocene.

6.2.2 Dry early Holocene and northern position of ITCZ

In spite of the wetter conditions, recorded from the Lake Valencia sediments (northern Venezuela) which had a high water level at ca. 9500 cal yr BP (Bradbury et al., 1981; Curtis et al., 1999), several sites in the Amazon region such as Laguna Loma Linda (Behling and Hooghiemstra, 1998), Laguna Sardinas (Behling and Hooghiemstra, 2000), Las Margaritas in Colombia (Vélez et al., 2005) and Comprido Lake near Monte Alegre City (Moreira et al., 2013) showed large savanna areas indicating drier climatic conditions during the early to mid-Holocene (11,200 to 7800 cal yr BP). This latitudinal difference is attributed to a more northerly position of the ITCZ during the early to mid-Holocene (Dias et al., 2009) that caused a long dry period in most regions of Amazonia, as well as in our study area (between 11,200-7500 cal yr BP). This long dry season trigged the savanna expansion on the Pleistocene hilly plain, which were covered by a former *Micropholis* forest.

6.2.3. Wetter mid-Holocene and ITCZ-SACZ coalesce

Palynological studies (table 2) from sites of the Llanos Orientales in Colombia (Fig. 5, Profiles 1-5) indicate that forest and palms increased from early to late Holocene in northern South America (illustrated by the increase of greenness in Fig. 5). However, studies on sites near the mouth of the Amazon River (Fig. 5, Profiles 7-9) together with one site from the *Caatinga* vegetation (Fig. 5, profile 10) document an opposite trend. The CUR record (Fig. 5, profile 6) has an intermediate position with the dominance of gallery forest (maximum greenness in Fig. 5) during the mid-Holocene. These two trends show that changes in precipitation over the northern and north eastern South America is a result of at least two different air circulation systems which met each other near the equator during the mid-Holocene.

The best compatible model to explain these trends is presented by Dias et al. (2009). According to this model, during the austral summer of the mid-Holocene, the combined northward shift of the SACZ and southward shift of the ITCZ resulted in these two systems to merge, causing higher precipitation in NE Brazil. The vegetation feedback enhanced the impact on the ITCZ and SACZ. They also suggest that the simulation of modern precipitation is much larger than what is observed in the SACZ region and is underestimated over the Amazon region.

Based on these conclusions and considering a wider domain for SACZ activity than Prado et al. (2013) proposed the gallery forest expansion and reduction of savanna area in the Curiaú region over a period of 2000 years is supported by ITCZ-STCZ merged system during Austral summer.

Table 2. Sites used in Fig 4.

Site No	Site name	Elevation (m a.s.l.)	Longitude	Latitude	Reference
1	Laguna Sardinas	80	4°58'N	69°28'W	Behling & Hooghiemstra, 1998
2	Laguna Angel	200	4°28'N	70°34'W	Behling & Hooghiemstra, 1998
3	Chenevo	150	4°05'N	70°21'W	Berrio et al., 2002
4	Las Margaritas	290	3°23'N	73°26'W	Velez et al., 2005
5	Laguna Loma linda	360	3°18'N	73°23'W	Behling & Hooghiemstra, 2000
6	Curiaú (CUR)	5	0°12'N	51°01' W	-
7	Lago Crispim	2	0°46'S	47°51' W	Behling & Costa 2001
8	Lagoa da Curuça (profile B)	35	0°46'S	47°51' W	Behling 2001
9	Lagoa do Caçó	120	2°58' S	43°25' W	Pessenda et al., 2005
10	Icatu River Valley	470	10°24'S	43°13'W	De Oliveira et al., 1999

6.2.4 Unstable mid- to late Holocene and stronger ENSO

During the late Holocene, orbital forcing and subsequent redistribution of solar energy pushed the Northern Hemisphere summer position of the ITCZ farther south compared to its position during the mid-Holocene. This led to summertime cooling of the Northern Hemisphere and triggered changes in temperature gradients in the world Oceans. These changes may have caused an intensified El Niño Southern Oscillation (ENSO) (Wanner et al., 2008). ENSO in turn exacerbates inter-annual variability of the SACZ movement (Trenberth et al., 1997) and its warm phase or El Niño is the main cause of rainfall decline during the wet season of northern South America (Marengo et al., 2012; Prado et al., 2013). According to Liebmann and Mechoso (2011) during modern times, this phenomenon reduces monsoonal rainfall near the equator between December and February which prolongs dry season over this region from 3 to up to 6 months. The unstable mid- to late Holocene and its two dry periods between 5600-3300 and 2300-1000 cal yr BP in Curiaú area can be attributed to the intensified ENSO. Although high resolution palaeo-climatic data from speleothem or coral reef is missing from the study area, several studies around the world (Donders et al., 2005, Langton et al., 2008) show that the intensity of ENSO has oscillated (with different timing) during the late Holocene. The relative higher gallery forest expansion between 3300 and 2300 cal yr BP is consistent with oxygen isotope studies in Porites microatolls from Christmas Island which indicate that interannual variations in ENSO sea-surface temperature and precipitation were less intense between 3800 and 2800 cal yr BP (Woodroffe et al., 2003).

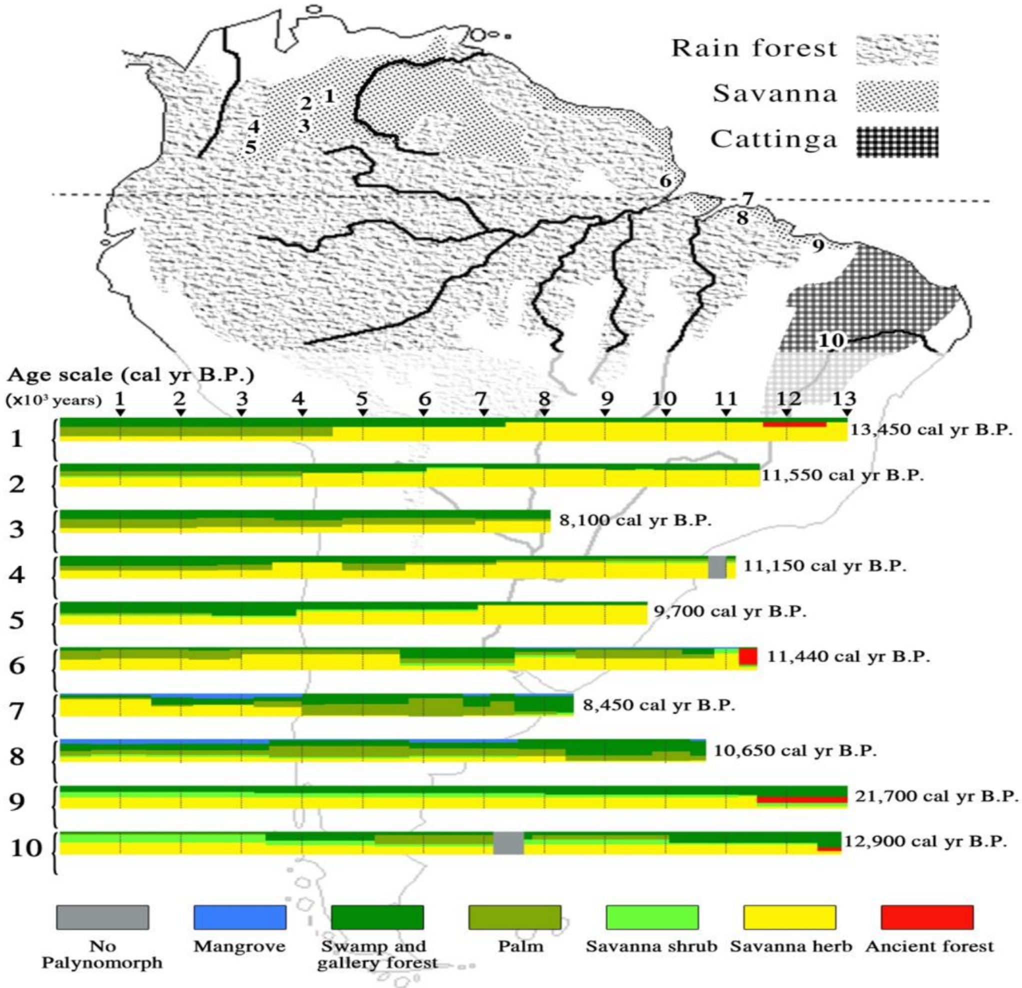

Figure 5. Schematic illustration of vegetation history. These 9 records are from savanna ecosystems located North (profiles 1-5) and South (profiles 7-9) of the Equator beside a caatinga (profile 10) and the new study site Curiaú (CUR) (profile 6). Only 13,000 years of records is demonstrated here even if they are older. Age mentioned at the right end of each row shows the oldest limit of the core. All ^{14}C radiocarbon dates from original literatures which used un-calibrated dates were calibrated using the same method explained in the text.

6.3 Soil and geomorphology

Little is known about soil composition of Macapá, but in a geological survey report Wrather (1949) mentioned that at a depth of 1 to 3 m below the old (Pleistocene) surface, a zone of ferruginous and aluminous nodules occurs. Since many plant species are sensitive to micromolar concentrations of Al (Delhaize and Ryan, 1995), this metal may be considered as edaphic factor controlling vegetation in the region. However, the history of vegetation shows periods with expansion of forests/gallery forests in riparian zone around depressions. Considering that Pleistocene plain has been the main source of sediments accumulated in the depressions, it can be concluded that the soil chemistry does not play a very important role regarding the occurrence of savanna. Nevertheless, the topography and edaphic properties permeability may be important factors controlling the geomorphologic evolution and vegetation dynamics.

6.4 Fire and humans

Since interactions between tree growth rates and fire frequency limits the forest development in the savanna region (Murphy, 2012), high concentrations of charcoal in the record CUR imply significant role of fire for the maintenance of savanna during the Holocene. This fire might be anthropogenic or natural. Although archeological sites in 100-400 km distance of the study area shows a long term presence of human in the area, because of two reasons anthropogenic origin of fire is less acceptable. First, until today, neither near the study area nor in the mentioned archeological sites evidence of big-game hunters who used fire to open the landscape for hunting is found. Second the simultaneous trends of charcoal particles concentration with climatic events support the natural origin of fire. For example, the concentration of charcoal was lower during the mid-Holocene wet period (Fig. 4b, zone CUR.IV, 7000-6000 cal yr BP) but for the period before and after mid-Holocene when the area experienced a longer dry season and dominant savanna vegetation, charcoal concentration has been always high.

7. Conclusion

The following main conclusions can be made from this study: i) Similar to many regions in lowland Amazonia, a unique forest type without modern analog grew near the mouth of Amazon River at the beginning of the Holocene. ii) Savanna had been continuously present in the coastal area of Amapá State at least since the beginning of the Holocene (11,500 cal yr BP). iii) In this region savanna has an intermediate position between interhemispheric shifts of atmospheric convection systems. The early Holocene drier climate is similar to the condition in Llanos Orientales savanna in Colombia which was under influence of ITCZ in its northern position. During the mid-Holocene, when the study area received higher precipitation due to the merge of ITCZ and SACZ, dense arboreal vegetation expanded and the area of savanna reduced. The recorded mid- to late Holocene dry episodes are comparable with the drier periods in northeast Brazil which is under influence of interaction between SACZ and ENSO. iv) Fire acted as an important factor to maintain the savanna and humans might have been the trigger of fire, but climatic factors such as the shift of ITCZ and SACZ as well as ENSO in the context of the specific regional geomorphology were the principle driving factors for the continuous occurrence of savanna in the coastal area of Amapá during the Holocene. v) Sea level rise promoted mangrove development and vegetation changes (*Mauritia* swamp versus swamp forest) in the network of palaeo-channels and palaeo-lakes during the early Holocene, but did not have a significant effect on savanna in the coastal area of Amapá State.

Acknowledgment

We would like to thank Dr. Thomas Giesecke (University of Göttingen), who kindly supervised statistical analysis of this investigation. We sincerely appreciate Professor Vera Markgarf (INSTAAR, University of Colorado Boulder) for her sage advice on both language and scientific aspect of the paper. We thank also Suzette G.A. Flantua manager of Latin American Pollen Database from the Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, for the useful advice on the literature review. Fieldwork of this study was financed by CNPq (Process 473635/2012-7 and Process 565054/2010-4). This work was funded by a scholarship awarded to Kamaleddin Alizadeh from Erasmus Mundus program under the framework of the SALAM project.

References

Absy, M.L., 1985. Palynology of Amazonia: The history of the forests as revealed by the palynological record. In: Prance, G.T., Lovejoy, T.E. (Eds.), Key Environments of Amazonia. Pergamon, Oxford, pp. 72-82.

Behling, H., 1996. First report on new evidence for the occurrence of Podocarpus and possible human presence at the mouth of the Amazon during the Lateglacial. Veget Hist. Archaeobot 5, 241-246.

Behling, H., 2001. Late Quaternary environmental changes in the Lagoa da Curuça region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. Veget Hist. Archaeobot. 10, 175-183.

Behling, H., Costa, M.L., 2000. Holocene environmental changes from the Rio Curuça record in the Caxiuan~a region, eastern Amazon basin. Quat. Res. 53, 369-377.

Behling, H., Costa, M.L., 2001. Holocene vegetational and coastal environmental changes from the Lago Crispim record in northeastern Pará State, eastern Amazonia. Rev. Palaeobot. Palyno. 114, 145-155.

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

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

Behling, H., Hooghiemstra, H., 2001. In: Markgraft, V. (Ed.), Neotropical Savanna Environments in Space and Time: Late Quaternary Interhemispheric Comparisons. Elsevier, pp. 307-323.

Behling, H., Keim, G., Iron, G., Junk, W., Mello, J.N., 2001. Holocene environmental changes in the Central Amazon basin inferred from Lago Calado (Brazil). Palaeogeogr. Palaeoclimatol. Palaeoecol. 173, 87-101.

Berrio, J.C., Hooghiemstra, H., Behling, H., Botero, P., Borg, K., 2002. Late-Quaternary savanna history of the Colombian Llanos Orientales from Lagunas Chenevo and Mozambique: a transect synthesis. Holocene 12 (1), 35-48.

Blaauw, M., 2010. Methods and code for ‘classical’ age-modelling of radiocarbon sequences. Quat. Geochronol. 5, 512-518.

Bradbury, J.P., Leyden, B.W., Salgado-Labouriau, M., Lewis Jr., W.M., Schubert, C., Binford, M.W., Frey, D.G., Whitehead, D.R., Weibezahn, F.H., 1981. Late Quaternary environmental history of Lake Valencia, Venezuela. Science 214, 1299-1305.

Bush, M.B., De Oliveira, P.E., Colinvaux, P.A., Miller, M.C., Moren, J.E., 2004. Amazonian paleoecological histories: one hill, three watersheds. Palaeogeogr. Palaeoclimatol. Palaeoecol. 214, 359-393.

Carreira, L.M.M., Barth, O.M., 2003. In: Atlas de pólen da vegetaç~ao de canga da Serra de Carajáas, Par_a, Brasil. Illustrated. Museu Paraense Emílio Goeldi, (Belém, Pará).

Carvalho, F.P., Costa Neto, S.V., Costa, W.J.P., Coutinho, R.S., Figueira, Z.R., Figueiredo, S.L., 2006. Atla Zoneamento Costeir Estuarino Do Estado Do Amapá. Macap_a, PNMA/SQA/MMA.

Castro, J.W.A., Suguio, K., Seoane, J.C.S., Da Cunha, A.M., Dias, F.F., 2014. Sea-level fluctuations and coastal evolution in the state of Rio de Janeiro, southeastern Brazil. An. Acad. Bras. Ciênc. 86, 671-683.

Cohen, M.C.L., Pessenda, L.C.R., Behling, H., Rossetti, D.F., França, M.C., Guimarães, J.T.F., Friaes, Y., Smith, C.B., 2012. Holocene palaeoenvironmental history of the Amazonian mangrove belt. Quat. Sci. Rev. 55, 50-58.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia. For. Cool. Glacial Times. Sci. 274, 85-88.

Colinvaux, P.A., De Oliveira, P.E., Moreno, E., 1999. Amazon Pollen Manual and Atlas e Manual e Atlas Palinol_ogico da Amaz^onia. Hardwood Academic, Amsterdam.

Costa Neto, S.V., 2004. Relat_orio de vegetaç~ao: Subsídio ao diagnostico sócio ambiental. Relat_orio T_ecnico. Macapá, IEPA/GERCO.

Costa Neto, S.V., Silva, M.S., 2004. Vegetaç~ao do setor costeiro estuarino do estado do Amapá. Instituto de Pesquisas Científicas e Tecnol_ogicas do Estado do Amapá. Governo do Estado do Amap_a. Cap. 5. Projeto Zoneamento Econômico-Ecol_ogico do setor costeiro estuarino: Diag-n_ostico s_ocio ambiental participativo do setor costeiro estuarino, pp. 72-96.

Costa Neto, S.V., Senna, C., Tostes, L.C.L., Silva, S.R.M., 2007. Macrófitas aquáticas das Regiões dos Lagos do Amapá, Brasil. Rev. Bras. Biociênc. 5, 618-620.

Curtis, J.H., Brenner, M., Hodell, D.A., 1999. Climate change in the Lake Valencia Basin, Venezuela, ~12,600 yr BP to present. Holocene 9, 609-619.

Delhaize, E., Ryan, P.R., 1995. Aluminum toxicity and tolerance in plants. Plant Physiol. 107, 315-321.

De Oliveira, P.E., Barreto, A.M.F., Suguio, K., 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco River. Palaeogeogr. Palaeoclimatol. Palaeoecol. 152, 319-337.

Dias, Turcq, B., Dias, M.A.F., Braconnot, P., Jorgetti, T., 2009. Mid-Holocene climate of tropical South America: a model-data approach. In: Vimeux, F., Sylvestre, F., Khodri, M. (Eds.), Past Climate Variability in South America and Surrounding Regions. Springer, pp. 259-281.

Donders, T.H., Wagner, F., Dilcher, D.L., Visscher, H., 2005. Mid- to late-Holocene El Niño-Southern oscillation dynamics reflected in the subtropical terrestrial realm. PNAS 102 (31).

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analyses, fourth ed. Wiley, New York.

Fan, Y., Li, H., Miguez-Macho, G., 2013. Global patterns of groundwater table depth. Sci 339, 940-943.

Faribanks, R.G., 1989. A 17,000-years glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature 342, 637-641.

Gagan, M.K., Hendy, E.J., Haberle, S.G., Hantoro, W.S., 2004. Postglacial evolution of the Indo-PacificWarm Pool and El Niño-Southern Oscillation. Quat. Int. 118-119, 127-143.

Grace, J., San Jos_e, J., Meir, P., Miranda, H.S., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savannas. J. Biogeogr. 33, 387-400.

Grimm, E.C., 1987. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13-35.

Guilherme, F.A.G., Nakajima, J.N., Vanini, A., Ressel, K., 2013. Tree community structure in a neotropical swamp forest in southeastern Brazil. Biosci. J. Uberlândia 29 (4), 1007-1016.

Guimarães, J.T.F., Cohen, M.C.L., Pessenda, L.C.R., França, M.C., Smith, C.B., Nogueira, A.C.R., 2012. Mid and late-Holocene sedimentary process and palaeovegetation changes near the mouth of the Amazon River. Holocene 22, 359-370.

Guimarães, J.T.F., Cohen, M.C.L., França, M.C., Pessenda, L.C.R., Souza, E.J., Nogueira, A.C.R., Alves, R., 2013. Recent effects of tidal and hydrometeorological changes on coastal plains near the mouth of the Amazon River. Earth Surf. Process. Landf. 39 (13), 1535-1549.

IBGE, 2002. Mapa de clima do Brasil. Instituto Brasileiro de Geografia e Estatistica, Rio de Janeiro.

Langton, S.J., Linsley, B.K., Robinson, R.S., Rosenthal, Y., Oppo, D.W., Eglinton, T.I., Howe1, S.S., Djajadihardja, Y.S., Syamsudin, F., 2008. 3500 yr record of centennial-scale climate variability from the Western Pacific Warm Pool. Geol. Soc. Am. 36 (10), 795-798.

Ledru, M.P., Cordeiro, R.C., Dominguez, J.M.L., Martin, L., Mourguiart, P., Sifeddine, A., Turcq, B., 2001. Late-glacial cooling in Amazonia inferred from pollen at Lagoa do Caçó, northern Brazil. Quat. Res. 55, 47-56.

Liebmann, B., Mechoso, C.R., 2011. The South American monsoon system. In: Chang, C., Ding, Y., Lau, N.C., Johnson, R.H., Wang, B., Yasunari, T. (Eds.), The Global Monsoon System: Research and Forecast, second ed. World Scientific Publishing Co.

Lima, M.I.C., Bezerra, P.E., Araújo, H.J.T., 1991. Sistematizaçao da Geologia do Estado do Amapá. In: Simpósio de geologia da Amazônia, Belem, Anais, SBG. 3, 322-335.

Lorenzi, H., 1992. Coleção Árvores Brasileiras, vol. I. Instituto Plantarum, São Paulo, Brazil.

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

Marengo, J.A., Liebmann, B., Grimm, A.M., Misra, V., Silva Dias, P.L., Cavalcanti, I.F.A., Carvalho, L.M.V., Berbery, E.H., Ambrizzi, T., Vera, C.S., Saulo, A.C., Nogues- Paegle, J., Zipser, E., Seth, A., Alves, L.M., 2012. Recent developments on the South American Monsoon system. Int. J. Climatol. 32, 1-21.

McGuire, K.L., 2007. Common ectomycorrhizal networks may maintain in a tropical rain forest. Ecology 88 (3), 567-574.

Moreira, L.S., Moreira-Turcq, P., Cordeiro, R.C., Turcq, B., Caquineau, S., Viana, J.C.C., Brandini, N., 2013. Holocene paleoenvironmental reconstruction in the eastern Amazonian Basin: comprido Lake. J. South Amer. Earth Sci. 44, 55-62.

Murphy, B.P., Bowman, D.M., 2012. What controls the distribution of tropical forest and savanna? Ecol. Lett. 15 (7), 748-758.

Nimer, E., 1989. Climatologia Do Brasil, second ed. Fundação IBGE, Rio de Janeiro.

Oksanen, J., 2013. Multivariate Analysis of Ecological Communities in R: Vegan Tutorial.

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., O'Hara, R., 2016. Vegan: community ecology package. R Packag. 2.3-3. doi:10.4135/9781412971874.n145

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Koppen-Geiger climate classification. Hydro. Earth Syst. Sci. 11, 1633-1644.

Peh, K.S.-H., Lewis, S.L., Lloyd, J., 2011. Mechanisms of monodominance in diverse tropical tree-dominated systems. J. Ecol. 99, 891-898.

Pessenda, L.C.R., Ledru, M.P., Gouveia, S.E.M., Aravena, R., Ribeiro, A.S., Bendassoli, J.A., Boulet, R., 2005. Holocene palaeoenvironmental reconstruction in northeastern Brazil inferred from pollen, charcoal and carbon isotopes records. Holocene 15 (6), 814-822.

Prado, L.F., Wainer, I., Chiessi, C.M., Ledru, M.-P., Turcq, B., 2013. A mid-Holocene climate reconstruction for eastern South America. Clim. Past. 9, 2117-2133.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatt_Z, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 Years cal BP. Radiocarbon 55 (4).

Roosevelt, A.C., 1991. Mound builders of the Amazon: Geophysical Archaeology on Marajo Island. Brazil.

Roosevelt, A.C., Costa, M.L., Machado, C.L., Michab, M., Mercier, N., Valladas, H., Feathers, J., Barnett, Silveira, Henderson, A., Sliva, J., Chernoff, B., Reese, D.S., Holman, J.A., Toth, N., Schick, K., 1996. Paleoindian Cave Dwellers in the Amazon: the peopling of the Americas. Science 272, 373-384.

Roubik, D.W., Moreno, P.J.E., 1991. Pollen and Spores of Barro Colorado Island. Monographs in Systematic Botany. Missouri Botanical Garden.

Scholes, R.J., Hall, D., 1996. The carbon budget of tropical savannas, woodlands and grasslands. SCOPE 56. In: Breymeyer, A.I., Hall, I.D., Melillo, J.M., Agren, G.I. (Eds.), Global Change, Effects on Coniferous Forests and Grasslands. John Wiley, New York, pp. 69-100.

Smith, C.B., Cohen, M.C.L., Pessenda, L.C.R., França, M.C., Guimarães, J.T.F., 2012. Holocenic proxies of sedimentary organic matter and the evolution of Lake Arari-Northern Brazil. Catena 90, 26-38.

Snow, J.W., 1976. The climate of northern South America. In: Schwerdtfeger, W. (Ed.), Climates of Central and South America. World Survey of Climatology, vol. 12. Elsevier, Amsterdam, pp. 295-403.

Souza, E.J., 2010. Geologia da regi~ao costeira do Amapâ comênfase na estratigrafia, morfotectônica e geomorfologia. Faculdade de Geologia. Universidade Federal do Par_a. Monografia de Conclusão de Curso, Belém.

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

Thomaz, O., Neto, C., Tostes, L., 2004. Inventário florístico das ressacas das bacias do Igarapé da Fortaleza e do rio Curiaú. In: Takyyama, L.R., Silva, A.Q. (Eds.), Diagnóstico de ressacas do Estado do Amapá: Bacias do Igarapé da Fortaleza e do rio Curiaú. JM Editora Gráfica, Macapá, AP, Brasil, pp. 13-32.

Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. Holocene 13, 499-505.

Tissot, C., Marius, C., 1992. Holocene evolution of the mangrove ecosystem in French Guiana: a palynological study. In: Singh, K.P., Singh, J.S. (Eds.), Tropical Ecosystem, Ecology and Management. Wiley Eastern, New Delhi, pp. 333-347.

Toledo, M.B., Bush, M.B., 2007. A mid-Holocene environmental change in Amazonian savannas. J. Biogeogr. 34, 1313-1326.

Toonen, W.H.J., Kleinhans, M.G., Cohen, K.M., 2012. Sedimentary architecture of abandoned channel fills. Earth Surf. Process. Landf. 37, 459-472.

Trenberth, K.E., 1997. The definition of El Niño,. B. Am. Meteor. Soc. 78, 2771-2777.

Van der Hammen, T., 1963. A palynological study on the Quaternary of British Guyana. Leidse Geol. Meded. 29, 126-168.

Vélez, M.I., Wille, M., Hooghiemstra, H., Metcalfe, S., 2005. Integrated diatom-pollen based reconstruction of environmental change from Laguna Las Margaritas in the western Colombian savanna area. Holocene 15, 1184-1198.

Waliser, D.E., Jiang, X., 2014. Tropical Meteorology: intertropical convergence zone. In: North, G.R., Pyle, J.A., Zhang, F. (Eds.), Encyclopedia of Atmospheric Sciences, second ed. Elsevier.

Wanner, H., Beer, J., Butikofer, J., Crowley, T.J., Cubasch, U., Fluckiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Kuttel, M., Muller, S.A., Prentice, C., Solomina, O., Stocker, T.F., Tarasov, P.,Wagner, M., Widmann, M., 2008. Quat. Sci. Rev. 27, 1791-1828.

Weischet, W., 1996. Regionale Klimatologie. 1. Die Neue Welt. Teubner, Stuttgart.

Wijmstra, T.A., 1971. The Palynology of the Guiana Coastal Basin. Ph.D. Thesis, University of Amsterdam, Amsterdam, 62 pp.

Woodroffe, C.D., Beech, M.R., Gagan, M.K., 2003. Mid-late Holocene El Niño variability in the equatorial Pacific from coral microatolls. Geophys. Res. Lett. 30 (7), 1358-1361.

Wrather, W.E., Chapman, O.L., 1949. Geologic Investigations in the American Republics. Geological survey bulletin, United States department of the interior.

III. A review on response of vegetation to equivocal climate history of the Amazon Basin during the Late Glacial-Holocene transition

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Abstract

Studies on precipitation history of South America proposed two opposite hydroclimatic scenarios (wet vs. dry) for Amazon Basin during the Late Glacial-Holocene transition (LG-HT) between ca. 13-10 kilo cal yr BP (ka). Investigating the dynamics of Amazon forests during the LG-HT using palynological records can deliver reliable evidence to support/oppose the authenticity of these hydroclimatic scenarios. Here we analyze 8 palynological records from 5 different ecosystems located in lowland Amazonia and adjacent savannas. In all records, the signal from arboreal pollen (AP) increased during the LG-HT with almost the same magnitude of the AP signals during the late Holocene but with some multi-centennial fluctuations. This suggests an episodic forest expansion during the LG-HT under a climate that was as wet as the late Holocene but not with the same stability. A review on hydroclimatic records from South America reveals that the palynological evidence is in agreement with the scenario of a wet LG-HT caused by millennial scale precipitation events over the Amazon Basin. As insolation at southern latitudes was at its minimum values during the LG-HT, the episodic intensified rainfall events must be driven by factors other than Earth's precessional cycle.

Keywords: Late Glacial; Holocene; forest dynamics; ITCZ; AMOC; Paleoclimatology

1. Introduction

Long term multi-decadal analysis on dynamics of Amazon forests demonstrated that a key factor affecting these dynamics is severe drought (Phillips et al. 2009). In the hydroclimate history of the Amazon Basin, occurrence of such severe drought is suggested during the LG-HT in particular the Younger Dryas (YD) by δ^{18}O analysis on a marine sediment core, collected from the Amazon River Fan (Maslin and Burns 2000; Maslin et al. 2011). This is the only record that reconstructs Amazon River discharge in the past and can be considered as an indicator for the basin scale precipitation changes. Results indicated that the Amazon River discharge decreased from 75% of its modern amounts at ca. 13 ka to 60% during the YD and again reached ca. 80% at around 10 ka. The authors suggested that during the YD the Amazon Basin experienced the driest period since the Late Glacial more likely due to the northern position of Intertropical Convergence Zone (ITCZ) under insolation forces. Similarly, the δ^{18}O analysis of calcite from Lake Junín (Seltzer et al. 2000) located in the Peruvian highland Andes, suggested a drier tropical South America during the Late Glacial followed by a long term increase in effective moisture during the Holocene.

In addition, new analyses of a sediment core taken from Lake Pata located in lowland Amazon forests suggests that despite what has been reported in previous publication form the lake (Colinvaux et al. 1996), the sedimentary and pollen records are discontinuous indicating episodic pauses in sedimentation. Additionally predominance of herbs and taxa which belong to seasonally dry forests during the glacial part of the record especially between 35-11 ka implies establishment of a seasonal climate (D'Apolito et al. 2013).

In contrast, several studies propose the occurrence of episodic wet condition in the Amazon Basin during the LG-HT. For instance, results from δ^{18}O analysis on speleothems collected in cave del Tigre Perdido in the foothills of Peruvian Andes (van Breukelen et al. 2008) suggested that the YD was as wet as the late Holocene. Besides, despite the results from Lake Junín (Seltzer et al. 2000), Thompson et al. (2000) recognized a YD like cooling interval in Huascarán ice core (225 km northwest of Lake Junín at 6048 m a.s.l.). They introduced this interval as deglaciation climate reversal. During this period they found less dust concentrations, implying wetter climatic condition. Also multi-proxy study (palynology, carbon and nitrogen isotope and Ti/Ca ratio) on marine sediment cores located off the northeastern Brazilian coast (Jennerjahn et al. 2004; Jaeschke et al. 2007; Burckel et al. 2015) and speleothem δ^{18}O profiles from the eastern flank of the Andes in northern Peru (western Amazonia, Cheng et al., 2013) show millennial-scale abrupt prevalence of wet climate corresponding with the Younger Dryas (YD) and Heinrich events (Cheng et al. 2013; Burckel et al. 2015). These wet episodes are in phase with speleothem records from southern (Cruz et al. 2005; Wang et al. 2006) and northeastern Brazil (Wang et al. 2004; Cruz et al. 2009), high altitude central Peruvian Andes (Kanner et al. 2012) and the Lake Titicaca record (Baker et al. 2001) implying rapid increase in monsoon rainfall during the YD owing to the southward displacement of ITCZ (Cheng et al. 2013). The same conclusion can be achieved from several pollen records such as those from Colombian Llanos Orientales (Behling and Hooghiemstra 1998, 1999) that suggest higher moisture levels under colder conditions prevailed during the El Abra stadial (YD equivalent). The recent hydroclimatic studies suggest that the position of ITCZ during the LG-HT was under influence of millennial climate changes around the North Atlantic rather than insolation forces (Cheng et al. 2013; Schneider et al. 2014).

According to these studies our understanding of precipitation patterns in Amazon Basin during the LG-HT remains equivocal because while the basin scale precipitation reconstruction (Maslin and Burns 2000; Maslin et al. 2011) shows a general aridity, other hydroclimatic records, mainly from outside the lowland Amazon Basin, imply a wet LG-HT. Unfortunately in the recently published record from Paraíso cave located in lowland eastern Amazonia there is a gap between 15-10.9 ka (Wang et al. 2016) and so it cannot help to understand the hydroclimatic history of the whole LG-HT.

One reliable approach to support either precipitation scenario of LG-HT is reconstructing the large scale Amazon forest dynamics using palynological records. As in palynology the increase in arboreal pollen percentage (AP%) and influx (API) is interpreted as prevalence of wetter or less seasonal climatic condition, the change in AP% and API of 8 palynological records from 5 different ecosystems distributed in lowland Amazonia and adjacent savannas are investigated in this study.

2. Materials and methods

2.1. Study areas

The palynological records are from 5 different ecosystems (Fig. 1 and Supplementary Table S1) including the savanna of Colombian Llanos Orientales (Behling and Hooghiemstra 1998, 1999), central part of the Colombian Amazonia (Behling et al. 1999), northern Brazilian coastal savanna belt (Alizadeh et al. 2015), northern Brazilian coastal unflooded terra firme Amazon forests (Behling 2001) and edaphic savanna on the plateau of Serra Sul dos Carajás in southeastern Amazonia (Hermanowski et al. 2012, 2014). The sedimentation environments are lakes and swamps with different catchment sizes which are found at elevations ranging from 5 to 740 m a.s.l. Length of the dry seasons differs from zero dry months in Colombian Amazonia to five dry months in Serra Sul dos Carajás. Therefore the modern topographic and climatic setting varies among the sites. Detailed information about topography, vegetation and climate can be found for each site in the Supplementary Table S1.

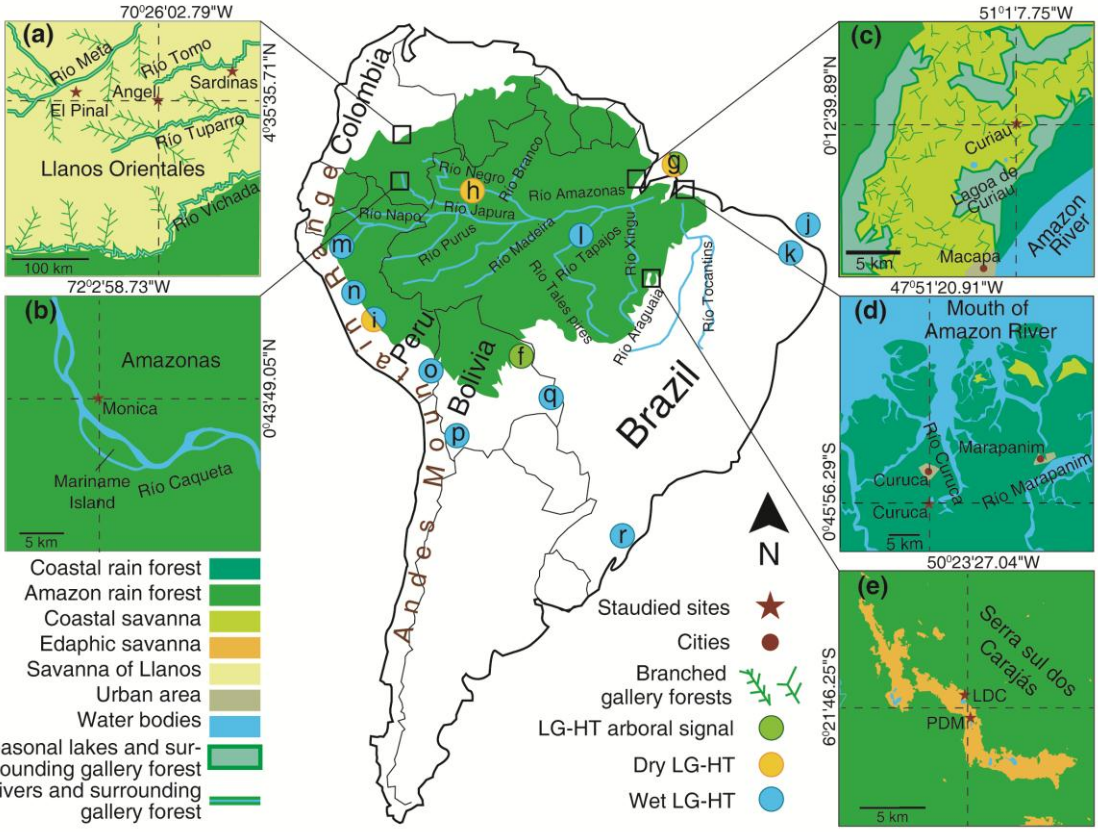


Fig 1. Location of palynological and hydroclimatic records. (a) Lakes Laguna El Pinal (Behling and Hooghiemstra 1999), Laguna Sardinas (Behling and Hooghiemstra 1998) and Laguna Angel (Behling and Hooghiemstra 1998) in savanna of Llanos Orientales. (b) Swamp Pantano de Monica in Colombian Amazon forest(Behling et al. 1999). (c) Swamp Curiaú in coastal savanna belt (Alizadeh et al. 2015). (d) Lake Lagua da Curuça in coastal Amazon rainforest (Behling 2001). (e) Wetland Pántano da Maurítia (PDM) (Hermanowski et al. 2012) and lake Lagoa da Cachoeira (LDC) (Hermanowski et al. 2014) in edaphic savanna on the plateau of Serra Sul dos Carajás. (f) Huanchaca Mesetta palm swamp, northeastern Bolivia (Maezumi et al. 2015). (g) Site 942, Amazon River Fan (Haberle Mark A. Maslin et al. 1999; Maslin and Burns 2000). (h) Lake Pata, central lowland Amazonia(Colinvaux et al. 1996). (i) Lake Pumacocha (Bird et al. 2011) and lake Junín(Seltzer et al. 2000), Peruvian Andes. (j) Site GeoB, located off the northeastern Brazilian coast (Jennerjahn et al. 2004; Jaeschke et al. 2007). (k) Rio Grande do Norte, northeastern Brazil (Wang et al. 2004; Jaeschke et al. 2007; Cruz et al. 2009). (l) Cave Paraíso, eastern lowland Amazonia(Cheng et al. 2013). (m) Caves Tigre Perdido (van Breukelen et al. 2008), El Condor and Dimante (Cheng et al. 2013), western Amazonia, (n) Huascarán ice cap, Peruvian Andes (Thompson et al. 2000). (o) Lake Titicaca, Bolivian and Peruvian highland Andes (Baker et al. 2001), (p) Lakes Poopo, Coipasa and Uyuni, southern Bolivian Altiplano (Placzek et al. 2006). (q) Lake Gaiba, lowland Bolivia(Metcalfe et al. 2014). (r) Cave Botuverá, southern Brazil (Cruz et al. 2005; Wang et al. 2006). Circles with two colors show two adjacent sites with different climate or vegetation signals. For the color image please visit the online version. The map is created using Landsat 8 images downloaded from United States Geological Survey Earth Explorer system and World Imagery in ArcGIS for desktop 10.2 and is graphically enhanced in Adobe Illustrator CS6

2.2. Chronology

The chronology in this study suffers from two sources of uncertainty:

i. The use of different age-depth modeling methods in the original studies corresponding to the 8 palynological records. To avoid this, the ^{14}C dates (Supplementary Table S2) are calibrated by using the calibration curves IntCal13 (Reimer 2013) and SHCal13 (Hogg et al. 2013) for records from northern and southern hemispheres respectively. Then the age-depth models are recreated for all 8 records in Oxcal (Bronk Ramsey 2001) (Supplementary Fig. S4-S11).

ii. The radiocarbon plateaus in the ^{14}C calibration curves during the LG-HT and the different number of radiocarbon dates among the records. To reduce effect of these uncertainties, age probability distribution with 95% confidence interval is calculated for each subsample that shows higher AP% at the boundary between Pleistocene and Holocene. The age probability distribution delivers the temporal extent of the interpolated age for each subsample and the probability of each chosen range in this temporal extent. This approach can reduce the uncertainties when detecting synchronous events in different records is desired. The weighted average interpolated age for each subsample is used to calculate sedimentation rate (cm/yr) and pollen influx. However, due to the effect of the plateaus in the calibration curves on estimation of sedimentation rate, the calculated influx must be considered with caution.

2.3. Palynology

The palynological records have been investigated and published by the third author and his colleagues. These records are selected because: i. they are well distributed in Amazon basin, ii. they are from various ecosystems and climates and iii. they cover approximately the last 13 ka. All records are checked for taxonomical nomenclature before plotting the percentage diagram. The AP% is calculated by dividing the sum of arboreal pollen (including savanna shrubs) into the total sum for the terrestrial pollen grains. Where present, pollen grains of *Mauritia, Mauritiella* and mangrove trees are excluded from sum of arboreal pollen because i) palms of *Mauritia* and *Mauritiella* in general surround the coring sites and their pollen grains represent a local rather than regional signal; ii) mangroves dynamics depend on the sea level fluctuations rather than the atmospheric climatic events.

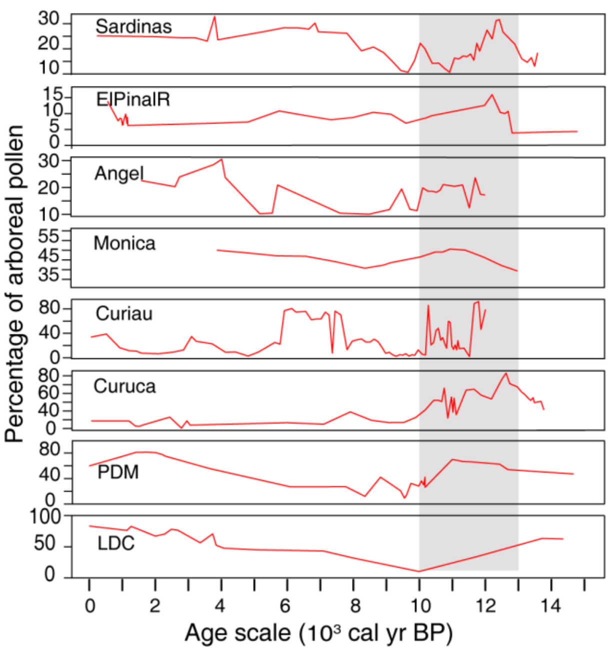
2.4. Principal Component Analysis (PCA)

The aim of PCA in this study is to test and illustrate the differences between pollen assemblages of subsamples corresponding to LG-HT and those of other subsamples in each record. The PCAs cover 13 ka of each record even if the record is longer. In the site Monica the data for the last 4 ka is not available. Therefore the variation in pollen percentage data in Monica dataset is not comparable with those in other records. Thus pollen zones (clusters) resulted from cluster analysis of Monica dataset cannot fulfill the aim of PCA in this study and the PCA for this record is not plotted. To plot the PCA for each of the other records, the pollen percentage data of all terrestrial taxa with percentage > 1% (except *Mauritia*, *Mauritiella* and mangrove) are first square root transformed. Then the constrained cluster analysis is done using CONISS in R by package Rioja (Juggins 2015). The cluster analysis allows separation of subsamples based on the dissimilarities in their pollen assemblage and categorizes them into different pollen zones (clusters). The PCA is plotted using the package Vegan (Oksanen et al. 2016), and clusters are shown on PCA by the function ordihull (Oksanen et al. 2016).

3. Results

3.1. Palynology and chronology

Despite the differences in modern climate, topography and vegetation cover among the records, in general, the diagrams for AP% (Fig. 2) and API (Fig. 3) for most of the records show maxima at the Pleistocene-Holocene boundary. The sum of the age probability distributions (black line in Fig. 4) for the subsamples constituting these maxima indicates that with 95% confidence interval they occurred between 13 and 10 ka (LG-HT). Only the record Laguna El Pinal does not show a maximum of API in this period, most probably because of the very low pollen concentration due to the sandy nature of the grey-greenish sediment accumulated between 12.8 and 11.2 ka. The long distance between Laguna El Pinal and Amazon rainforest and the location of the site may also cause the low API during the LG-HT. Despite Laguna Angel and Sardinas that are located in depression, Laguna El Pinal is located on a hill and is surrounded by a narrow fringe of gallery forest. In the record Lagoa da Cachoeira (LDC), the maxima for both AP% and API, are partly out of the LG-HT interval. This might be because of the relatively long temporal distance between the two radiocarbon dates before and after LG-HT or/and the plateau in ^{14}C calibration curves that may cause some uncertainties in the age estimation. The illustration of the data (Fig. 2 and 3) clearly show that the maxima in AP% and API during the LG-HT are comparable with those maxima during the late Holocene when moister climatic conditions in general prevailed in tropical South America according to palaeoecological studies (Behling et al. 2001; Mayle et al. 2004). For the site Pántano de Monica (Monica) the data for the last 4 ka was not available, however in the original published paper (Behling et al. 1999) authors showed that the AP% reaches ca. 90% after 4 ka (Supplementary Fig. S1). Although in this record the maxima in AP% during the LG-HT is not comparable with that of the late Holocene, it is higher compared to the period before 13 ka and the period between 10 and 4 ka. In the records Laguna El Pinal (Behling and Hooghiemstra 1999), Pántano da Maurítia (PDM) (Hermanowski et al. 2012) and LDC (Hermanowski et al. 2014) that reach back to the Last Glacial Maximum (LGM), the AP% during the LG-HT was the strongest compared to the period between the LGM and the LG-HT (Supplementary Fig. S2).



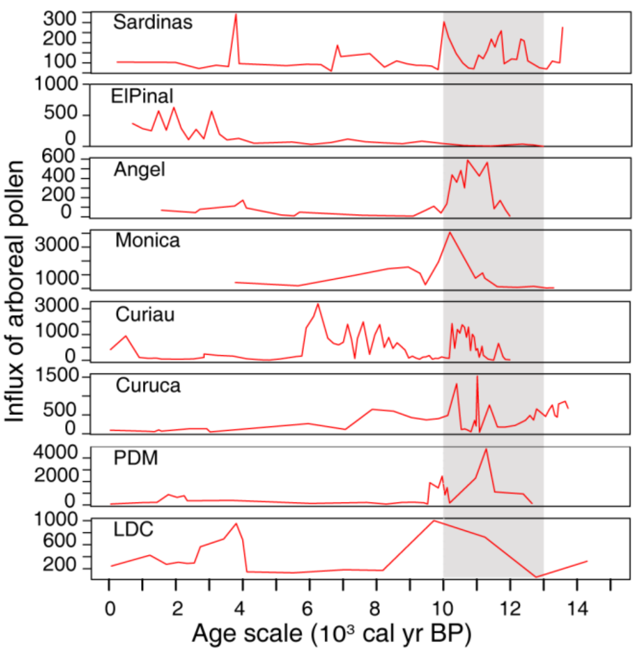


Fig 2. The pattern of AP% changes in the 8 palynological records

Fig 3. The pattern of API changes in the 8 palynological records

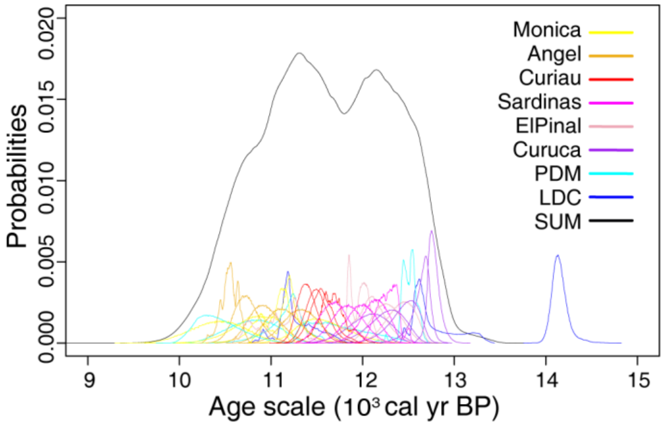


Fig 4. The age probability distributions for each subsample with higher values of AP% during the LG-HT are shown. Each color corresponds to one site and each peak belongs to one subsample. The black line shows the sum of probability distributions and the age range when the maxima in AP% occurs. For the color image please visit the online version

Furthermore, in the records Sardinas, Curiaú and Curuça several fluctuations in the AP% can be detected during the LG-HT. The range of these fluctuations is larger than fluctuations during the late Holocene (and also mid-Holocene in Curiaú). This proposes that the forest expansion during the LG-HT occurred in some short multi-centennial episodes and the area of forest was more dynamics compared to the late Holocene. The rate and timing of fluctuations in AP% during the LG-HT vary among the records probably because of i) dissimilar subsampling intervals for pollen analysis in the records, ii) site specific characteristics such as edaphic factors and microclimates, iii) centennial scales variations in occurrence of climatic events in different sites and iv) chronological issues such as number of radiocarbon dates for each site and the effect of plateaus in calibration curve.

3.2. Principal Component Analysis (PCA)

The result of PCA is shown in Figure 5 and Supplementary Figure S3. The first two principal components (PC) are plotted. The first PCs account for 20-43% of variation in our dataset. This value for the second PCs is between 12-21%. Contribution from each of the other PCs to the variation in our dataset is negligible. The red diamonds (solid diamonds in black and white print) represent the subsamples with maxima in AP% that constitute the LG-HT cluster.

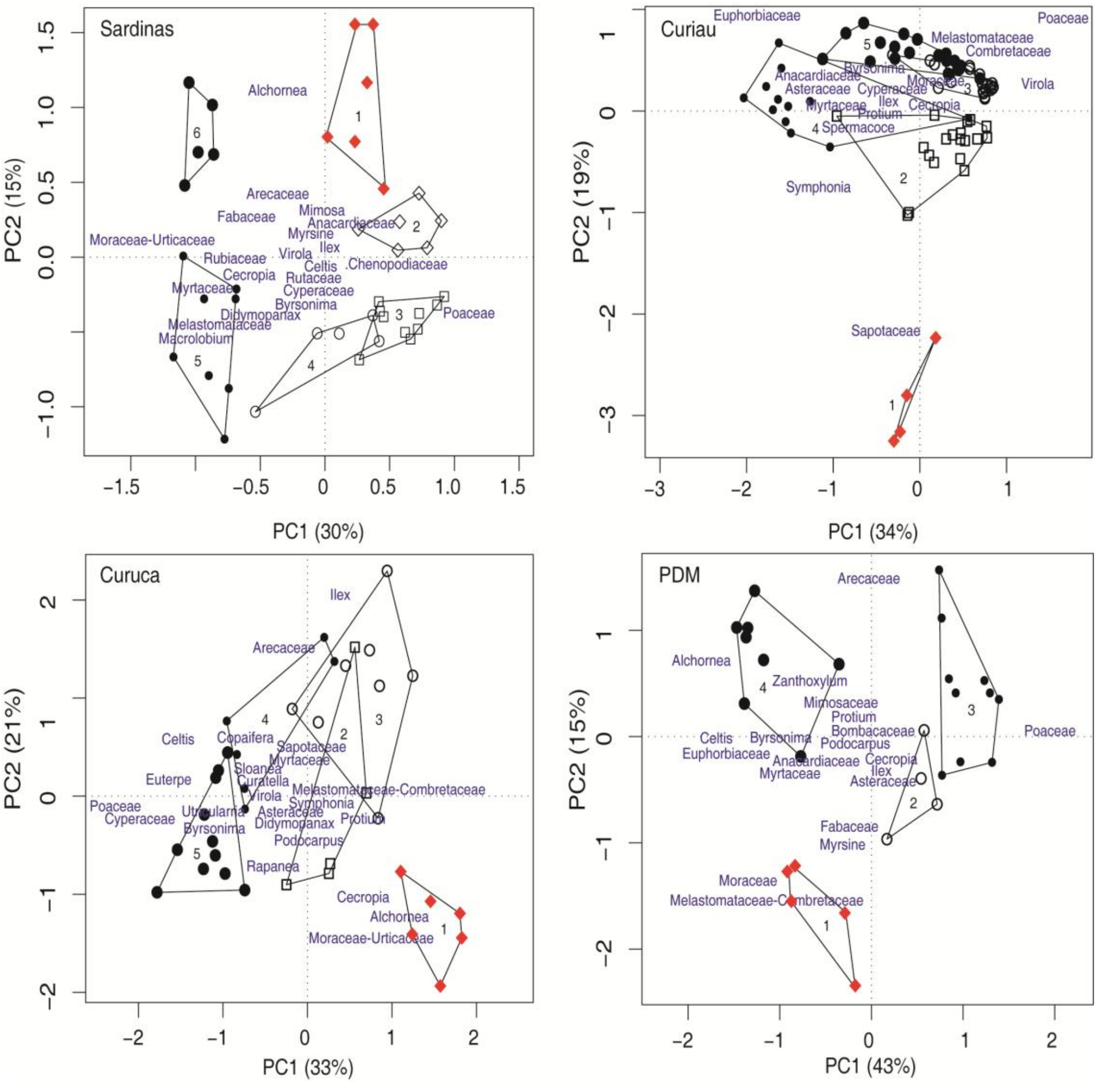


Fig 5. PCA for the records Sardinas, Curiaú, Curuça and PDM. The red diamonds (solid diamonds in black and white print) represent samples which constitute the cluster corresponding to the LG-HT. The plant taxa close to this cluster demonstrate the predominance taxa during the LG-HT. The numbers in the clusters indicate the order of clusters from older to younger. For the color image please visit the online version

The plant taxa near these clusters are the dominant taxa of that period. As the relative position of each cluster compared to others depends on the similarities/dissimilarities in the pollen assemblages, the isolated position of the LG-HT cluster in most of the records implies that its vegetation composition was different from the younger part of the corresponding records. The degree of isolation differs among the sites with most obvious isolation in Curiaú to no isolation in Angel. These variations could naturally occur due to the site specific characteristics. For example in the record Curiaú (Alizadeh et al. 2015) the dominant taxa of the LG-HT was *Micropholis* (Sapotaceae), whereas the pollen of this plant was not found after 11.2 ka. In the record Sardinas, *Alchornea* was frequent during both LG-HT and the late Holocene. In the record Curuça pollen of Moraceae/Urticaceae, *Cecropia* and *Alchornea* were more frequent during the LG-HT. In the record El Pinal, *Celtis* is closer to the LG-HT cluster. Although the records PDM and LDC are located close together, the LG-HT was dominated by Melastomataceae/Combretaceae and Moraceae/Urticaceae in PDM while in LDC cold adapted taxa *Podocarpu*s and *Hedyosmum* are important trees of that period.

4.1. The maxima in AP signal (AP% and API)

There were maxima in AP signals during the LG-HT in almost all palynological records used in this study that implies a forest expansion at the boundary between Pleistocene and Holocene. The AP signals of LG-HT are stronger than the AP signals during the period between the LGM and the LG-HT and in most of the records their strength is comparable with the AP signals during the wetter late Holocene. Increased frequency of arboreal pollen in palynology is interpreted as prevalence of wetter climatic conditions. In particular presence of pollen from Moraceae/Urticaceae, Melastomataceae/Comberataceae, *Alchornea* and *Celtis* is indicator for occurrence of moist rain forests (Marchant et al. 2002; Gosling et al. 2009). This evidence suggests that the LG-HT was wetter than LGM and as wet as the late Holocene. Such conclusion can be made also based on the following hydroclimatic records.

The studies on water level changes in large palaeo-lakes located in southern Bolivian Altiplano reported the Coipasa deep lake cycle dated between 13 and 11 ka. Since lake cycles on the Bolivian Altiplano are under influence of moisture content in the Amazon Basin and enhanced transport of that moisture onto the Altiplano, it can be concluded that the Amazon Basin was not dry during the LG-HT (Placzek et al. 2006).

In the stalagmite retrieved from cave del Tigre Perdido (van Breukelen et al. 2008) the δ^{18}O values of the YD period are almost equal to the modern δ^{18}O values in this record suggesting that during the YD, northern Peruvian Andes received the same amount of precipitation as modern time (~1500 mm/yr). The striking similarity in the trends of the Holocene δ^{18}O curves of the Tigre Perdido (foothills of the Andes) and Huascarán records (highland Andes) means that the latter record accumulated from essentially the same moisture that first produced the rainfall trapped in the Tigre

Perdido record. This study suggests that during the YD both lowland and highland Andes received rainfall equal to the modern time. Thus because a large part of the rainfall in western Amazonia and Andes is produced by the moisture transported from eastern Amazonia (Sun and Barros 2015), a wetter LG-HT in the lowland Amazon Basin can be concluded as well. Similarly, in the records Paraíso cave located in eastern lowland Amazonia (Cheng et al. 2013) and lake Pumacocha (Bird et al. 2011) located close to the lake Junín in Peruvian highlands, the values of $\delta^{18}O$ around 11 ka is similar to those during the late Holocene.

4.2. Multi-centennial fluctuations in AP signals during the LG-HT

Such variable AP signals of LG-HT in comparison with the almost stable AP signals during the late Holocene can suggest that the climate of LG-HT was not a stable wet climate similar to the late Holocene, but the wet conditions more likely prevailed in some multi-centennial episodes. This aspect of forest dynamics and climatic condition can be explained by the following hydroclimatic studies.

Speleothem records from southern (Cruz et al. 2005; Wang et al. 2006) and northeastern (Wang et al. 2004; Cruz et al. 2009) Brazil as well as eastern and western Amazonia (Cheng et al. 2013) delivered the most recent comprehension of precipitation patterns in South America (Fig. 6). The orbital scale shifts in $\delta\ ^{18}O$ profiles of the records from northeastern Brazil and eastern Amazonia are not in phase with those from southern Brazil and western Amazonia. But during the glacial periods and YD there were several synchronous millennial scale shifts in the $\delta\ ^{18}O$ profiles of these records and in Ti/Ca ratio of marine sediment cores located off the northeastern Brazilian coast (Jennerjahn et al. 2004; Jaeschke et al. 2007; Burckel et al. 2015). These synchronous shifts imply precipitation events that lasted for a thousand years during stadials such as YD and Heinrich events and covered more likely many locations of South America and Amazon Basin (Cheng et al. 2013). During the late Pleistocene the climate of the Greenland experienced consecutive cold (stadial) and warm (interstadial) phases leading to abrupt changes in world ocean currents and reduction in Atlantic Meridional Overturning Circulation (AMOC) during stadials. AMOC slowdowns preceded some of the large South American rainfall events during stadials and it presumably caused these millennial scale precipitation events (Burckel et al. 2015).

Change to an episodic wetter climatic condition is reported also from lake Gaiba located in lowland Bolivia. This record demonstrated a marked change at about 12.2 ka to a wetter climate with rising lake levels that was interrupted by periodic drying. From ca. 11.8 to 10 ka stable, deeper water conditions persisted (Metcalfe et al. 2014).

4.3. Dissimilar taxa composition of forests during the LG-HT

In each record, the forests of LG-HT show some dissimilarity in taxa composition compared to the forests in other periods of Holocene in the same record. The dominant tree taxa of LG-HT, however, were not the same among different records even from sites that are located close together in one ecosystem (e. g. PDM and LDC). Such heterogeneous forest taxa composition among sites that are closely located proposes that during the LG-HT there was not any particular climatic condition that could homogenize forest taxa composition. It seems that the short precipitation events could only cause the tree taxa around each site to expand locally.

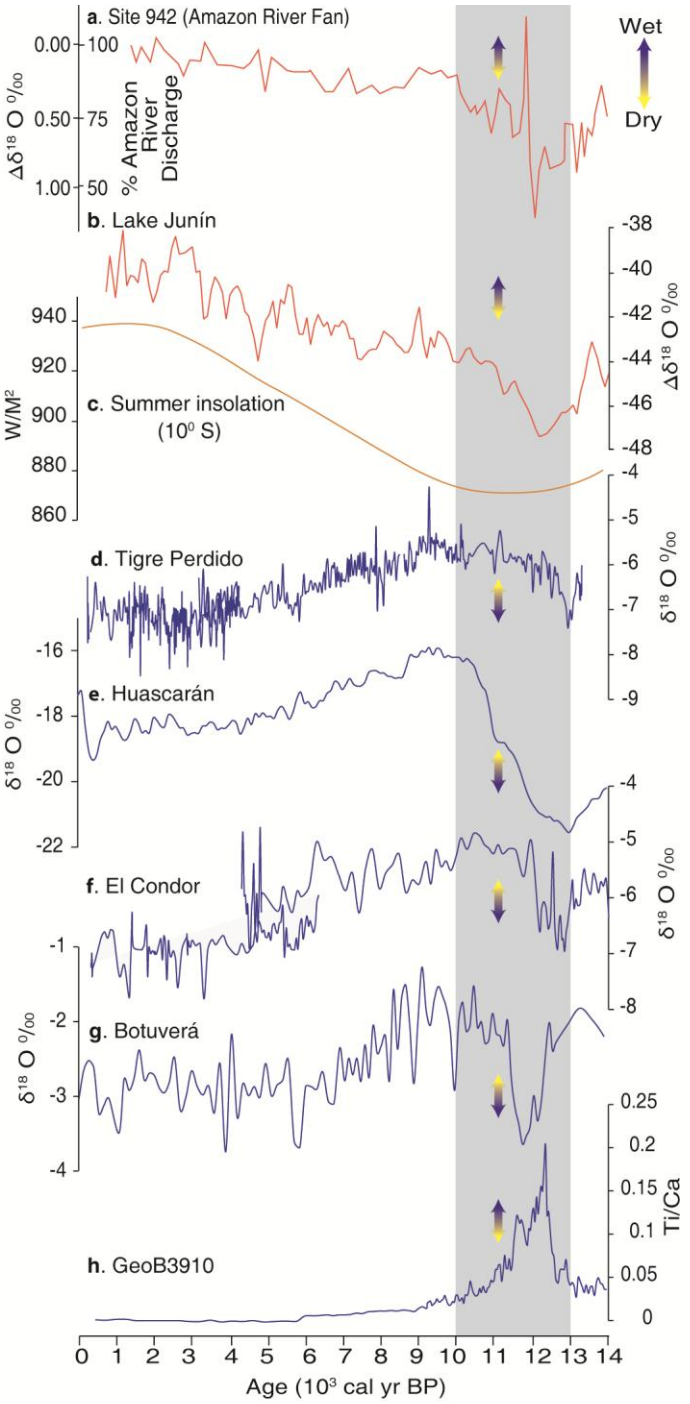


Fig 6. Hydroclimatic evidence for dry (red) and wet (blue) climatic scenarios. (**a**) Planktonic foraminifera δ^{18}O composition of marine core taken at site 942 and reconstructed Amazon River discharge (Maslin and Burns 2000). (**b**) The δ^{18}O composition of foramineferal calcite from Lake Junín (Seltzer et al. 2000). (**c**) Summer insolation at 10° S (Berger 1978). (**d-g**) δ^{18}O values for records from cave Tigre Perdido (van Breukelen et al. 2008), Huascarán ice cap(Thompson et al. 2000), cave El Condor (Cheng et al. 2013) and cave Botuverá (Cruz et al. 2005; Wang et al. 2006) respectively and (**h**) sedimentary Ti/Ca ratios in marine sediment cores GeoB (Jaeschke et al. 2007). For the color image please visit the online version

The only palynological signal that can be attributed to a basin scale particular climatic condition, is the occurrence of *Podocarpus* and some associated cold adapted taxa in the records Curuça (Behling

2001), PDM (Hermanowski et al. 2012), LDC (Hermanowski et al. 2014) as well as the record from lake Pata located in central lowland Amazonia (Colinvaux et al. 1996), the marine core from Amazon River Fan (Haberle Mark A. Maslin et al. 1999) and the record Huanchaca Mesetta palm swamp located in northeastern Bolivia (Maezumi et al. 2015). This signal indicates a colder climatic condition during the LG-HT. A nearly 5° C cooling between 40 and 11.5 ka (Stute et al. 1995) over the lowlands of northern South America is also reported from analyzing the concentration of atmospheric noble gas dissolved in ^{14}C-dated ground water in northeastern Brazil.

5. Conclusion

According to the reconstructed dynamics of Amazon forests, prevalence of an unstable wetter and colder climate condition during the LG-HT can be concluded. This conclusion is in agreement with climatic scenario of millennial scale precipitation events in South America resulted from the abrupt increase in monsoon rainfall related to a southward shift in the mean position of the ITCZ. Incidence of such events was not under insolation forces but was due to the consecutive oscillation in the climate of Greenland that could affect the world ocean currents. This scenario is mainly based on the hydroclimatic records located outside the lowland Amazonia, however, the moisture made by evapotranspiration from Amazon Basin can be distributed in the whole continent by several mechanisms such as Amazon biotic pump (Syst et al. 2006) and Low Level Jet (Marengo et al. 2004). Therefore records outside the Amazon Basin can also reflect precipitation changes in this basin.

The records studied or cited in this paper are broadly distributed in tropical South America so that they can provide robust evidence for the scenario of basin scale precipitation events during the LG-HT. However, as some hydroclimatic records can show, due to the size of Amazon Basin, a homogenous climate cannot be considered for the whole area. For example the deep lake cycles in palaeo-lakes of Bolivian Altiplano as an indicator of moisture availability in Amazon Basin did not occurred synchronously (Placzek et al. 2006) during the glacial periods. The Ouki highstand was in phase with the wet periods recorded in speleothems from southern Brazil (Cruz et al. 2005) synchronous with the February insolation at 30°S (Wang et al. 2004). In contrast the Tauca highstand shows synchrony with the wet periods in speleothem record from northeastern Brazil (Wang et al. 2004) that are in phase with the austral autumn insolation at 10°S. Therefore it is suggested that there is not a single season or latitude of precessional cycling that brings the moisture to the whole Amazon Basin. Maslin et al. (2011) also suggested that South American Summer Monsoon (SASM) is not a simple belt, but its northern and southern boundaries are independently dynamic and driven by temperature gradients within their individual hemispheres. Thus the moisture availability in tropical South America since the LGM experienced dynamic heterogenic changes. This heterogeneity in climate highlights the need for higher number of palynological and hydroclimatic records before creating more precise basin scale image of climatic condition during the LG-HT.

Acknowledgment

This research is carried out based on the results obtained during two decades of palynological studies by Prof. Hermann Behling and coworkers. Many funding institutes and personnel have contributed to these studies. We would like to acknowledge all the efforts and funds which helped preparation of this paper. Also we would like to appreciate the scientific comments that Dr. Vincent Montade made on our manuscript. This study is part of the first author's PhD that is funded by Erasmus Mundus, SALAM project, award number (SALA1204147).

References

Alizadeh K, Cohen M, Behling H (2015) Origin and dynamics of the northern South American coastal savanna belt during the Holocene – the role of climate, sea-level, fire and humans. Quat Sci Rev 122:51–62 . doi: 10.1016/j.quascirev.2015.05.009

Baker P a, Seltzer GO, Fritz SC, et al (2001) The history of South American tropical precipitation for the past 25,000 years. Science 291:640–643 . doi: 10.1126/science.291.5504.640

Behling H (2001) Late Quaternary enviornmental changes in the Lagoa da Curuca region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. Veg Hist Archaeobot 10:175–183 . doi: 10.1007/PL00006929

Behling H, Berrio JC, Hooghiemstra H (1999) Late Quaternary pollen records from the middle Caqueta river basin in central Colombian Amazon. Palaeogeogr Palaeoclimatol Palaeoecol 145:193–213 . doi: 10.1016/S0031-0182(98)00105-9

Behling H, Hooghiemstra H (1998) Late quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. Palaeogeogr Palaeoclimatol Palaeoecol 139:251–267 . doi: 10.1016/S0031-0182(97)00139-9

Behling H, Hooghiemstra H (1999) Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. J Paleolimnol 21:461–476 . doi: 10.1023/A:1008051720473

Behling H, Hooghiemstra H, Markgraf V (2001) Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons\rInterhemispheric climates linkages. 307–323

Berger A (1978) Long-term variations of caloric insolation resulting from the earth’s orbital elements. Quat Res 9:139–167 . doi: 10.1016/0033-5894(78)90064-9

Bird BW, Abbott MB, Rodbell DT, Vuille M (2011) Holocene tropical South American hydroclimate revealed from a decadally resolved lake sediment ??18O record. Earth Planet Sci Lett 310:192–202 . doi: 10.1016/j.epsl.2011.08.040

Bronk Ramsey C (2001) Development of the radiocarbon calibration program. Radiocarbon 43:355–363 . doi: papers2://publication/uuid/5B399323-3576-4144-BF98-497069142583

Burckel P, Waelbroeck C, Gherardi JM, et al (2015) Atlantic Ocean circulation changes preceded millennial tropical South America rainfall events during the last glacial. Geophys Res Lett 42:411–418 . doi: 10.1002/2014GL062512

Cheng H, Sinha A, Cruz FW, et al (2013) Climate change patterns in Amazonia and biodiversity. Nat Commun 4:1411 . doi: 10.1038/ncomms2415

Colinvaux P a., De Oliveira PE, Moreno JE, et al (1996) A Long Pollen Record from Lowland Amazonia: Forest and Cooling in Glacial Times. Science (80-) 274:85–88 . doi: 10.1126/science.274.5284.85

Cruz FW, Burns SJ, Karmann I, et al (2005) Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. Nature 434:63–66 . doi: 10.1038/nature03365

Cruz FW, Vuille M, Burns SJ, et al (2009) Orbitally driven east–west antiphasing of South American precipitation. Nat Geosci 2:210–214 . doi: 10.1038/ngeo444

D'Apolito C, Absy ML, Latrubesse EM (2013) The Hill of Six Lakes revisited: New data and re-evaluation of a key Pleistocene Amazon site. Quat Sci Rev 76:140–155 . doi: 10.1016/j.quascirev.2013.07.013

Gosling WD, Mayle FE, Tate NJ, Killeen TJ (2009) Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. Rev Palaeobot Palynol 153:70–85 . doi: 10.1016/j.revpalbo.2008.06.007

Haberle Mark A. Maslin SG, A.Maslin SGHM, Haberle SG, Maslin MA (1999) Late Quaternary Vegetation and Climate Change in the Amazon Basin Based on a 50,000 Year Pollen Record from the Amazon Fan, ODP Site 932. Quat Res 51:27–38 . doi: 10.1006/qres.1998.2020

Hermanowski B, da Costa ML, Behling H (2012) Environmental changes in southeastern Amazonia during the last 25,000yr revealed from a paleoecological record. Quat Res 77:138–148 . doi: 10.1016/j.yqres.2011.10.009

Hermanowski B, Da Costa ML, Behling H (2014) Possible linkages of palaeofires in southeast Amazonia to a changing climate since the Last Glacial Maximum. Veg Hist Archaeobot 24:279–292 . doi: 10.1007/s00334-014-0472-0

Hogg A, Hua Q, Blackwell PG, et al (2013) SHCal13 Southern Hemisphere Calibration, 0–50,000 Years cal BP. Radiocarbon 55:1889–1903 . doi: 10.2458/azu_js_rc.55.16783

Jaeschke A, Rühlemann C, Arz H, et al (2007) Coupling of millennial-scale changes in sea surface temperature and precipitation off northeastern Brazil with high-latitude climate shifts during the last glacial period. Paleoceanography 22:n/a–n/a . doi: 10.1029/2006PA001391

Jennerjahn TC, Ittekkot V, Arz HW, et al (2004) Asynchronous terrestrial and marine signals of climate change during Heinrich events. Science 306:2236–9 . doi: 10.1126/science.1102490

Juggins S (2015) rioja: Analysis of Quaternary Science Data, R package version (0.9-9).

Kanner LC, Burns SJ, Cheng H, Edwards RL (2012) High-Latitude Forcing of the South American Summer Monsoon During the Last Glacial. Science (80-) 335:570–573 . doi: 10.1126/science.1213397

Maezumi SY, Power MJ, Mayle FE, et al (2015) Effects of past climate variability on fire and vegetation in the cerr??do savanna of the Huanchaca Mesetta, NE Bolivia. Clim Past 11:835–853 . doi: 10.5194/cp-11-835-2015

Marchant R, Almeida L, Behling H, et al (2002) Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev Palaeobot Palynol 121:1–75 . doi: 10.1016/S0034-6667(02)00082-9

Marengo JA, Soares WR, Saulo C, Nicolini M (2004) Climatology of the low-level jet east of the Andes as derived from the NCEP-NCAR reanalyses: Characteristics and temporal variability. J Clim 17:2261–2280 . doi: 10.1175/1520-0442(2004)017<2261:COTLJE>2.0.CO;2

Maslin M a, Burns SJ (2000) Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. Science 290:2285–2287 . doi: 10.1126/science.290.5500.2285

Maslin MA, Ettwein VJ, Wilson KE, et al (2011) Dynamic boundary-monsoon intensity hypothesis: Evidence from the deglacial Amazon River discharge record. Quat Sci Rev 30:3823–3833 . doi: 10.1016/j.quascirev.2011.10.007

Mayle FE, Beerling DJ, Gosling WD, Bush MB (2004) Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. Philos Trans R Soc Lond B Biol Sci 359:499–514 . doi: 10.1098/rstb.2003.1434

Metcalfe SE, Whitney BS, Fitzpatrick KA, et al (2014) Hydrology and climatology at Laguna La Gaiba, lowland Bolivia: Complex responses to climatic forcings over the last 25 000 years. J Quat Sci 29:289–300 . doi: 10.1002/jqs.2702

Oksanen J, Blanchet F, Kindt R, et al (2016) Vegan: community ecology package. R Packag. 2.3-3 Available at: https://cran.r–project.org/web/packa

Phillips OL, Aragao LEOC, Lewis SL, et al (2009) Drought Sensitivity of the Amazon Rainforest. Science (80-) 323:1344–1347 . doi: 10.1126/science.1164033

Placzek C, Quade J, Patchett PJ (2006) Geochronology and stratigraphy of late Pleistocene lake cycles on the southern Bolivian Altiplano: Implications for causes of tropical climate change. Bull Geol Soc Am 118:515–532 . doi: 10.1130/B25770.1

Reimer P (2013) IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. Radiocarbon 55:1869–1887 . doi: 10.2458/azu_js_rc.55.16947

Schneider T, Bischoff T, Haug GH (2014) Migrations and dynamics of the intertropical convergence zone. Nature 513:45–53 . doi: 10.1038/nature13636

Seltzer G, Rodbell D, Burns S (2000) Isotopic evidence for late Quaternary climatic change in tropical South America. Geology 28:35–38 . doi: 10.1130/0091-7613(2000)28<35:ieflqc>2.0.co;2

Stute M, Forster M, Frischkorn H, et al (1995) Cooling of Tropical Brazil (5{degrees}C) During the Last Glacial Maximum. Science (80-.). 269:379–383

Sun X, Barros AP (2015) Impact of Amazonian evapotranspiration on moisture transport and convection along the eastern flanks of the tropical Andes. Q J R Meteorol Soc 141:3325–3343 . doi: 10.1002/qj.2615

Syst E, Syst E, License CC, et al (2006) Biotic pump of atmospheric moisture as driver of the hydrological cycle on land. Nucl Phys 2621–2673 . doi: 10.5194/hessd-3-2621-200

Thompson LG, Mosley-Thompson E, Henderson KA (2000) Ice-core palaeoclimate records in tropical South America since the last glacial maximum. J Quat Sci 15:377–394 . doi: 10.1002/1099-1417(200005)15:4<377::AID-JQS542>3.0.CO;2-L

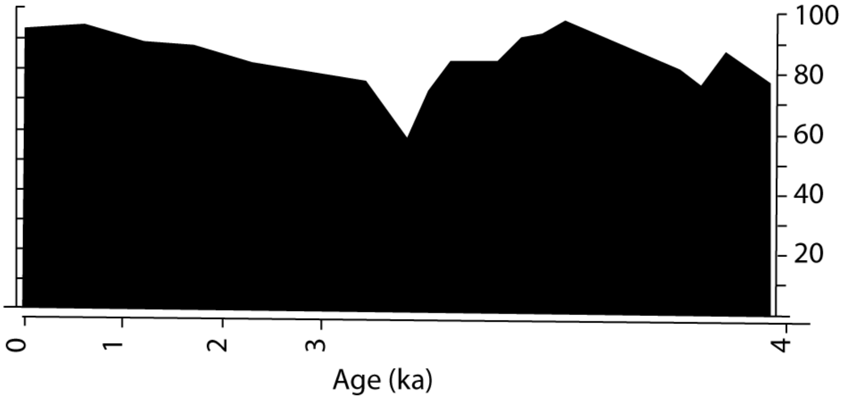
van Breukelen MR, Vonhof HB, Hellstrom JC, et al (2008) Fossil dripwater in stalagmites reveals Holocene temperature and rainfall variation in Amazonia. Earth Planet Sci Lett 275:54–60 . doi: 10.1016/j.epsl.2008.07.060

Wang X, Auler AS, Edwards RL, et al (2006) Interhemispheric anti-phasing of rainfall during the last glacial period. Quat Sci Rev 25:3391–3403 . doi: 10.1016/j.quascirev.2006.02.009

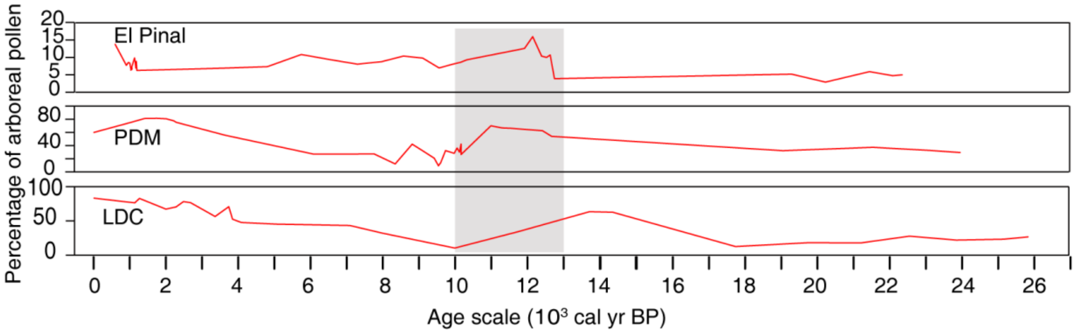
Wang X, Auler AS, Edwards RL, et al (2004) Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. Nature 432:740–743 . doi: 10.1038/nature03067

Wang X, Lawrence Edwards R, Auler AS, et al (2016) Hydroclimate changes across the Amazon lowlands over the past 45,000 years. Nature 541:204–207 . doi: 10.1038/nature20787

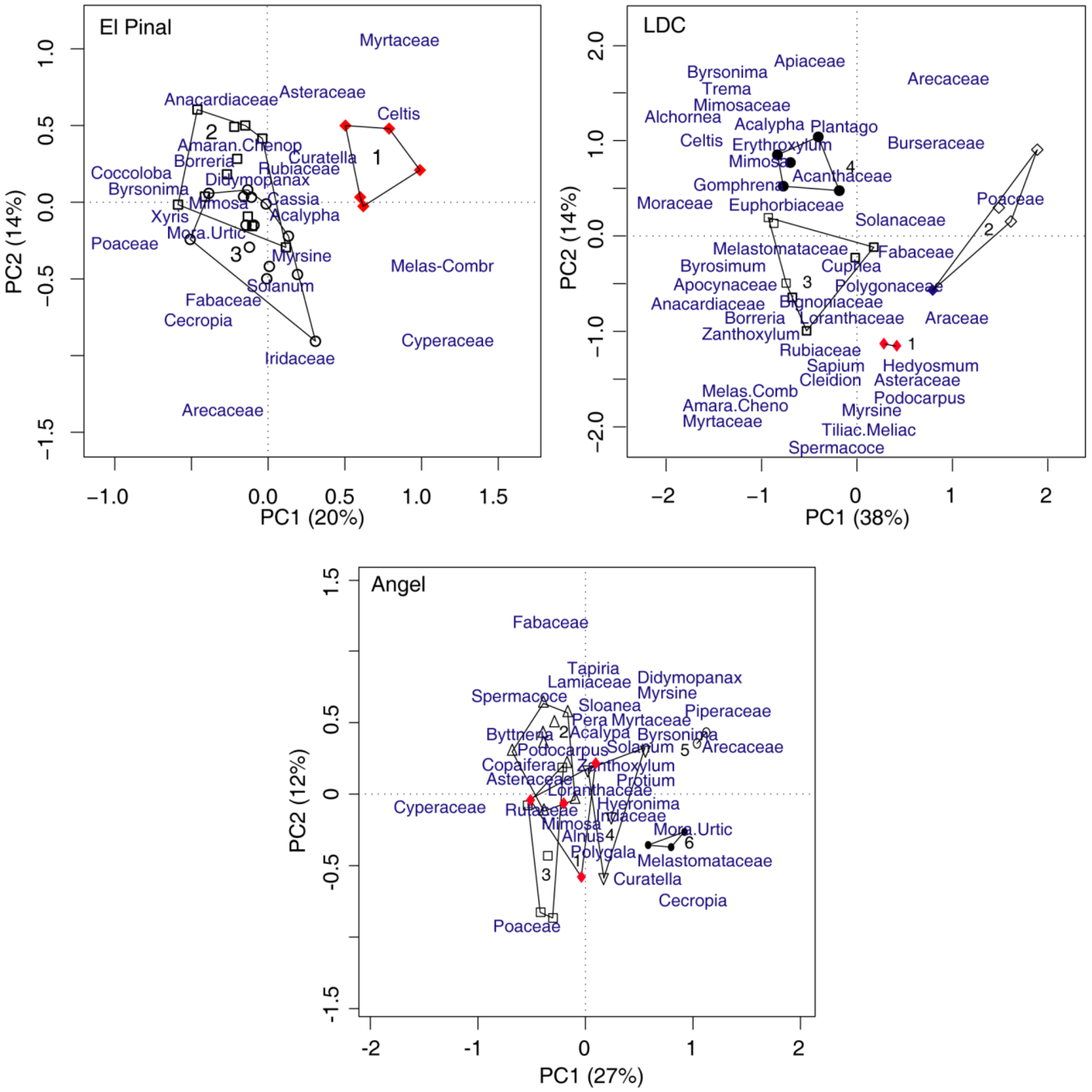
Supplementary materials of Chapter III



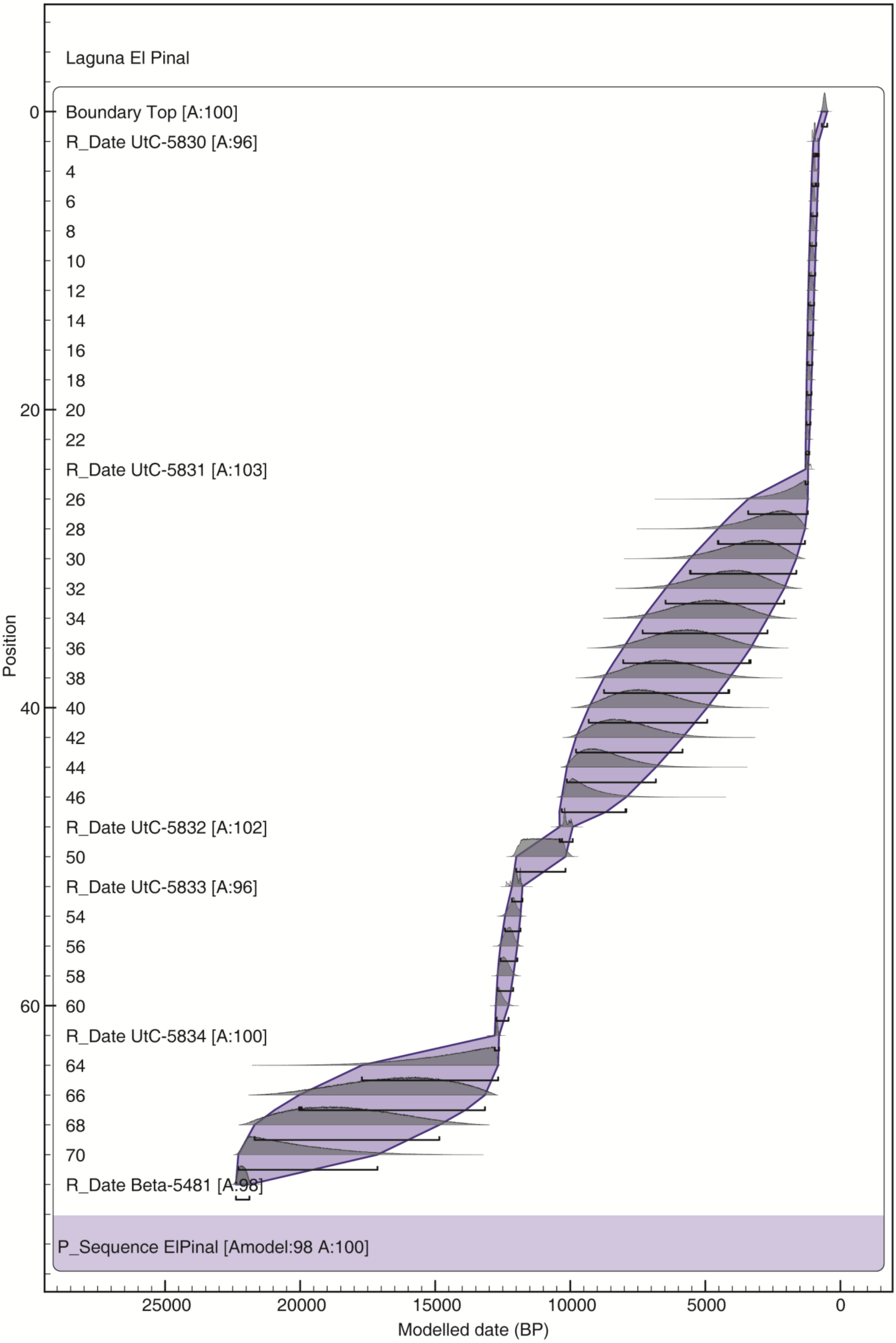
Supplementary Fig. 1. The pattern of AP% changes in the record Pantano de Monica during the last 4 ka. The fig is recreated in Adobe Illustrator based on the original pollen diagram.



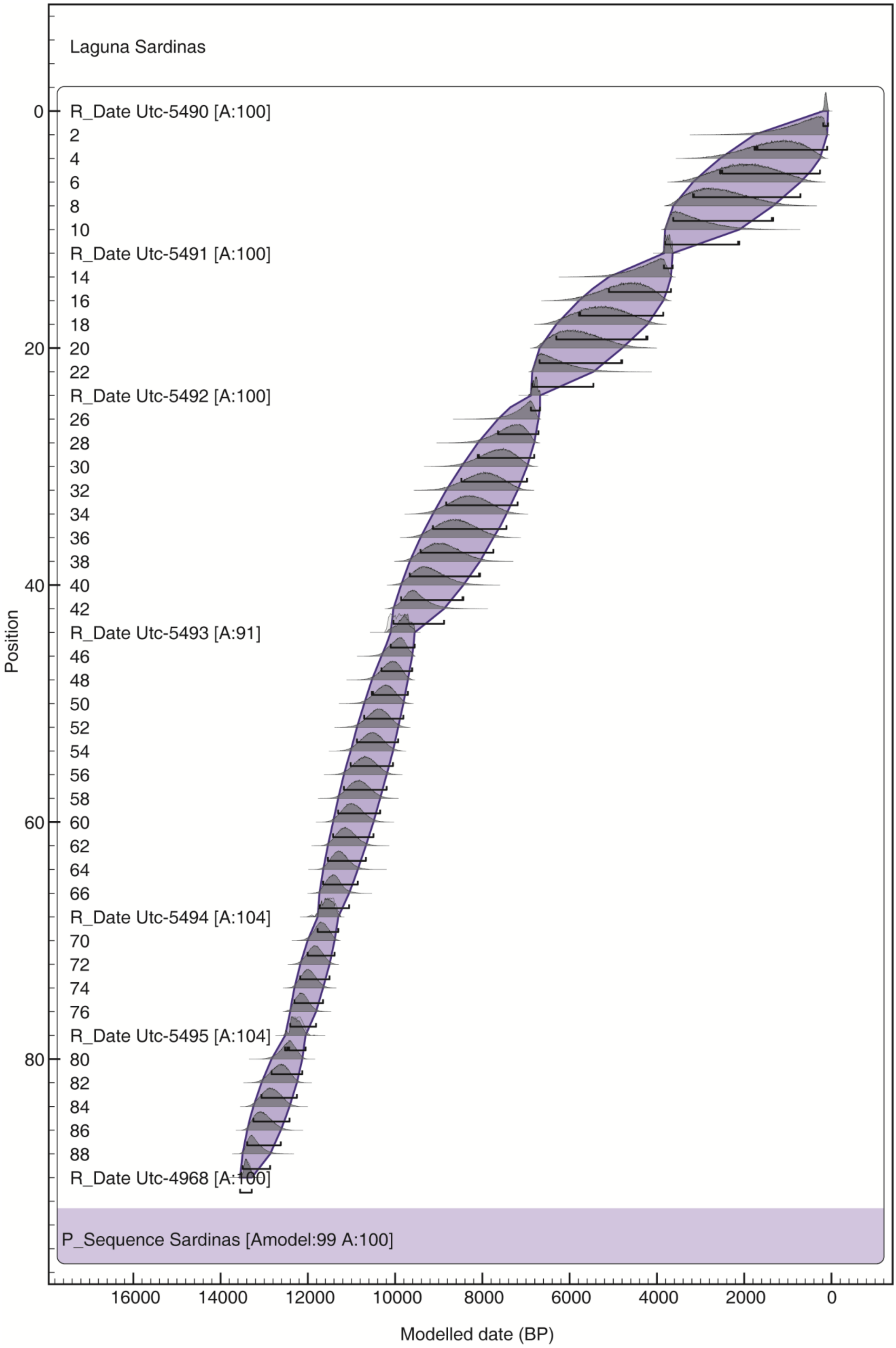
Supplementary Fig. 2. The pattern of AP% changes in the records Laguna El Pinal, Pántano da Maurítia, Lagoa da Cachoeira.



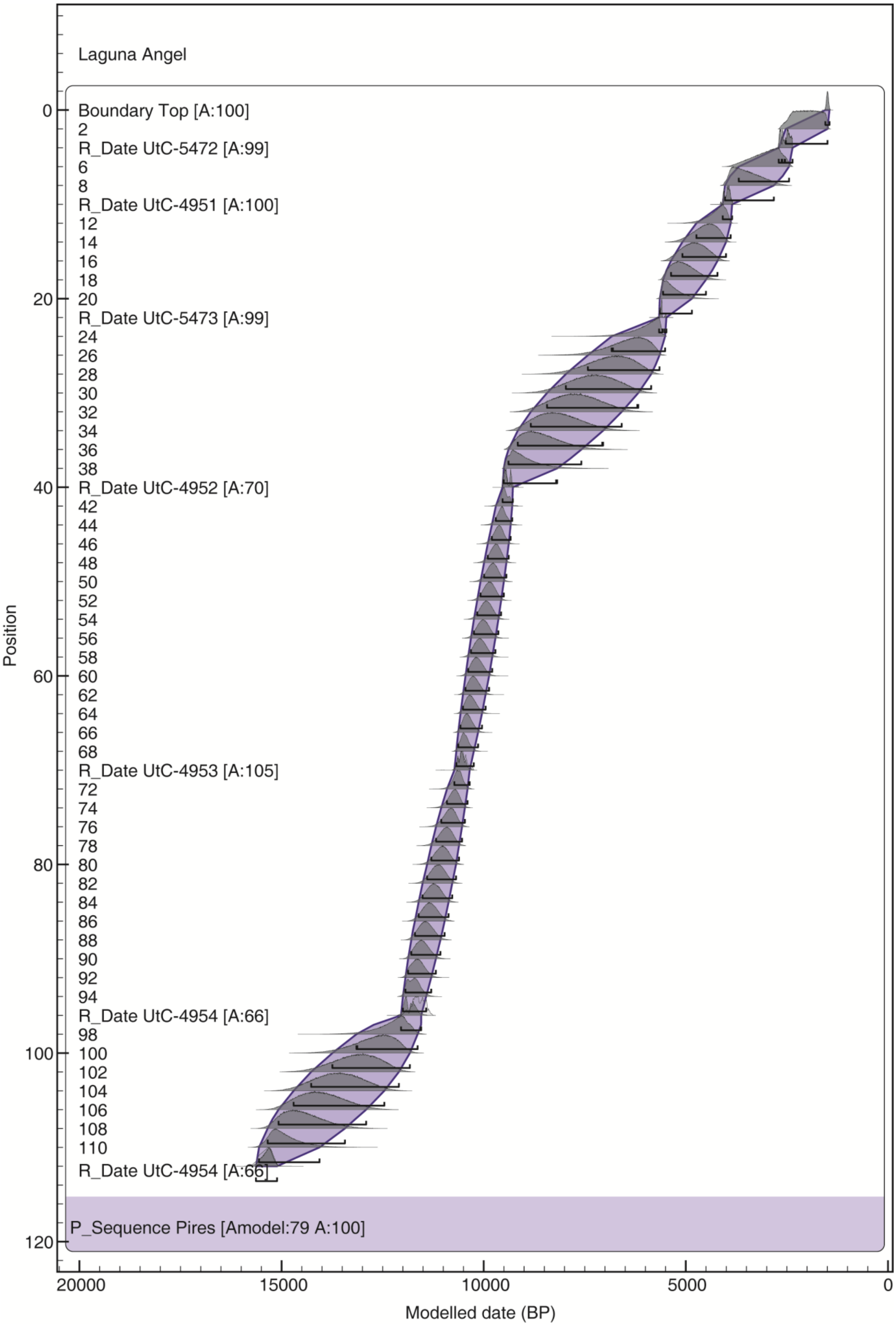
upplementary fig. 3. Principal Component Analysis for the records Laguna El Pinal, Lagoa da Cachoeira and Laguna Angel. The red diamonds (solid diamonds in black and white print) represent samples which constitute the cluster corresponding to the LG-HT. The plant taxa close to this cluster demonstrate the predominance taxa during the LG-HT. The numbers in the clusters indicate the order of clusters from older to younger.



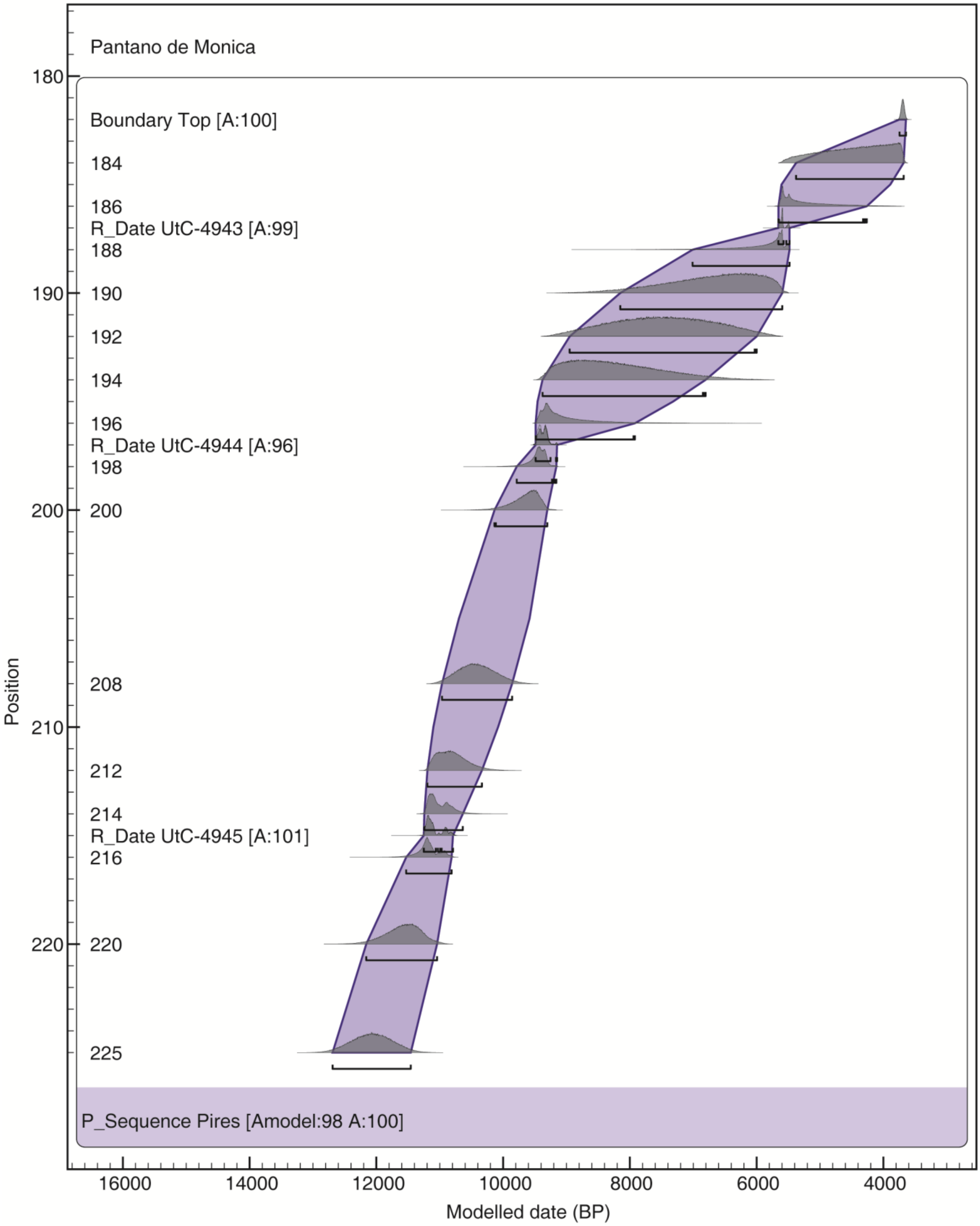
Supplementary fig 4. Age-depth model of the record Laguna El Pinal



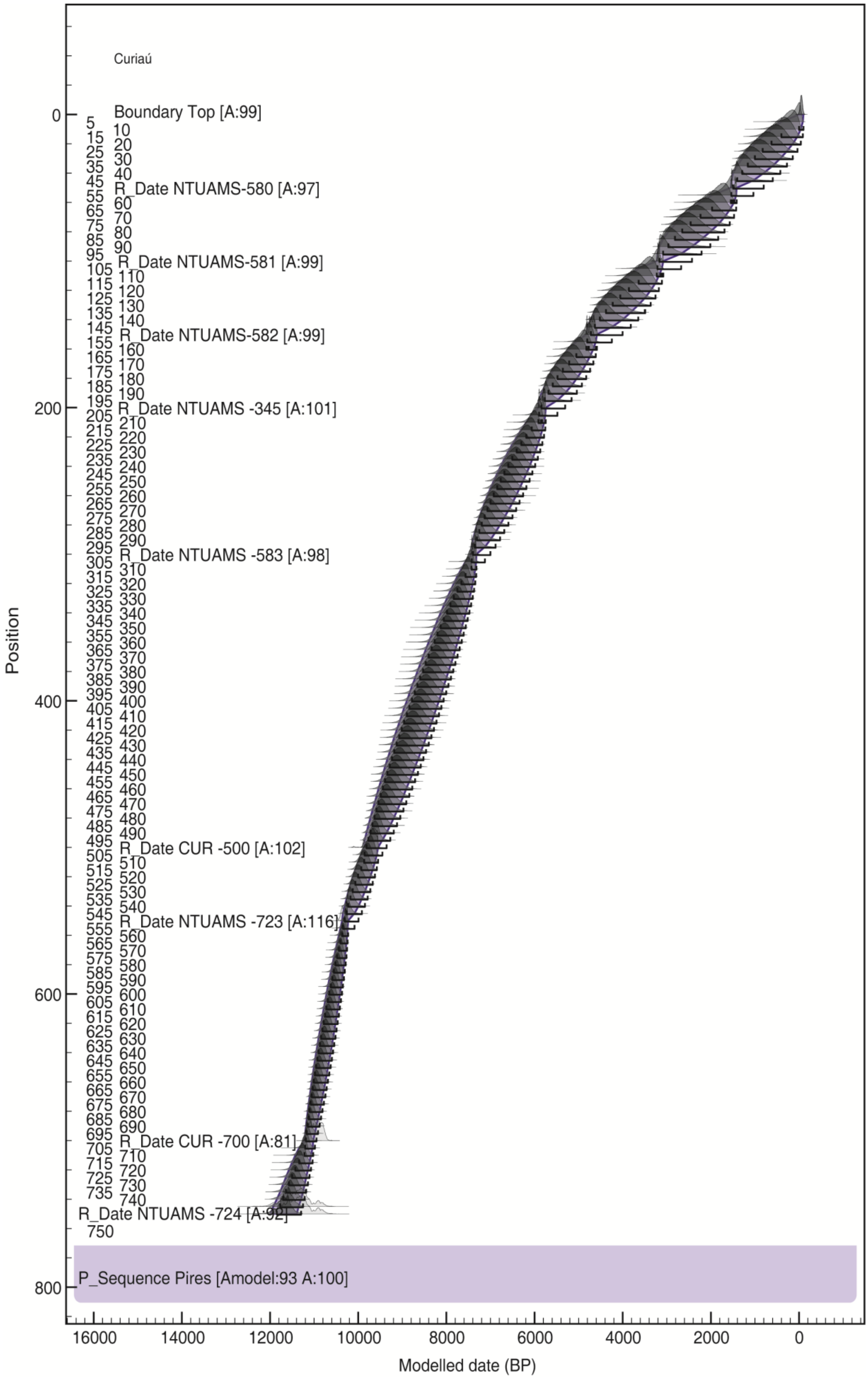
. **Supplementary fig. 5.** Age-depth model of the record Laguna Sardinas**.**



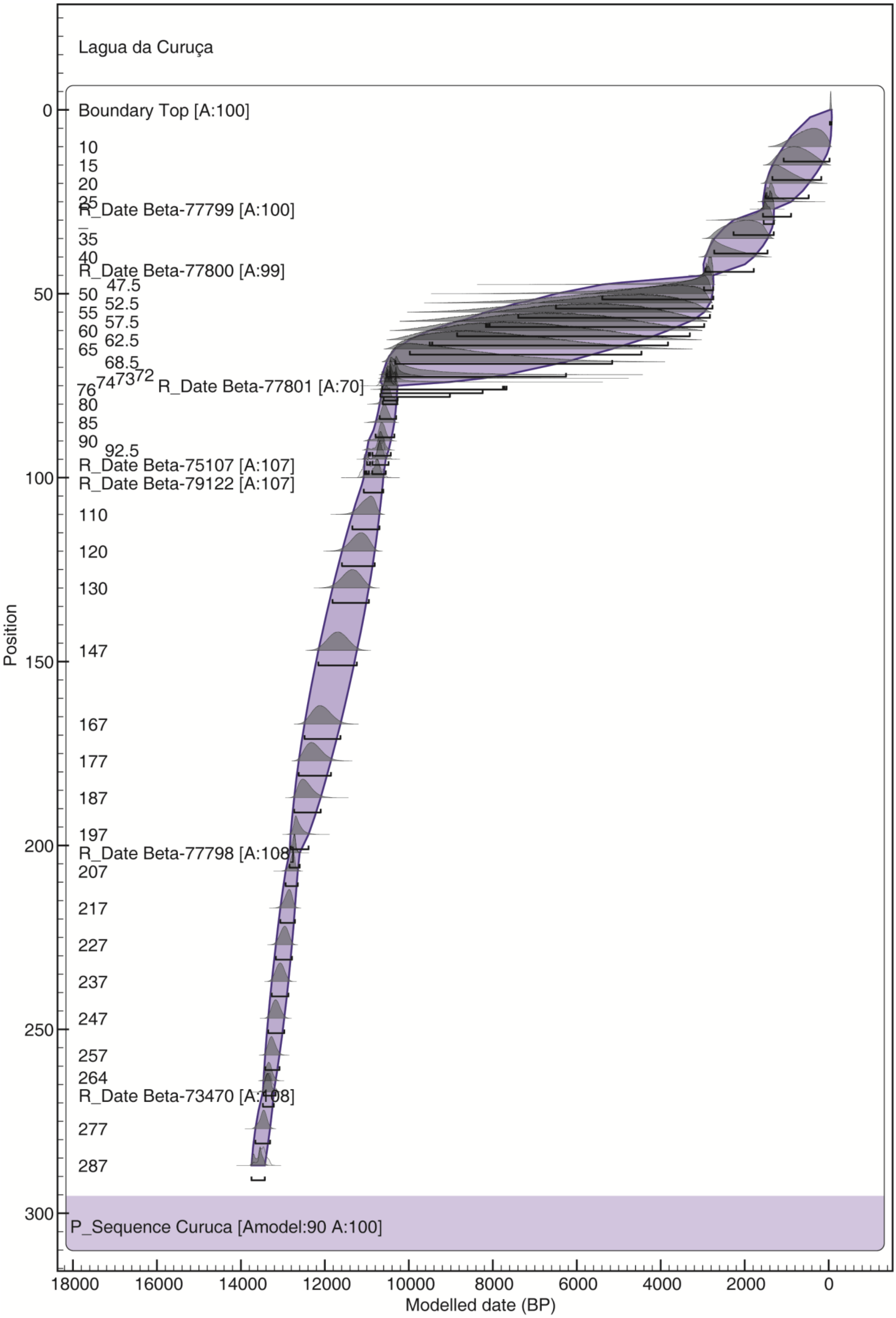
Supplementary fig. 6. Age-depth model of the record Laguna Angel**.**



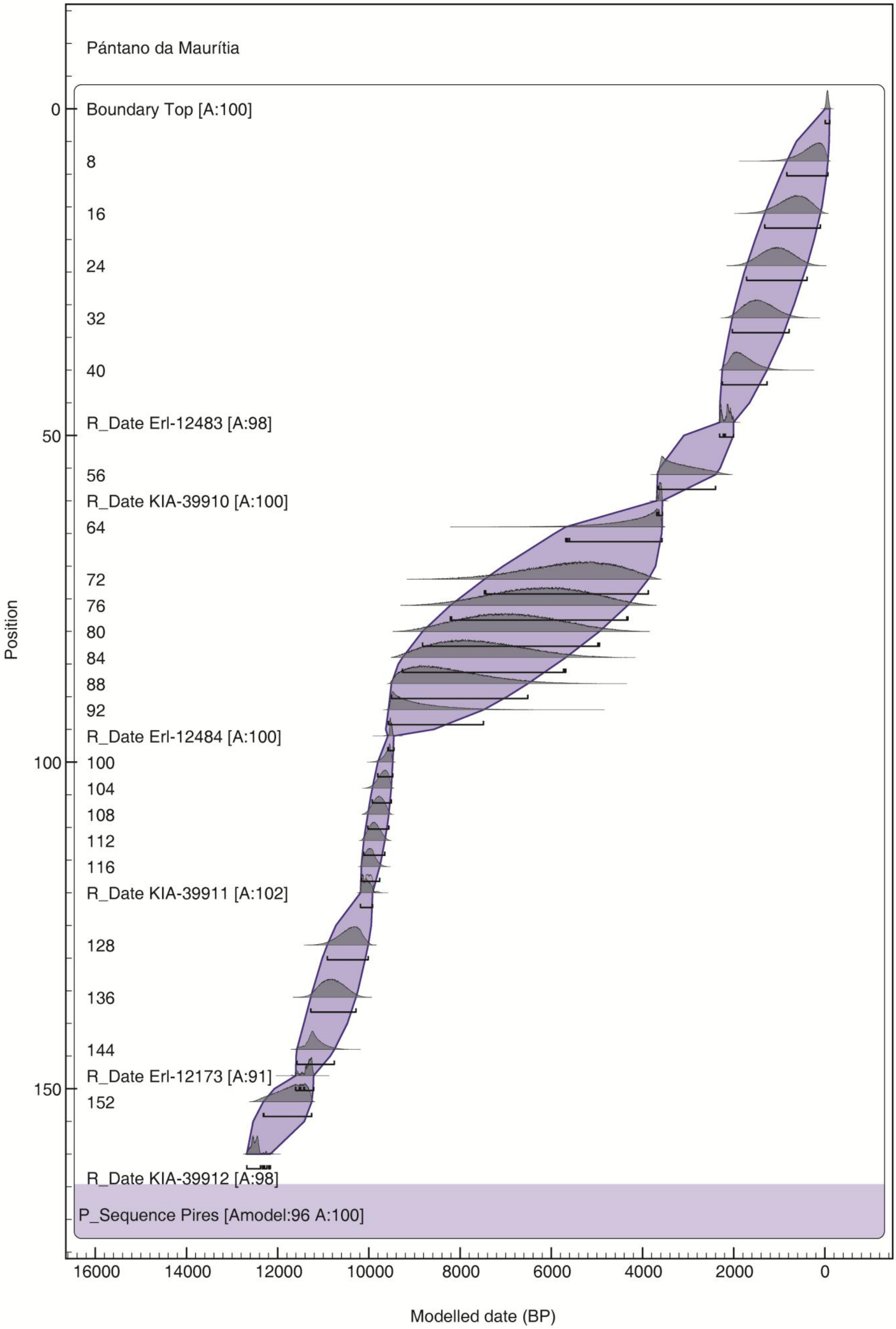
Supplementary fig. 7. Age-depth model of the record Pantano de Monica.



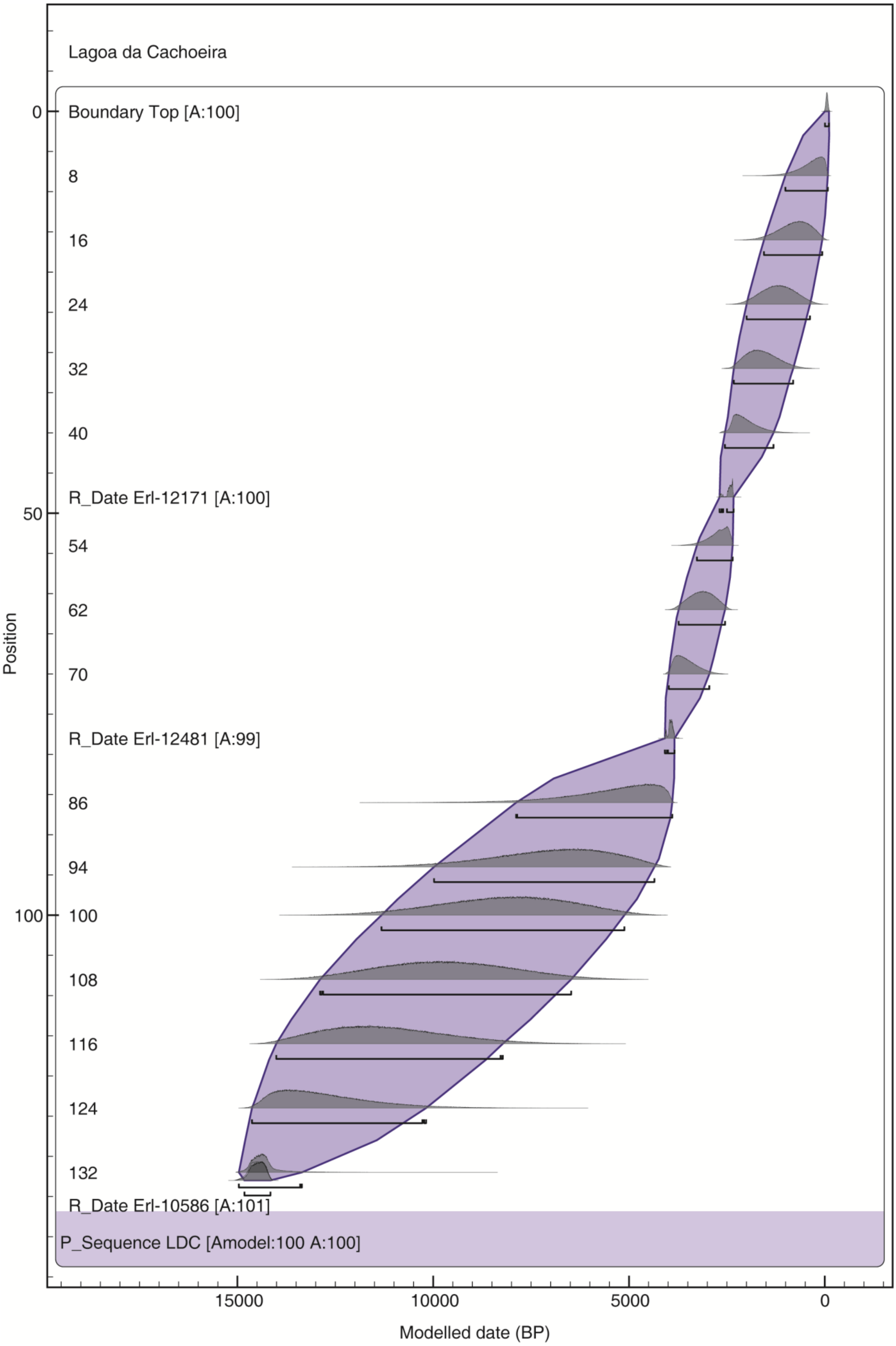
Supplementary fig. 8. Age-depth model of the record Curiaú.



Supplementary fig. 9. Age-depth model of the record Lagua da Curuça**.**



Supplementary fig. 10. Age-depth model of the record Pántano da Maurítia.



Supplementary fig. 11. Age-depth model of the record Lagoa da Cachoeira.

Supplementary table 1. Summary of geographical setting for the 8 study sites.

	Geographical coordinates	Elevation (m a.s.l.)	Location description	Ecosystem and vegetation	Climate and dry season	Mean annual rainfall (mm)	Mean annual temperature (°C)
Laguna El Pinal	4°39'40.81"N 71°27'10.51"W	150	100 km to Amazon rainforests	Grassy savanna with patches of gallery forest along the rivers and dense stands of *Mauritia* and *Mauritiell* around lakes	Tropical savanna climate November to March (four months)	2000 (90% falling during the wet season)	26.5
Laguna Sardinas	4°59'18.98"N 69°21'57.55"W	140	70 km to Amazon rainforests				
Laguna Angel	4°26'57.67"N 70°32'19.45"W	175	55 km to Amazon rainforests				
Pantano de Monica	0°42'0.00"S 72° 3'5.00"W	100	On the lower terraces of the Rio Caqueta	Central part of Colombian Amazon forests covered by dense, tall tropical rainforest	Tropical humid without seasonally dry periods	3060	25.7
Curiaú	0°12'40.00"N 51° 1'12.10"W	5	Near the mouth of Amazon River 30 km distance to eastern borders of Amazon rainforest	Coastal savanna on the Hilly plain with gallery forests along meandering palaeo-channels	Tropical humid September to November (three months)	2750	27.5
Lagua da Curuça	0°45'53.78"S 47°51'21.17"W	35	Near the mouth of Amazon river, 15 km distance to the Atlantic ocean	Coastal unflooded terra firme Amazon rainforest with coastal vegetation such as mangrove, salt marshes, restinga and campo de dunas	tropical warm and humid less rainfall from June to November	2277	25.9
Pántano da Maurítia	6°22'32.73"S 50°23'9.43"W	740	Located on ferruginous soil of plateau of Serra Sul dos Carajás km mean distance to Amazon forests	Edaphic savanna with xerophytic deciduous vegetation called 'Campo rupestre'	Tropical savanna June to October (five months)	2126	23.5
Lagoa da Cachoeira	6°21'18.00"S 50°23'35.00"W	705					

Supplementary table 2. List of the radiocarbon dates for the 8 palynological records.

	Lab. number	Depth (cm)	14C yr B.P.	Calendar age (cal yr B.P.) 95.4% probability
Laguna El Pinal	UtC-5830	2	1065 ± 36	1056-926
	UtC-5831	4	1261 ± 36	1283-1082
	UtC-5832	48	9020 ± 80	10394-9909
	UtC-5833	52	10280 ± 50	12379-11824
	UtC-5834	62	10790 ± 60	12792-12626
	UtC-5481	72	18290 ± 90	22391-21898
Laguna Sardinas	UtC-5490	0	83 ± 27	185-77
	UtC-5491	12	3475±39	3842-3641
	UtC-5492	24	5961±40	6892-6679
	UtC-5493	44	8840±90	10194-9624
	UtC-5494	68	10030±60	11802-11272
	UtC-5495	78	10380±60	12521-12016
	UtC-5468	90	11570±70	13551-1327
Laguna Angel	UtC-5472	4	2451±30	2705-2361
	UtC-4950*	9.5	3651±43	4091-3854 (A= 29.7%)
	UTC-4951	10	4830±60	5512-5318
	UtC-5473	22	4864±38	5662-5483
	UtC-4952	40	8450±60	9542-9310
	UtC-4953	70	9320±70	10700-10290
	UtC-4954	95.5	10070±60	11959-11328
	UtC-4955	112	12880±80	15680-15141
Pantano de Monica	UtC-4943	187	4855±38	5658-4482
	UtC-4944	197	8363±49	9491-9264
	UtC-4945	215	9720±70	11253-10789
	UtC-4946**	235	7260±60	8181-7968
Curiaú	NTUAMS-580	50	1606±10	1548-1416
	NTUAMS-581	100	2994±16	3228-3080
	NTUAMS-582	150	4162±26	4828-4586
	NTUAMS-345	200	5092±28	5914-5750
	NTUAMS-583	300	6471±30	7434-7322
	NTUAMS-346**	400	9268 ± 40	10569-10295
	CUR-500	500	8711±57	9890-9547
	NTUAMS-347**	600	10160±50	12053-11511
	NTUAMS-723	550	9165±38	10480-10236
	CUR-700	700	9610±67	11180-10744
	NTUAMS-724	745	9873±164	11977-10786
Lagua da Curuça	Beta-77799	25-30	1520±70	1527-1279
	Beta-77800	42-47	2740±60	2950-2740
	Beta-77801	72-77	9340±60	10661-10276
	Beta-75107	90-97	9430±70	11066-10303
	Beta-79122	366-374	9530±90	11131-10521
	Beta-77798	468-476	10850±80	12875-12562
	Beta-73470	532-541	11490±80	13451-13123
Pántano da Maurítia	Erl-12483	48-49	2140±40	2301-1935
	KIA-39910	60-61	3373±26	3641-3468
	Erl-12484	96-97	8547±51	9551-9432
	KIA-39911	120-121	8899±39	10169-9746
	Erl-12173	148-149	9900±54	11593-11176
	KIA-39912	160-161	10537±57	12647-12103
Lagoa da Cachoeira	Erl-12171	48-49	2374±41	2678-2183
	Erl-12481	78-79	3619±40	4061-3720
	Erl-10586	133-134	12414±38	14810-14191

* Radiocarbon date is excluded from age-depth model because of the low agreement index.

** Radiocarbon date is excluded from age-depth model because it shows a reversal age.

IV. Forest-savanna boundary shift on the plateau of Serra Sul dos Carajás (southeastern Amazonia) since the mid-Holocene; driving forces and limiting factors

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Published in *Quaternary International (2017) 499: 12–21*
https://doi.org/10.1016/j.quaint.2017.07.001

Abstract

The vegetation history of the savanna on the plateau of Serra Sul dos Carajás is well studied by three palynological records. Nonetheless there is no record from the forests around this plateau so that the forest-savanna boundary shift can be investigated. In this study, a sediment core taken from forests on the slopes of the plateau is studied using a multi-proxy analysis. The comparison of the results with the vegetation history of the adjacent savanna showed that well-established forests have been present around the plateau since 6600 cal yr BP. Since the mid-Holocene owing to a change to favorable climatic conditions, forests started to move toward the savanna and after 3400-4000 years reached their modern borders in the savanna region. Because during this long period forests borders shifted a relatively short horizontal distance, it can be concluded that there might be limiting factors that delayed forest expansion. Among different possible factors, fire and human may play an important role. However, the evidence suggests that the slow process of soil formation to produce a soil layer with sufficient depth is the main limiting factor that delayed the forest expansion. The southward shift of Inter Tropical Convergence Zone is more likely the trigger of forest expansion in the area.

Keywords: Carajás, vegetation history, palynology, soil properties, fire, Holocene

1. Introduction

The amount of atmospheric CO_2 that is absorbed, processed and stored by Amazon forests each year is more than twice the CO_2 emitted from fossil fuel combustion (Malhi and Grace, 2000). Therefore the role that Amazon forests plays to control the concentration of atmospheric CO_2 and thus offset the effect of climate change is critical. This huge carbon sink however, is vulnerable to marked climatic events like the severe drought occurred in 2005 that hampered trees growth and killed the trees selectively (Phillips et al., 2009). Hence investigating the long-term dynamics of Amazon forests, especially the shift in savanna-forest boundaries under substantial climate changes, affords an efficient way to understand the future of these forests under the upcoming climate changes.
During the last two decades, the plateau of Serra Sul dos Carajás has been a key area for such long-term palaeoecological studies. The reasons why this plateau is interesting for scientists are: i) it is vulnerable to position of Inter-Tropical Convergence Zone (ITCZ) (Peterson and Haug, 2006), moisture input from Atlantic Ocean and the surface temperature of Pacific Ocean (Liu et al., 2000; Marengo et al., 2001; Zheng et al., 2008), ii) it is located in "Amazonian Dry Corridor" (Bush, 1994; van der Hammen and Absy, 1994) where receive less rainfall compared to adjacent area (Absy et al., 1991), iii) it is developed upon “banded iron formation” covered by savanna and surrounded by tropical forests (Absy et al., 1991) and iv) this region has accommodated human since 10,000 cal yr BP (Kipnis et al., 2005; Magalhães, 2009).

These factors caused the Serra Sul dos Carajás to be subjected to several environmental changes through the Holocene. Two important changes in the time frame of this study are the mid- to late Holocene savanna expansion and the late Holocene forest expansion. The first change, with some temporal differences among different records, is agreed to be caused by dry periods alternating with slightly wetter periods. During this interval the repeated failed attempts for forest expansion into the savanna is evident implying that the wet periods were not long enough to support forest expansion (Absy et al., 1991; Fournier and Bruno, 1993; Hermanowski et al., 2012; Sifeddine et al., 2001). The second change that occurred at ca. 4500-3500 cal yr BP is associated with the return to wetter climate condition and forests boundary shift toward the savanna.

These environmental changes have been revealed through the studies carried out on the savanna of Serra Sul dos Carajás. So far the dynamics of the forest fringe on the slopes of the plateau have not been directly investigated through a sediment core taken from forested area. Therefore it is not clear how far the forest margins from their modern borders were and with which rate does forests shifted toward savanna. Also factors promoting/hampering the forest expansion are not clear. This study using multi-proxy analyses on a sediment core retrieved from forests surrounding the plateau aims to address these issues.

2. Study area

2.1 Climate

The regional climate of southeast Amazon is tropical wet and dry (type “Aw” in the Köppen system) or savanna climate (McKnight and Hess, 2000) with pronounced wet (November–May) and dry seasons (end of June–early October) (Lopes et al., 2013; Sifeddine et al., 2001). The average annual rainfall in Carajás is 2126 mm that increases with elevation so that lowlands receive 1500 mm and higher altitudes receive 1900 mm per year in average (IBAMA, 2003). The mean annual temperature ranges from 23.5 °C at 835 m a.s.l. to 26.2 °C at 203 m a.s.l. (Silva et al., 1996). The main drivers of seasonal precipitation are the position of the ITCZ and the coupled onset and intensity of convection in the Amazon. During the austral summer, warmer southern Atlantic sea surface temperature (SST) causes southward movement of the ITCZ and intensifies the convection, causing higher rainfall rates. Other factors influencing the regional rainfall are moist trade winds from the tropical Atlantic and evapotranspiration from the forests itself (Fu et al., 2001; Liebmann and Marengo, 2001; Marengo et al., 2001, 1993; Nobre and Srukla, 1996) (Fig. 1a).

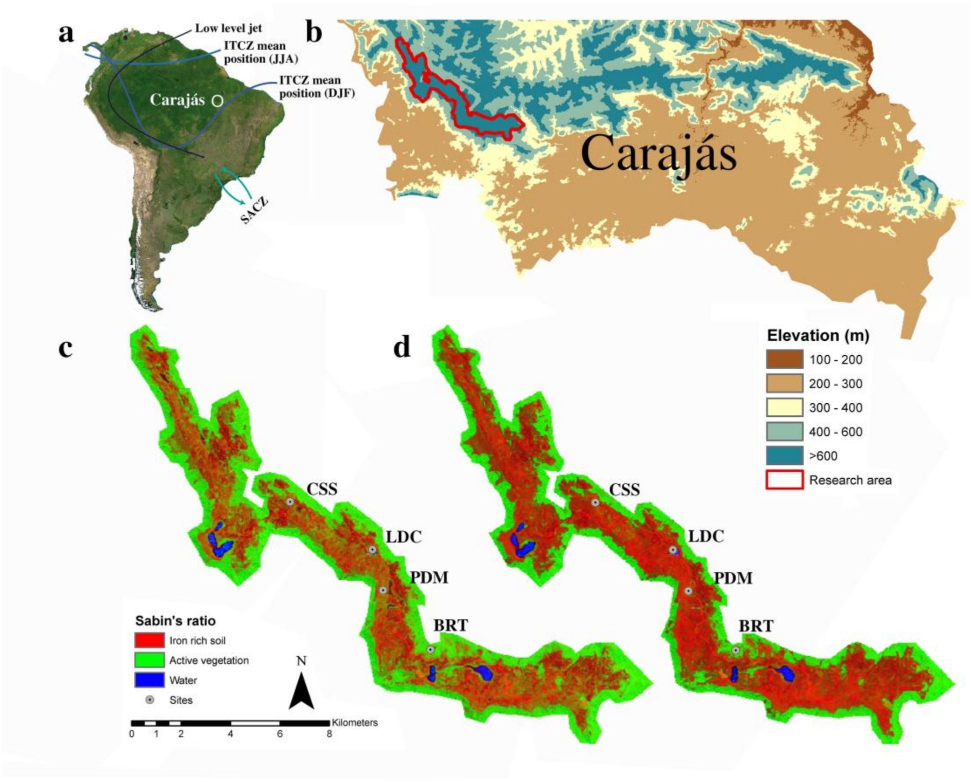

Fig.1. Map of the study area. (a) The position of Serra Sul dos Carajás in South America and the main air convection systems over the continent. (b) Regional topography of the study area. (c and d) Sabins colour composites for May and August respectively. These colour composites show the distribution of vegetation and the lateritic soil. For colour image please read the online version.

2.2 Topography and soil

The Serra Sul dos Carajás, is a narrow plateau located in the southeastern region of Amazonia and is comprised of several hilly plateaus ranging from 600 to 900 m in elevation (Fig. 1a and b). The plateau is developed upon a banded iron formation (Absy et al., 1991) which is covered by a thin layer of lateritic soil with high concentrations of iron oxyhydroxides and relatively lower amounts of aluminum. A thicker soil horizon with higher water content provides habitats for arboreal vegetation on the slopes around the plateau and in the depressions (Absy et al., 1991; Hermanowski et al., 2014, 2012; Nunes et al., 2015; Sifeddine et al., 2001; Soubiès et al., 1991).

2.3 Modern vegetation

The lateritic substrate underlying the superficial soil horizon causes a series of restrictions to plant establishment, such as forming shallow and patchy infertile soils with low water content, high energy absorption from sunshine, raised temperatures, and soil poisoning (Meirelles et al., 1997). Four different vegetation units present in the area are separated according to the soil depth gradient whereby herbaceous *campo rupestre*, shrubby *campo rupestre*, *capão* forests and upland (rather than montane) forests grow in shallower to the deeper soil respectively (Nunes et al., 2015). In *campo rupestre*, Poaceae, Myrtaceae, and Asteraceae are the most common families and the genera *Borreria* and *Byrsonima* are also frequent. Herbaceous *campo rupestre* is an open vegetation covered by small shrubs, with *Vellozia glochidea* (Velloziaceae) growing on the grassy layer. Taxa such as several *Croton* species, *Cuphea tenella*, and *Mimosa* are also common. Dense or shrubby *campo rupestre* is supported on more fragmented ironstone cap (canga) that provides a softer medium for root development. Vegetation is composed of tall shrubs and herbaceous plants with dominance of Mimosaceae, *Byrsonima*, *Ficus nymphaeifolia*, *Miconia*, *Tibouchina*, Myrtaceae and Rubiaceae. *Capão* forests form isolated small islands of semi-deciduous forest within *campo rupestre* vegetation. Upland forests are dense ombrophilous forest established on the margin of plateau in the transition (ecotone) between *campo rupestre* and the forests of the lower slopes of the plateau (Nunes et al., 2015).

2.4 Location of the coring site

The studied core is called Buriti (BRT) and was collected from a narrow depression in a small forest hollow (6°23'28.95" S, 50°22'18.29" W, 710 m a.s.l.) surrounded by upland forests. The site is 250 m distant from the modern forest-savanna boundary. The core name is derived from the local name for *Mauritia* palm that occurred in a small population at the location.

Former palaeoecological records from Serra Sul dos Carajás (Fig. 1c and d) are i) Pântano de Mauritia (PDM, (Hermanowski et al., 2012)), a swamp located in the savanna area at 740 m a.s.l, with 700 m mean distance from the forest borders on both the eastern and western sides, iii) Lagoa da Cachoeira (LDC, (Hermanowski et al., 2014)) at 705 m a.s.l., that is today connected to forests on the eastern side and is surrounded by a broad area of savanna from the other 3 sides with 1 km mean distance from the forest borders on the western side, and iii) CSS2 and CSS10 (Absy et al., 1991; Sifeddine et al., 2001) are located about 9 km to the northwest of BRT; Here only pollen records from Hermanowski et al. (2012 and 2014) will be discussed and compared beside the record BRT.

3. Material and methods

3.1 Coring, lithology and Fe measurement

For this study in 2005, a core with a length of 93 cm was collected using a Russian corer. Sediments were transported to the Geoscience Institute at the Federal University of Pará (UFPA) in Belém and stored in dark and cold (4°C) conditions.

Lithological description was done based on the color and texture of the sediment core. To measure amount of soil extractable Fe, 19 sediment subsamples were taken in intervals of 5 cm along the core plus one additional subsample at 93 cm. Subsamples were dried for 48 hours in 70°C and 100 mg dry weight of each subsamples were treated through digestion in HNO3 acid 65%. Digestion was carried out in closed digestion vessels for 12 hours at the temperature of 195°C (modified protocol from Department of Plant Ecology and Ecosystem Research, University of Göttingen). The contents were then measured in an Inductively Coupled Plasma (ICP) machine in the same department.

3.2 Age depth modeling

Table 1 shows the details of the 5 subsamples, taken from the core and sent for radiocarbon dating to the Accelerator Mass Spectrometry (AMS) laboratory, Department of Geosciences, National Taiwan University. Based on the results of the 5 radiocarbon-dated samples the age-depth model was plotted by Bacon 2.2 package (Blaauw and Christeny, 2011) in R studio using Southern Hemisphere terrestrial calibration curve SHCal13 (Hogg et al., 2013). The same method was used to obtain new age-depth models for the records LDC and PDM.

Table 1. Detail of samples sent for AMS ^{14}C dating and their results

AMS Lab ID	Depth (cm)	Material	Radiocarbon date	Weighted mean Calibrated date (cal yr BP)
NTUAMS-1771	33	Organic material	1295±6	1240
NTUAMS-1166	53	Charcoal	2745±16	2782
NTUAMS-1167	53	Organic material	4320±26	4898
NTUAMS-2019	80-82	Bulk sediment	5270±20	5949
NTUAMS-1772	83	Plant remains	814±5	722

3.3 Pollen and charcoal analysis

For pollen and micro-charcoal analysis, 19 sediment subsamples were taken at the same depths of subsampling for Fe measurement. Based on the knowledge obtained from the 4 test subsamples, an uneven subsampling approach is adopted. The first 50 cm from the top of the core are characterized by a higher content of pollen, therefore subsamples of 0.25 cm^3 sediment were taken. Before further procedure in the lab, 3 *Lycopodium* tablets were added as exotic markers (Stockmarr, 1971) for later concentration and influx calculations. In the lower part of the core, 0.5 cm^3 of sediment was taken and 2 *Lycopodium* tablets were added. Subsamples were prepared following the standard procedure by Faegri and Iversen (1989) including HF 70% treatment. Pollen and spores were identified according to the literature (Roubik and Moreno, 1991; Colinvaux et al., 1999; Carreira and Barth, 2003) and pollen reference collection available at the Department of Palynology and Climate Dynamics, University of Göttingen. Pollen counting was done until two criteria were fulfilled. First, to reach at least 300 terrestrial pollen grains and second, to reach at least 100 *Lycopodium* spores. In the two subsamples from bottom of the core only 150 pollen grains were counted due to the very low pollen concentration. Micro-charcoal particles (10 to 120 µm) were counted on the pollen slides.

Pollen and charcoal percentages, concentration and influx have been calculated and plotted in software packages TILIA and TILIAGRAPH, version 2 (http://www.ncdc.noaa.gov/paleo/tiliafaq.html). Percentages were calculated based on the terrestrial pollen sum, excluding fern spores. Pollen and spore data was grouped into forest trees, shrubs, lianas-scandent-vine, herbs, palms, wetland trees and ferns. This categorization was done according to the online plant species list in Brazil (floradobrasil, 2016) and floristic studies on the area (Cleef and da Silva, 2008; Nunes et al., 2015, 2009; Silva et al., 1996). The group “unidentified” represents broken grains which could not be identified and the group “unknown” represents pollen grains which were intact but difficult to recognize the plant of origin. Influx and concentration diagrams were also plotted besides the pollen percentages diagrams. The percentages and concentration diagram for sum of each vegetation group of the records Lagoa da Cachoeira (LDC) and Pântano da Mauritia (PDM) for the last 7000 cal yr BP, were also plotted to be compared with BRT. Since BRT, LDC and PDM are characterized by different catchment size and deposition systems and LDC is surrounded by sharp slopes from the eastern side which may cause stronger input of sediment after changing to the wetter climate conditions, application of influx data for comparison between sites is avoided (Hicks and Hyvärinen, 1999).

3.4 Remote sensing

Cloud free Landsat 8 / OLI satellite images captured in May and August 2013 were used to map the lateritic soil and vegetation distribution. After radiometric calibration (top of atmosphere reflectance) the Normalized Difference Vegetation Index (NDVI) was calculated to quantify vegetation differences throughout the landscape and to measure the seasonal change in vegetation cover. Aster Global Digital Elevation Model (GDEM) with 30 meters horizontal and vertical resolution was assigned providing elevation information.

To map the vegetation and ferruginous soil, spectral band ratios red/SWIR1 (4/6) and red/blue (4/2) and SWIR1/SWIR2 (6/7) have been calculated and combined in red, green and blue channels respectively to create Sabin's Color composite (Sabins, 1999). Ground based information obtained through several fieldworks can confirm the authenticity of the produced color composite map. The relation between vegetation distribution, ferruginous soil and elevation was examined by means of correlation matrix between NDVI, band ratio 4/2 and Aster DEM. The whole remote sending part was carried out in ArgGIS for desktop 10.2.

4. Results

4.1 Lithology, chronology and Fe measurement

The lithology of the sediment core can be divided into three zones. The first zone, from 93 to 70 cm, mainly contains detrital constituents comprised of yellow-orange coarse fragments of iron rich crust and almost without OM. The second section from 70 to 50 cm forms a transition zone characterized by increase in OM content and decrease in the size of the lateritic crust fragments. The section from 50 cm to the top of the core consists of dark, organic rich, silty clay sediment with plant remains on uppermost part of the core (Fig. 2a).

Table 1 shows the result of radiocarbon dating. The date (ca. 722 cal yr BP) at 83 cm core depth shows a reverse age because the isolated plant remains was probably a root of much younger age. This age has been not included in the model. At 53 cm a charcoal piece (ca. 2745 cal yr BP) and small fragments of OM in the sediment (ca. 4320 cal yr BP) were dated. As there is no logic reason to exclude one of these dates, two age-depth models are created. Each model includes one of these dates and excludes the other date. Both models show that the bottom of the core goes back to 6600 cal yr BP (Fig. 2 b and c).

Chemical analysis of the sediment shows a sharp descending trend in the content of Fe from the bottom to the top of the core (Fig. 3b). In the lower 30 cm of the core, concentration of Fe is 23 times higher than their concentrations at the surface.

4.2 Pollen and charcoal record

In total 78 terrestrial pollen types were identified including 6 unidentified types. The 39 most frequent taxa are illustrated in the pollen diagram (Fig. 3a).

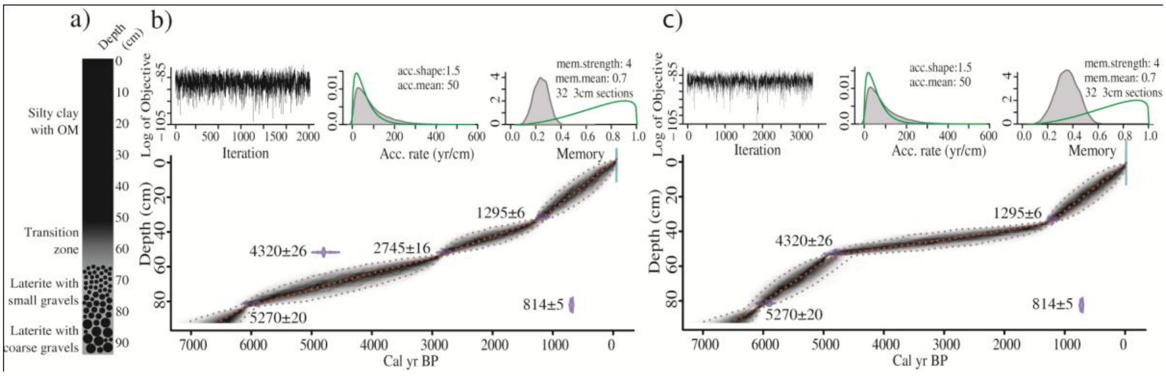

Fig.2. Lithology and age-depth models. (a) Lithology of the core BRT showing changes in the colour and gravel size of the sediment. (b and c) Age-depth models of the core BRT according to the dates from piece of charcoal and the organic material respectively. Numbers on the model show the C^{14} dates.

The percentages diagram (Fig. 3 a and b) indicates the constant dominance of taxa which are more frequent in the upland forest including the groups "forest trees" and "wetland trees" (called arboreal vegetation in the text) at the site since 6600 cal yr BP. Plants which are indicative of savanna such as herbs and shrubs have been always less frequent compared to arboreal vegetation. A slight ascending trend in percentages of forest trees and palms and a gentle descending trend in percentages of shrubs, wetland trees, and herbs are evident from bottom to the top of the core. Pollen of lianas, scandents and vines show almost the same mean percentages throughout the whole record.

Influx (Fig. 3b) and concentration (Fig. 4a) diagrams show minimum values at the lowermost part of the core between 93 and 80 cm and subsequently maximum values in all groups (except palms) between 80 and 70 cm. After these maxima, the influx and percentage of forest trees and palms show overall increasing trends through the core while these values for savanna herbs and shrubs and wetland trees demonstrate overall decreasing trends.

Influx of charcoal particles gradually increases from 80 cm and reaches the maximum influx at 55 cm and decreases markedly in the following sample and become rare afterward.

4.3 Remote sensing results

Fig. 1c and 1d show Sabins color composite images which belong to May and August, respectively. Since May is in the wet season, Fig. 1c looks greener than Fig. 1d which is a composite of bands captured in August (dry season), when semi-deciduous forests shed leaves and herbaceous plants die.

The red shade represents iron rich lateritic crusts and its gravels. The green fringe around both images (Fig. 1c and 1d) demonstrates evergreen forests that do not show change in phenology across seasons.

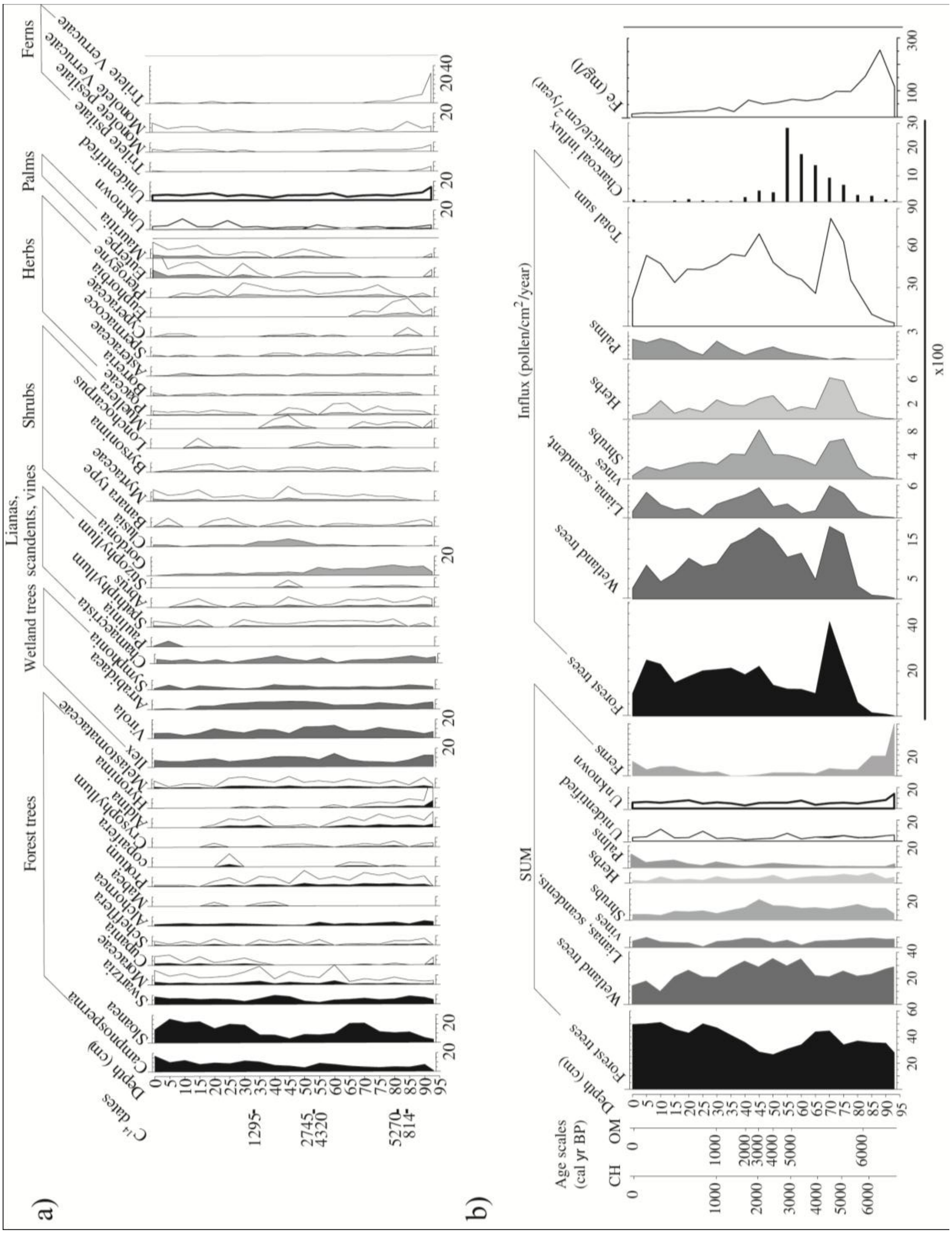

Fig.3. Pollen diagrams of the site BRT. (a) Detailed percentages pollen diagram of the record BRT showing the most frequent taxa and ecological grouping. (b) Percentage of pollen sums, the pollen and charcoal influx and the change in exchangeable Fe content of the record BRT. CH and OM are age scales based on the age-depth models produced by including charcoal and organic material respectively.

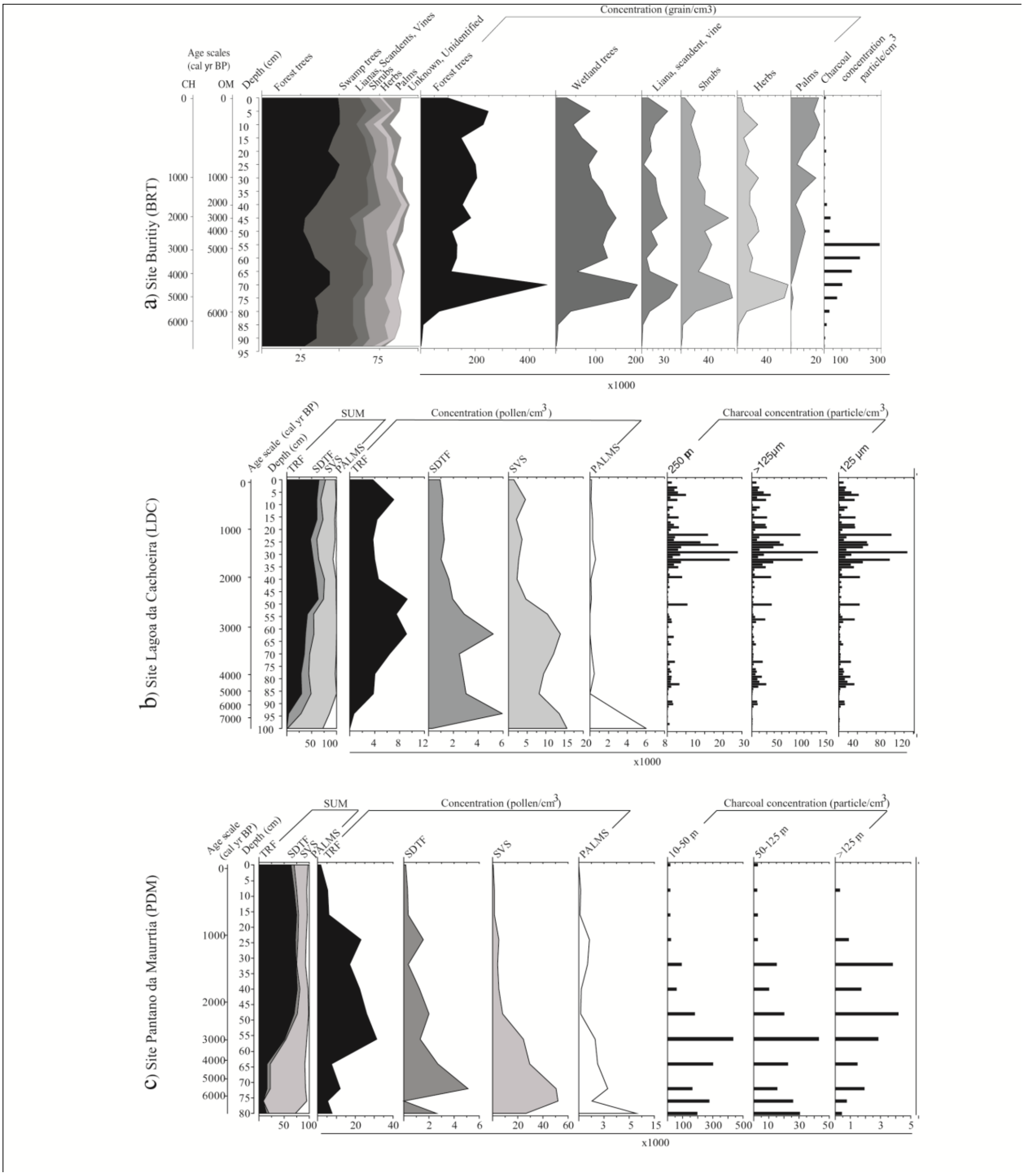

Fig.4. Pollen diagrams of the site BRT, LDC and PDM. (a) Percentage of pollen sums as well as pollen and charcoal concentration diagram of the record BRT. (b and c) Percentages of pollen sums and concentration of pollen and charcoal for sites LDC and PDM respectively. TRF = Tropical Forests, SDTF = Semi-deciduous Dry Tropical Forest, SVS = Savanna Vegetation System.

The magenta rings around the lakes reflect iron rich lateritic stones (iron ore) on the margin of the lakes. Some temporary wetlands are formed in the area during the wet season and dry out completely during the dry season.

There is a negative correlation (-45) between NDVI of May (wet season) and band ratio 4/2 that represents the ferruginous soil. This negative correlation is bigger (-73) for August (dry season) when deciduous and herbaceous vegetation are absent and the contrast between bare lateritic surface of plateau and surrounding forests is more obvious. This confirms that evergreen forests are limited to the margin of ferruginous plateau.

From the negative correlations between elevation and vegetation (≈ -40) and the positive correlation between elevation and the ferruginous soil (≈ +45) it can be concluded that ferruginous soils are located on the higher elevated areas and vegetation occur on the lower parts like depressions or on the slopes of the plateau.

5. Interpretation and discussion

5.1 Change in lithology and chronology

Lithology of the BRT sediment core shows a gradual transition from yellow-orange sediment associated with coarse gravels and little OM to a black organic rich material. Coincident with lithological change, the accumulation rate also gently increases throughout the record. These changes may demonstrate a shift to wetter conditions that led to higher biomass production and formation of an organic soil layer on top of the former lateritic base. Accumulation of voluminous OM is the reason for higher sediment accumulation rate in upper parts of the core. Such transition to organic rich sediment has been also reported in other palaeoecological studies from Serra Sul dos Carajás. Sifeddine et al. (2001) reported resumption of organic sedimentation from 3800 cal yr BP. Hermanowski et al. (2012) showed that in the record PDM, OM started to accumulate at ca. 5000 cal yr BP. In the record BRT, the timing of the transition to OM accumulation must be estimated based on two different age depth models. If the date from charcoal particle (2782 cal yr BP) is accepted then the transition in the sedimentation regime has occurred between ca. 4560 and 2500 cal yr BP (Fig. 2b). If the date from the piece of OM in the soil (4898 cal yr BP) is considered then the transition has occurred between 5550 and 4050 cal yr BP (Fig. 2c). Considering the chronology of the record BRT and the timing for onset of OM accumulation in other records in the area, it can be estimated that OM gradually increased in the core BRT approximately between 5000 and 3000 cal yr BP.

5.2 Vegetation and fire history in Serra Sul dos Carajás

According to both age-depth models (Fig. 2a and b) and the percentages diagram of the record BRT (Fig. 3b), the vegetation composition during the last 6600 cal yr BP was relatively stable with continuous dominance of the local forest vegetation around the study site. A slight increase in pollen percentages of forest trees and a gentle decrease in percentages of shrubs and herbs may suggest that forest borders shifted toward savanna and therefore the distance between the site BRT and savanna became longer. This in turn may imply better climatic conditions such as less seasonality in rainfall regime. The small decrease in populations of *Ilex, Symphonia, Virola* and *Arrabidae* taxa, which all can be found in the lowland seasonal floodplains and wetland ecosystems (Marchant et al., 2002), may also confirm the less seasonality in rainfall.

Despite the record BRT, pollen diagrams of LDC and PDM (Fig. 4b and 4c) show marked shifts toward higher percentages of forest taxa after a period of savanna dominance that started at ca. 10,200 cal yr BP due to a seasonal climate (Hermanowski et al., 2014, 2012). In the LDC (Fig. 4b) the tropical forests (TRF) expansion started at ca. 6500 cal yr BP from around 4% of forest taxa that reached the value of 60% at ca. 2400 cal yr BP and afterward the area of forests were more or less stable. Although PDM diagram shows a mean value of 25% for tropical forest taxa since ca. 7000 cal yr BP, a marked increase in forest taxa started at ca. 4000 cal yr BP and reached the value of 75% at ca. 2500 cal yr BP. The group Semi-deciduous Dry Tropical Forest (SDTF) is not considered in the calculation because the source of pollen for this group is more likely *capão* forests, whereas the shift in upland forest around the plateau is important here. Near the CSS record (Absy et al., 1991) establishment of forests occurred at ca. 3200 cal yr BP.

Therefore, in LDC, PDM and CSS the signal of arboreal vegetation that comes from surrounding forests (Absy et al., 1991) reached its maximum approximately 3400-4000 years later compared to BRT. In the lake LDC where there is a bigger catchment area that is mainly covered by a broad savanna, the percentages of forest taxa never reached a similar amount in BRT and PDM. Also the increment in percentages of forest taxa has a slower rate in LDC than in PDM.

Considering the point that LDC (705 m a.s.l.) and BRT (705 m a.s.l.) are at the same elevation, it can be concluded that the forest borders did not have a large altitudinal shift since 6600 cal yr BP, but moved horizontally into the savanna area on the plateau.

The pollen concentration and influx at the lowermost part of BRT (approximately before 5800 cal yr BP according to both age-depth models) show the minimum values. As these minimum values occurred in all vegetation groups it can be interpreted as inappropriate soil condition for pollen preservation rather than a long distance between forests border and site BRT during that period. Because if the forests were away from the site, then the signal from savanna taxa must have been higher in percentage, concentration and influx diagrams of BRT. However none of these diagrams show such signal. The sediment at the bottom of the core BRT was very hard, dry and contains large detrital constituents. In such soil condition the pollen cannot be preserved. In addition, the minimum in pollen concentration in BRT coincides with the maxima in concentration of savanna taxa in PDM and LDC and seasonal dry tropical forest taxa in LDC. This confirms the drier climate condition that can also hinder pollen preservation.

Coincident with the transition zone in the lithology of the core BRT, the influx of charcoal particles increased implying that the fire events were more frequent in the landscape between 5000 and 3000 cal yr BP (Fig. 3b). This change suggests that the transition zone in the record BRT shows a period when the climate was returning to a wetter condition. Therefore on one hand enough biomass (fuel) could be produced to feed the fire and on the other hand the dry season was still long enough to support natural fire. After the transition zone, when a dark organic rich material started to accumulate, fire events at site BRT became very rare. However the fire activity continued for a longer time in adjacent savanna (records LDC and PDM, Fig. 4b and 4c). Therefore the very low charcoal influx in the upper part of the core BRT, when still fire events were frequent in adjacent savanna, may indicate favorable climatic conditions such as less seasonality in rainfall that: i) reduced the fire events in the small forest hallow where the site BRT is located and ii) caused further expansion of forests into the savanna. The forest expansion isolated site BRT from the fire events in the neighboring savanna. This forest expansion and isolation of the site BRT can also be confirmed by other signals in the record BRT; for example i) slightly lower percentages of Poaceae pollen as the main savanna herb, ii) the decrease in percentages of shrubs (especially *Gordonia*) which form the ecotone between forests and savanna iii) the higher concentration of forest pollen grains after ca. 3000 cal yr BP in LDC and PDM.

5.3 Forest-savanna boundary shift

The records from savanna of Serra Sul dos Carajás indicate that mid to late Holocene was associated with a seasonal climate in the area. The dry seasons were longer than today and hindered the forest expansion toward the savanna. These long dry seasons were alternated with short wet seasons with enough precipitation to support swamp formation in site PDM. This can be confirmed by presence of *Sagittaria* and a maximum of Arecaceae in that record. At this time forests existed on the slopes around the savanna but away from their modern boundaries and with less density. The occurrence of Anacardiaceae, Bignoniaceae, Euphorbiaceae, Fabaceae, and *Zanthoxylum* in PDM has been also interpreted as predominance of forests similar to modern semi-deciduous dry tropical forests in southwest Amazonia that can survive in climate with longer dry seasons (Gosling et al., 2009; Hermanowski et al., 2012). In LDC, the presence of *Alchornea/Aparisthmium* and the pioneer *Celtis*, together with low abundance of Melastomataceae/Combretaceae and Moraceae/Urticaceae can be indicative of the first reoccupation of savanna by forest trees (Hermanowski et al., 2014). Also in the records CSS, abundance of sponge spicules and pollen of the pioneer *Piper* imply a dry period that was alternating with brief periods of humid condition. These alternating dry and wet periods are the reason for moderate increase in detrital constituents that can be accumulated when the plateau does not experience severe erosions as would be the case if the droughts were permanent. In general this period was associated with failed attempts for forest reestablishment due to alternating long dry seasons with short wet seasons (Sifeddine et al., 2001).

During the late Holocene after ca. 4000 cal yr BP, the signal from tropical forests increased in the records from savanna (Absy et al., 1991; Hermanowski et al., 2014, 2012; Sifeddine et al., 2001) implying the expansion of forests toward the savanna. This period coincides with increased abundance of the pioneers such as *Piper, Celtis* and *Trema* (Marchant et al., 2002) that suggests a gradual successive expansion of tropical forests from the slopes toward the savanna. Higher frequency of pollen from *Alchornea*/*Aparisthmium* and Moraceae/Urticaceae proposes reduced water stress during this period due to increased precipitation (Hermanowski et al., 2014).

In summary, since the mid-Holocene, the savanna of Serra Sul dos Carajás experienced an environmental change from a seasonal climate with failure in forest reestablishment to a wet climatic condition with forest incursion into the savanna region. The lithology changed from detrital constituents with little OM to an organic rich sediment. The change in sedimentation regime of cores taken from savanna region is similar to that of BRT. However the pollen percentage diagram of the record BRT does not show any marked change in vegetation similar to the records from savanna. It suggests that the small surface area of the forest hollow where the core BRT was taken has been always covered by herbaceous vegetation similar to savanna region and was surrounded by forest. Therefore with the change toward a wetter climatic condition, higher biomass production from herbaceous plants contributed to accumulation of OM rich sediment (similar to lithology of records from savanna) while the dominant source of pollen is still surrounding forests. In addition, lack of pollen from pioneers in the record BRT indicates that well-established forests have been present around the site since the mid-Holocene.

The comparison of BRT vegetation history with the records from savanna proposes that the expansion of forests into the savanna took approximately 3300 to 4000 years. This interpretation cannot be affected by the different age depth models for BRT as both models show the age of 6600 for the bottom of the core. Even if just the dates from 33 cm core depth and that from organic material at 53 cm core depth are taken into account the resulting age depth model (is not shown here) suggest a bottom age of 8850 cal yr BP that makes the difference between the vegetation history of forests and savanna even more significant.

5.3.1 Limiting factors for forest-savanna boundary shift

The site BRT is not located far from the modern forest-savanna boundaries. Therefore since the mid-Holocene the forests did not shift a long distance to reach its modern borders. Thus the 3400-4000 years difference between the maximum signal of arboreal vegetation in BRT and those in LDC, PDM and CSS suggests that there might be limiting factors that delayed forest expansion. In the following paragraphs possible limiting factors are discussed.

Micro-climates. Occurrence of a microclimate around the site BRT might support the forests to survive around this site even during the seasonal climate with longer dry season. However presence of signal from forest vegetation in pollen diagrams of LDC, PDM and CSS even during the former seasonal climate indicates that the fringe of forest has been always present around the whole plateau. Thus the difference in vegetation history of savanna and forests is not due to the occurrence of a microclimate only around site BRT.

Climate. The site BRT is not far from the study sites on the savanna region (LDC, PDM and CSS) and they are located almost at the same elevation. Therefore differences in climatic conditions between sites cannot explain the delay in forest expansion.

Fire. Either natural or manmade, fire events have been occurred in the area even during the wetter late Holocene. Presence of charcoal together with pollen of pioneering taxa in the savanna records implies a continuous succession for forest reestablishment (Hermanowski et al., 2014, 2012) and fire-forest interaction. Therefore fire can be considered as one of the factors that prevents forest expansion during the wetter late Holocene.

Human. The archaeological studies revealed human occupation in the area since 10,000 cal yr BP. Thus hunting-gathering activities and anthropogenic fires can be included among limiting factors (Kipnis et al., 2005; Magalhães, 2009).

Ferruginous soil. Our results show that the amount of bio-available Fe has decreased through the record. This decrease was coincident with the environmental changes in the area including start of forest expansion and accumulation of organic material. This may support the idea that high concentration of Fe in the soil hindered the forest expansion. In addition, the negative correlation between NDVI and band ratio 4/2 resulted from remote sensing also may confirms that the ferruginous soil is the main limiting factor for forest expansion. However a new study on the properties of the soil under the four different vegetation types (*campo rupestre*, shrubby *campo rupestre*, *capão* forests and upland forests) show that the amount of Fe in the record BRT, except in one subsample, has been always in the tolerable range for forests (*capão* forests = 429 mg/l, upland forests = 149 mg/l, (Nunes et al., 2015)). In addition, this study concluded that there is no evidence to support the idea that high levels of extractable Fe (such as Fe^{2+}) is the reason for vegetation differences among sites, since most Fe is present in soil as Fe^{3+}, that is insoluble and non-available.

Soil depth. Studies by Nunes et al. (2015) showed that soil depth can be the principle limiting factor for establishment and development of the forests. Different vegetation types in Serra Sul dos Carajás can be separated according to the soil effective depth from shallower to thicker as herbaceous *campo rupestre* (8.7 cm) <shrubby *campo rupestre* (38.4 cm) <*capão* forests (93.1 cm) <upland forests (113.7 cm). The surface of the forest hollow where the site BRT is located was covered by a hard lateritic substrate at ca. 6600 cal yr BP. Since that time a soil layer of 93 cm has formed that is still

not sufficient for upland forests establishment. This data suggest that the 4000 years delay in forest expansion might be spent on the slow process of soil formation.

In hilly plateaus, such as Serra Sul dos Carajás, lower water level and steep hillsides of the crest facilitate drainage and erosion, allowing for the transfer of weathered materials downward to the less drained plains. By this process, a ferruginous rocks remains on top of the hills. In contrast, the results of weathering are transported downhill and together with the dead biomass form the soil in the depressions and on the slopes of the plateau. This process causes a topographic inversion with different soil depths and compositions through an altitudinal gradient (Bernadelli et al., 1983; Gleeson et al., 2003) that in turn affects the vegetation distribution. This inference can be supported also by the result of image processing that shows the modern vegetation distributes on the lower elevations while ferruginous crust occurs mainly at higher elevations.

5.3.2 Driving forces for forest-savanna boundary shift

The most accepted reason for the change to wetter climatic conditions during the mid- to late Holocene is orbital scale southward shift of the ITCZ due to the changes in the seasonality of insolation associated with the 21,000 years precession component of Milankovitch forcing (Burbridge et al., 2004; Haug et al., 2001; Mayle et al., 2000; Peterson and Haug, 2006; Silva Dias et al., 2009). ITCZ influenced tropical South America during the mid- to late Holocene and changed the landscape for the last 6000 cal years. Slightly reduced Northern Atlantic SST during the late Holocene (Ruhlemann et al., 1999) probably led to the intensified moisture transport from the tropical Atlantic and a stronger Amazon convection. In Serra Sul dos Carajás, the ITCZ brought humidity which was necessary for forest expansion.

6. Conclusion

The slopes around the plateau of Serra Sul dos Carajás were covered with well-established forests during the last 6600 years. Incidence of wetter climate conditions probably due to southward shift of ITCZ prompted forest expansion toward the savanna and through a process of 3400-4000 years the forests reached their modern borders. Since the study site BRT is located near the modern forest borders and almost at the same elevation, it can be concluded that during this long period forests had a short horizontal shift. Therefore the possibility of interference from some limiting factors which slow down the forest expansion is proposed. The presence of pollen from pioneers together with frequent charcoal particles in the records from savanna region imply successive reestablishment of forests and highlight the role of fire and human to delay the forest expansion. However, the relation between the soil depth and the distribution of different vegetation types suggests that the soil depth is the key factor for forest development on the savanna of Serra Sul dos Carajás. Thus the slow process of soil formation is more likely the main limiting factor that delayed forest expansion.

Our results suggest that climatically triggered changes in vegetation may be delayed by soil properties. This conclusion is very important for the palaeoecological reviews that look for synchronous climatically derived vegetation changes in different region of the world.

Acknowledgements

We would like to appreciate here Dr. Stephan Erasmi from the Department of Cartography, GIS & Remote Sensing, University of Göttingen for his revision and comments on the remote sensing section of the paper. Our sincere thanks also go to Olivia Box for her precise English edition. We thank the Vale do Rio Doce Company for logistical support and IBAMA for the permission to carry out fieldwork in the reserve Serra Sul dos Carajás.

Funding: The fieldwork of the project was funded by CNPq (Proc.471 109/03-7). This study is part of the first author's PhD and is funded by Erasmus Mundus scholarship under framework of the SALAM project.

References

Absy, M.L., Cleef, A., Fournier, M., Martin, L., Servant, M., Sifeddine, A., Ferreira da Silva, M., Soubiès, F., Suguio, K., Turcq, B., Van der Hammen, T., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le Sud-Est de l'Amazonie au cours des 60 000 dernières années : première comparaison avec d'autres régions tropicales. Comptes Rendus l'Académie des Sci. Paris 2, 312, 673–678.

Blaauw, M., Christeny, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. doi:10.1214/11-BA618

Bernadelli, A., Melfi, A.J., Oliveira, S.M.B., Trescases, J,J., 1983. The Carajás nickel deposits, in Lateritisation processes, Melfi AJ, Carvalho A, [Eds]. Instituto Astrônomico e Geofísico, University of São Paulo: 107–118.

Burbridge, R.E., Mayle, F.E., Killeen, T.J., 2004. Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. Quat. Res. 61, 215–230. doi:10.1016/j.yqres.2003.12.004

Bush, M.B., 1994. Amazonian Speciation: A Necessarily Complex Model. J. Biogeogr. 21, 5–17. doi:10.2307/2845600

Carreira, L.M.M. & Barth, O.M., 2003. Atlas de pólen da vegetação de canga da Serra de Carajás, Pará, Brasil. Illustrated ed. Museu Paraense Emílio Goeldi, Belém, Pará.

Cleef, A.M., da Silva, M.F.F., 2008. Plant communities of the Serra Dos Carajás (Pará), Brazil. Bol.Mus.Para.E.Goeldi.sér.Bot. 10, 269–281.

Colinvaux, P.A., De Oliveira, P.E., Moreno, E., 1999. Amazon Pollen Manual and Atlas - Manual e Atlas Palinológico da Amazônia. Hardwood Academic, Amsterdam.

Faegri, K. & Iversen, J., 1989. Textbook of Pollen Analyses, 4th ed. Wiley, New York.

Flora do Brasil, 2016. http://floradobrasil.jbrj.gov.br

Fournier, M., Bruno, A.N.D., 1993. Martin 1993 Southern Oscillation Signal in South American Paleoclimatic Data.Pdf 346, 338–346.

Fu, R., Dickinson, R., Chen, M., Wang, H., 2001. How do tropical sea surface temperatures influence the seasonal distribution of precipitation in the equatorial Amazon? J. Clim. 4003–4026. doi:10.1175/1520-0442(2001)014<4003:HDTSST>2.0.CO;2

Gleeson, S.A., Butt, C.R.M., Elias, M., 2003. Nickel laterites: A review: Society of Economic

Geologists Newsletter 54: 10–16.

Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. Rev. Palaeobot. Palynol. 153, 70–85. doi:10.1016/j.revpalbo.2008.06.007

Haug, G.H., Hughen, K. a, Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. Science 293, 1304–1308. doi:10.1126/science.1059725

Hermanowski, B., Da Costa, M.L., Behling, H., 2014. Possible linkages of palaeofires in southeast Amazonia to a changing climate since the Last Glacial Maximum. Veg. Hist. Archaeobot. 24, 279–292. doi:10.1007/s00334-014-0472-0

Hermanowski, B., da Costa, M.L., Behling, H., 2012. Environmental changes in southeastern Amazonia during the last 25,000yr revealed from a paleoecological record. Quat. Res. 77, 138–148. doi:10.1016/j.yqres.2011.10.009

Hicks, S., Hyvärinen, H., 1999. Pollen influx values measured in different sedimentary environments and their palaeoecological implications. Grana 38, 228–242. doi:10.1080/001731300750044618

Hogg, A., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., Turney, C.S.M., Zimmerman, S.R., 2013. SHCal13 Southern Hemisphere Calibration, 0–50,000 Years cal BP. Radiocarbon 55, 1889–1903. doi:10.2458/azu_js_rc.55.16783

IBAMA - Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, CVRD – Companhia Vale do Rio Doce and STCP – STCP Engenharia de Projetos LTDA. 2003. Plano de manejo para uso múltiplo da Floresta Nacional de Carajás.

Kipnis, R., Caldarelli, S.B., Oliveira, W.C. De, 2005. Contribuição para a cronologia da colonização amazônica e suas implicações teóricas. Rev. Arqueol. 18, 81–93.

Liebmann, B., Marengo, J.A., 2001. Interannual variability of the rainy season and rainfall in the Brazilian Amazon Basin. J. Clim. 14, 4308–4318. doi:10.1175/1520-0442(2001)014<4308:IVOTRS>2.0.CO;2

Liu, Z., Kutzbach, J., Wu, L., 2000. Modeling climate shift of El Niño variability in the Holocene. Geophys. Res. Lett. 27, 2265–2268. doi:10.1029/2000GL011452

Lopes, M.N.G., De Souza, E.B., Ferreira, D.B. da S., 2013. Climatologia Regional Da Precipitação

No Estado Do Pará. Rev. Bras. Climatol. 12, 84–102.

Magalhães, M.P., 2009. Evolução antropomorfa da Amazônia. Rev. História da Arte e Arqueol. n^{o}12 5–38.

Malhi, Y., Grace, J., 2000. Tropical forests and atmospheric carbon dioxide. Trends Ecol. Evol. 15, 332–337. doi:10.1016/S0169-5347(00)01906-6

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-Garćia, S., Hooghiemstra, H., Ledru, M.P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev. Palaeobot. Palynol. 121, 1–75. doi:10.1016/S0034-6667(02)00082-9

Marengo, J.A., Druyan, L.M., Hastenrath, S., 1993. Observational and modelling studies of Amazonia interannual climate variability. Clim. Change 23, 267–286. doi:10.1007/BF01091619

Marengo, J.A., Liebmann, B., Kousky, V.E., Filizola, N.P., Wainer, I.C., 2001. Onset and end of the rainy season in the Brazilian Amazon Basin. J. Clim. 14, 833–852. doi:10.1175/1520-0442(2001)014<0833:OAEOTR>2.0.CO;2

Mayle, F.E., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of southern Amazonian rain forests. Science 290, 2291–2294. doi:10.1126/science.290.5500.2291

McKnight, T. L., Hess, D., 2000. "Climate Zones and Types: The Köppen System". Physical Geography: A Landscape Appreciation. Upper Saddle River, New Jersey: Prentice Hall 235–237.

Meirelles, S.T., Mattos, E.A., Silva, A.C., 1991. Potential desiccation tolerant vascular plants from Southeastern Brazil. Polish Journal of Environmental Studies. 6(4), 17-21.

Nobre, P., Srukla, J., 1996. Variations of Sea Surface Temperature, Wind Stress, and Rainfall over the Tropical Atlantic and South America. J. Clim. doi:10.1175/1520-0442(1996)009<2464:VOSSTW>2.0.CO;2

Nunes, J.A., 2009. Florística, estrutura e relações solo-vegetação em gradient fitofisionômico sobre canga, na Serra Sul, FLONA de Carajás—Pará. Dissertação apresentada á Universidade Federal de Viçosa, como parte das exigências do Programa de Pś-Graduação em Botânica, para obtençâo do titulo de Magister Scientiae.

Nunes, J.A., Schaefer, C.E.G.R., Júnior, W.G.F., Neri, A. V., Correa, G.R., Enright, N.J., 2015. Soil-vegetation relationships on a banded ironstone “island”, Carajás Plateau, Brazilian Eastern Amazonia. An. Acad. Bras. Cienc. 87, 2097–2110. doi:10.1590/0001-376520152014-0106

Peterson, L.C., Haug, G.H., 2006. Variability in the mean latitude of the Atlantic Intertropical Convergence Zone as recorded by riverine input of sediments to the Cariaco Basin (Venezuela). Palaeogeogr. Palaeoclimatol. Palaeoecol. 234, 97–113. doi:10.1016/j.palaeo.2005.10.021

Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. t., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. Science (80-.). 323, 1344–1347. doi:10.1126/science.1164033

Roubik, D.W., Moreno P.J.E., 1991. Pollen and spores of Barro Colorado Island. Monographs in Systematic Botany. Missouri Botanical Garden.

Ruhlemann, C., Mulitza, S., Muller, P.J., Wefer, G., Zahn, R., 1999. Warming of the tropical Atlantic Ocean and slowdown of thermohaline circulation during the last deglaciation. Nature 402, 511–514. doi:Doi 10.1038/990069

Sabins, F.F., 1999. Remote sensing for mineral exploration. Ore Geol Rev 14, 157–183.

Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubiès, F., Cordeiro, R.C., Suguio, K., 2001. Variations of the Amazonian rainforest environment: A sedimentological record covering 30,000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 168, 221–235. doi:10.1016/S0031-0182(00)00256-X

Silva Dias, P.L., Turcq, B., Silva Dias, M.A.F., Braconnot, P., Jorgetti, T., 2009. Mid-Holocene Climate of Tropical South America: A Model-Data Approach, in: Past Climate Variability in South America and Surrounding Regions. pp. 259–281. doi:10.1007/978-90-481-2672-9

Silva, M., Secco, R., Lobo, M., 1996. Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. Acta Amaz. 26, 17–44. doi:10.1590/1809-43921996261044

Soubiès, F., Suguio, K., Martin, L., 1991. The Quaternary lacustrine deposits of the Serra dos Carajás

(State of Pará, Brazil): ages and other preliminary results. Bol. IG-USP, 8, pp. 223–243.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores. 13, 615–621.

van der Hammen, T., Absy, M.L., 1994. Amazonia during the last glacial. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109, 247–261. doi:10.1016/0031-0182(94)90178-3

Zheng, W., Braconnot, P., Guilyardi, E., Merkel, U., Yu, Y., 2008. ENSO at 6ka and 21ka from ocean-atmosphere coupled model simulations. Clim. Dyn. 30, 745–762. doi:10.1007/s00382-007-0320-3

V. The Holocene population dynamics of *Mauritia flexuosa* in tropical South America

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Ongoing study

Abstract

Mauritia flexuosa is one of the most successful tropical South American palm trees distributed widely in Amazon and Orinoco basin and in surrounding savannas such as Gran Sabana and Central Brazilian Cerrado. Almost all parts of this palm is used by human. The cause for its widespread expansion especially during the mid- and late Holocene is still an open question to palaeoecologists. Some scientists think that the human activities in particular savanna selective burning are the cause for the expansion of *Mauritia*. This study aims to investigate the relation between fire frequency and abundance of *Mauritia* during the Holocene by examining a new sediment core and reviewing already published records. In addition other potential factors such as topography and elevation of sites, the sea level fluctuations and the effect of ENSO will be discussed. Finally the history of human settlement in Amazonia will be reviewed. At this preliminary stage the results and the first interpretation based on current results and two formerly published records from eastern Amazonia are presented.

1. Introduction

Mauritia flexuosa L.f. has a very broad distribution across tropical South America in particular in Amazonis and Orinico basin as well as tropical savannas almost between the latitudes 12° N and 20° S. This palm is restricted to lowlands below 1000 m a.s.l. where the warm and moist climate fulfills its ecological needs (Rull, 1998). But it is absent from the Andes, the Pacific coasts and the eastern Brazilian Atlantic coasts. This palm can successfully grow mixed with rainforest taxa, however its noticeable habitat is permanently flooded soils where it can form a monodominant palm swamps (Rull and Montoya, 2014).

It is suggested that *M. flexuosa* was not abundant during the dry glacial periods and reestablished in the tropical South America during the wetter and warmer Holocene. Synchrony of the late Holocene large expansion of this palm with the time of human settlement (Behling and Hooghiemstra, 1998) and frequent burning in the landscape (Rull and Montoya, 2014) cause the rise of this hypothesis that human might promote the expansion of this palm in tropical savannas. The extensive use of almost all parts of this palm by human also provides additional support for this hypothesis (Rull and Montoya, 2014).

In this study one new sediment core is analyzed. In addition other records from eastern Amazonia and the sites from different parts of tropical South America are reviewed in order to investigate the reason for episodic expansion of *Mauritia* particularly during the late Holocene.

2. Study area

The sediment core Vereda (VRD) was retrieved from a small swampy strip of gallery forest (00°09'50.00" N, 51°04'16.0" W, 10 m a.s.l) dominated with *Mauritia*. The swamp area is situated 7 km north of the City Macapá (capital city of the State of Amapá) near the mouth of Amazon River (Fig. 1).

2.1 Climate

Based on Köppen climate classification (Peel et al., 2007), the area is mainly under the influence of the tropical monsoon climate "Am" and also partly tropical savanna climate "Aw". The study area receives 2500 - 3000 mm annual rainfall with the wet season between December and August and three dry months (September, October and November) with little precipitation. The temperature fluctuates between 23-32 ^{o}C with a mean annual of 27 ^{o}C (IBGE 2002).

2.2 Geomorphology and vegetation

The coastal savanna in the State of Amapá occurred on a hilly plain that has formed by erosion and deposition of sediments due to sea level changes and tectonic movements during the Holocene. The narrow depressions between these hills provide a network of meandering channels. On the more flat areas there are several lakes (such as Lake Curiaú) which are connected to these channels (De Toledo and Bush, 2007; Guimarães et al., 2013). This low-laying channel network is sensitive to changes in Atlantic sea level change and the amount of precipitation. Therefore the vegetation communities that are dependent up on these water bodies have been always subjected to marked changes. The most important plant communities are gallery forest composed mainly of Euphorbiaceae, Melastomataceae and Anacardiaceae as well as the palm *Mauritia*. The latter also forms monodominant populations around lakes and swamps.

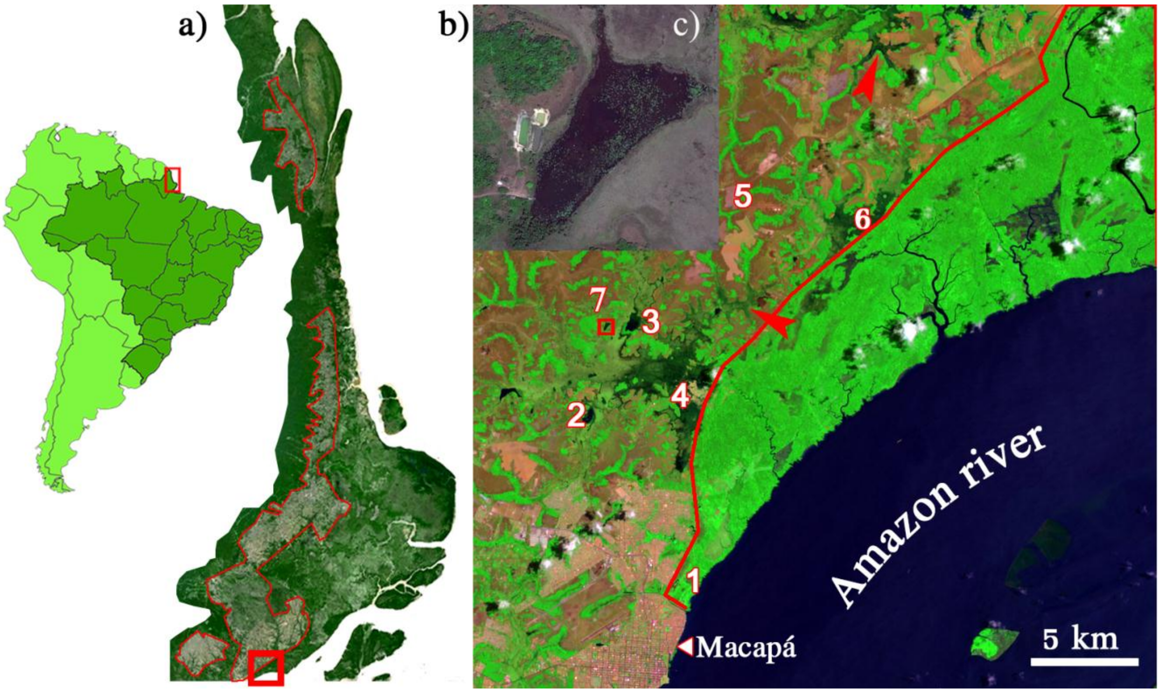


Figure 1. Study area: a) Amapá coastal belt. Red line shows approximate borders of the savanna compartment. b) False color map of the study area produced from Landsat 8. Red arrows show palaeo-channels. 1 = site Macapá (Guimaraes et al., 2012), 2 and 3 = Lakes Tapera and Marcio, respectively (De Toledo and Bush, 2007), 4 = Lake Curiau, 5 = site CUR, 6 = lake connected to CUR swamp by a palaeo-channel and 7 = Swamp where sediment core VRD is taken. In panel "b" the area bordered in red are Holocene deposited sediments of the river bank (Guimarães et al., 2013). c) Aerial image of the swamp where sediment core VRD is taken.

3. Material and methods

In November 2004 a 80 cm long sediment core VRD was taken using a Russian Corer and was transported to the Federal University of Pará and then to the Department of Palynology and Climate Dynamics, University of Göttingen to be stored in a dark cool (4 °C) condition.

3.1 Lithological description and age-depth modeling

Lithological description is carried out and based on the color, texture and grain size of the record. Table 1 shows the details of the 5 subsamples taken from the core and sent to the Accelerator Mass Spectrometry (AMS) laboratory, Department of Geosciences, National Taiwan University for radiocarbon dating. The results of this set of radiocarbon-dated samples are used to create the age-depth model by Bacon 2.2 package (Blaauw and Christeny, 2011) in R studio using Northern Hemisphere terrestrial calibration curve IntCal13 (Reimer, 2013).

Table 1: Details of samples sent to AMS ^{14}C laboratory and the results of dating.

AMS Lab ID	Depth (cm)	Material	^{14}C dates	Weighted mean calibrated date (cal yr BP)
NTUAMS-1168	34	Wood	438±1	485
NTUAMS-1773	47	Plant remains	1612±8	1425
NTUAMS-1449	58	Wood	2352±21	2355
NTUAMS-1169	75	Wood	1542±6	1446
NTUAMS-1774	77	Plant remains	2378±18	2465

3.2 Pollen and micro-charcoal analysis

For pollen and micro-charcoal analyses first 17 subsamples (0.5 cm³) were taken at 5 cm intervals along the sediment core. However, after analyzing this first set of samples, due to the need for a higher resolution analysis between 40 and 75 cm core depth, 7 additional subsamples were taken so that in this part of the core subsampling was carried out at 2.5 cm intervals. All subsamples were prepared using standard pollen analytical methods including application of HF 70% and acetolysis using dilute H_2SO_4 (Faegri and Iversen, 1989). Two exotic marker *Lycopodium clavatum* spores were added (Stockmarr, 1971) to each subsample for later pollen concentration and influx calculations. For each subsample pollen counting continued to reach a minimum of 300 terrestrial pollen grains. However in some subsample due to the very high abundance of *Mauriatia*, counting continued to higher numbers in order to detect also under represented pollen. The total pollen sum is based on the sum of terrestrial pollen excluding spores and pollen of aquatic taxa. Micro-charcoal particles (10 to 120 μm) were counted on pollen slides. Pollen identification was carried out according to relevant literature (Carreira et al., 1996; Carreira and Barth, 2003; Colinvaux et al., 1999; Roubik and Moreno, 1991) and the pollen reference collection in Department of Palynology and Climate Dynamics, University of Göttingen~~.~~ pollen data were grouped into palms, trees and shrubs, herbs and aquatics. For calculation and plotting of percentage and concentration for pollen counts and concentration of charcoal particles, Software packages TILIA and TILIAGRAPH were used.

3.3. Statistical analysis

To investigate the relation between number of charcoal particles and number of *Mauritia* pollen in the primary phase of this study, a simple linear regression was plotted in R. However for further examination of relationships between components of more complex data sets including *Mauritia* and charcoal counts and ENSO index values, Principle Component Analysis (PCA)) using R packages Vegan (Oksanen et al., 2016), Cluster (Maechler et al., 2015), Analogue (Simpson 2015) and Rioja (Juggins 2015) may be carried out.

4. Results

4.1 Lithology and age-depth model

The lower most 4 cm of the 80 cm long sediment core comprises of yellow clayish sediment accompanied with coarse sands and gravels. Between 74 cm core depth and the surface the sediment composed of dark organic material and the uppermost part of the core (upper 10 cm) contains some plant remains (Fig 2).

The result of 5 AMS radiocarbon dates is shown in table 1. The dated wood at 58 cm was probably transported from deeper levels due to the reworking. Therefore the model considers only the younger part of the age range (instead of weighted average of 2355 cal yr BP) provided from this dating. The wood piece at 75 cm core depth (1446 cal yr BP) belongs more likely to root of a plant and thus shows a much younger age compared to the subsequent date at 77 cm (2465 cal yr BP). This date is excluded by Bacon from the model. Although these unfit dates bring some uncertainties to the model, the age-depth model still can suggest a late Holocene age about 2500 calibrated years for the record.

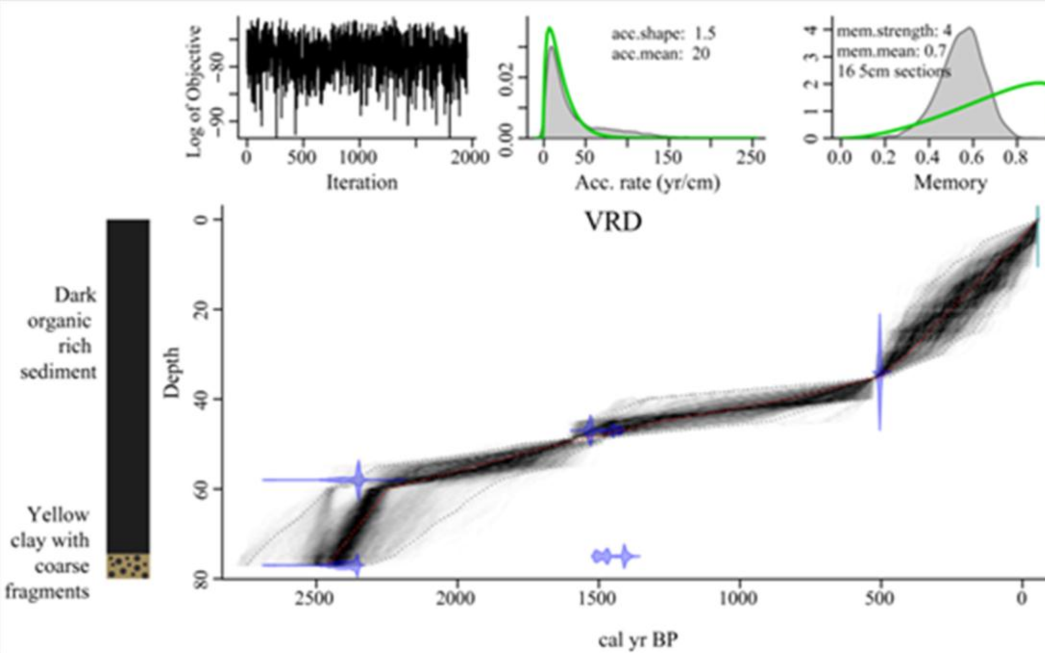


Fig. 2. Lithological illustration and age-depth model of the records Vereda.

4.2 Pollen and micro-charcoal

The pollen assemblages were saturated by *Mauritia* pollen and therefore the diversity of pollen types in the record is low. In total 35 pollen types were recognized among them 7 types could not be identified. The identified pollen types were categorized into four ecological groups: i) palms that comprises mainly of *Mauritia* and few grains of other members from Arecaceae, ii) trees and shrubs with very low contribution of gallery forest taxa, iii) herbs with dominance of Poaceae and episodic signals from Cyperaceae, iv) aquatics which are only *Ludwigia* pollen grains. The palynology of the core indicates that during the last 2500 years *Mauritia* has been the dominant plant at the swamp with background signal of savanna herbs (Fig. 3). The gallery forest trees and shrubs did not occur in the landscape frequently. The concentrations of pollen from all vegetation groups are higher between 2300 and 300 cal yr BP.

Charcoal particles were rare in the lowermost part of the record. Between ca. 2350 and 1000 cal yr BP the charcoal particles were more abundant and their number decreased afterward.

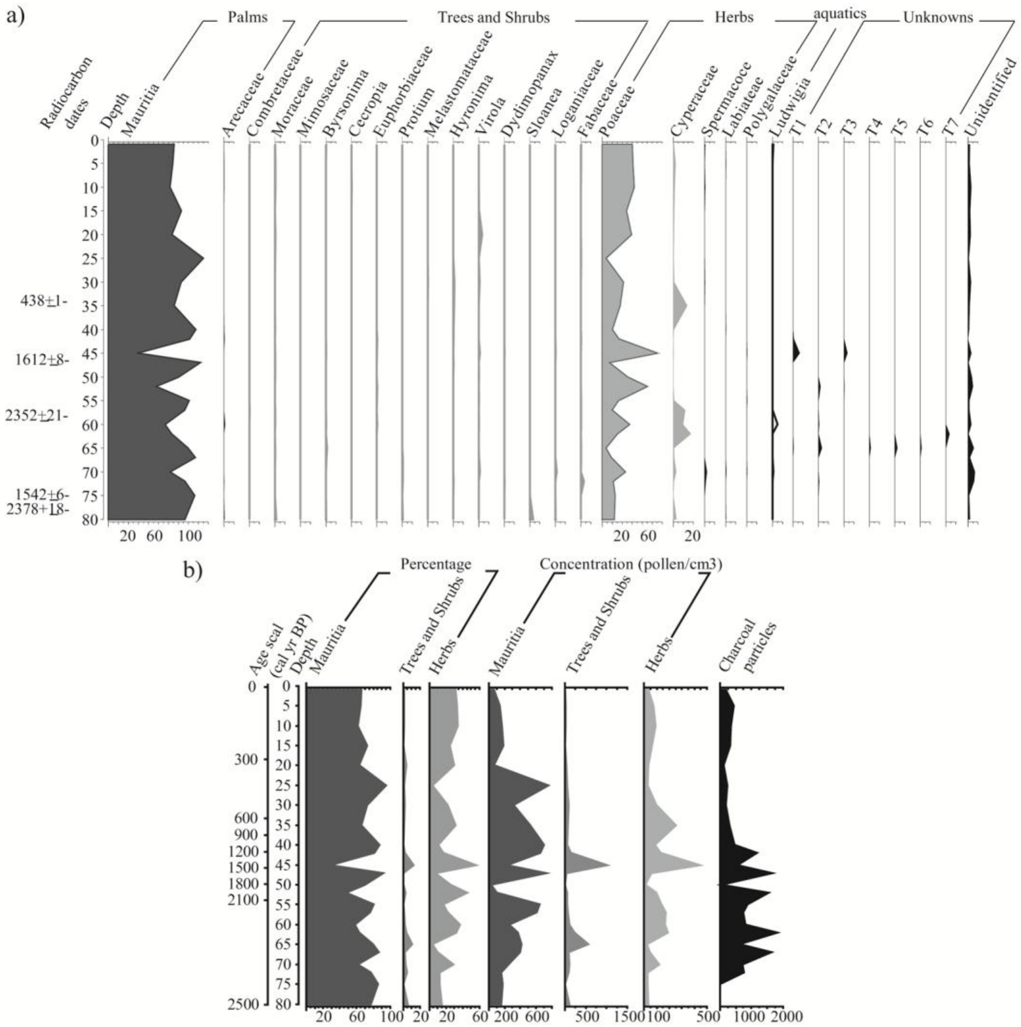


Fig. 3. a) pollen percentage diagram of the record Vereda, b) Pollen percentage and concentration for different ecological groups as well as number of charcoal particles.

4.3 Statistical analysis

Linear regression between number of charcoal particles and *Mauritia* pollen in three sites from eastern Amazonia (Current site, Curiaú (Alizadeh et al., 2015) and Curuça (Behling, 2001)) is shown in Figure 4. These plots show that there is no significant positive correlation between fire frequency and increase in population of *Mauritia*.

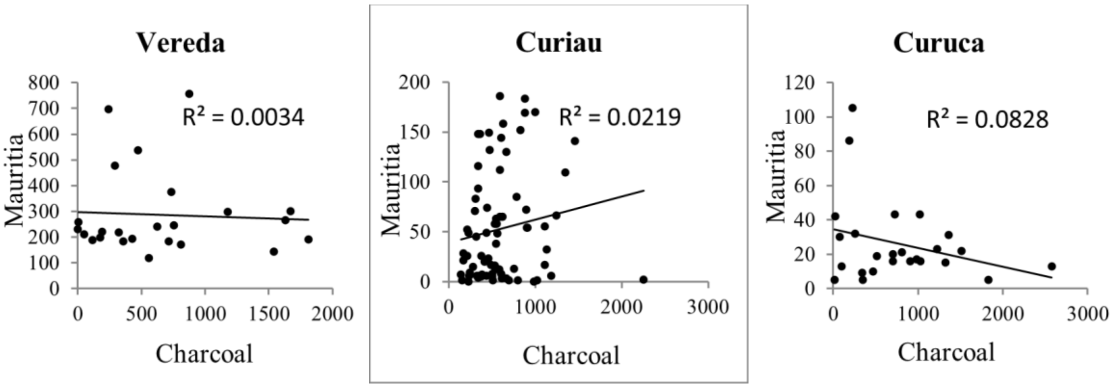


Fig. 4. The linear regression between number of charcoal particles and pollen of *Mauritia* for the records Vereda, Curiaú and Curuça.

5. Preliminary interpretation and perspectives

The results propose that in eastern Amazonia the occurrence of *Mauritia* is not synchronous with the increased fire events in the landscape. In addition a review on the records Curiaú and Curuça reveals that this palm has been present in the eastern Amazonia since the early Holocene with asynchronous population increase in different regions. For example around the lake Curuça the population of this palm shows increase between 11700-11200 cal yr BP (in profile A of the record) and 6000-3000 cal yr BP (profile B). However around the swamp Curiaú the population of this palm reached its maximum between 10000-8000 cal yr BP and after 3000 cal yr BP. Therefore three conclusions can be made here, i) the increase in population of *Mauritia* was not only a late Holocene event, ii) the anthropogenic origin for the late Holocene increased population of *Mauritia* at least based on charcoal data is questionable, iii) the asynchronous expansion of *Mauritia* in different regions imply that the dynamics of this palm may not be derived by climate alone but also by local factors like elevation and topography. If the climate was the principle driving force for expansion of *Mauritia* then its population increase must have been a synchronous event like the late Holocene forest expansion that is evident in the records from the whole tropical South America.

The further course of this study will investigate the following items:

1- The dynamics of *Mauritia* in other region of Amazonia and surroundings. For example in the records from Serra Sul dos Carajás (PDM (Hermanowski et al., 2012), LDC (Hermanowski et al., 2014)) and BRT (chapter IV)) or Llanos Orientales (Angel and Sardinas (Behling and

Hooghiemstra, 1998), El Pinal and Carimagua (Behling and Hooghiemstra, 1999)). Of special interest is investigating east-west or north-south trend/synchrony in dynamics of *Mauritia* as well as the role of topography and elevation of the study sites.

2- The impact of the early Holocene sea level rise and subsequently rise in water table on formation of coastal lagoons and *Mauritia* communities in low-laying coastal regions.

3- The effect of the late Holocene intensification of ENSO (Wanner et al., 2008) on the dynamics of *Mauritia*. Increased ENSO activities may cause several strong droughts in a decade that can selectively kill the trees (Phillips et al., 2009). Therefore it might kill the trees in the gallery forests that constitute the outer layer of vegetation around the water bodies. However it might not affect strongly the population of *Mauritia* that can expand into the shallow parts of the lakes and swamps.

4- The role of human to support the population of *Mauritia*. This item suffers from lack of sufficient number of archeological records hampers investigating the role of human activities. In a written correspondence with Professor Anna Roosevelt who pioneered archaeological studies in South America, she also mentioned that the expansion of *Mauritia* is natural and more likely due to the local hydrological changes rather than sort of pre-Colombian agricultural activities.

References

Alizadeh, K., Cohen, M., Behling, H., 2015. Origin and dynamics of the northern South American coastal savanna belt during the Holocene – the role of climate, sea-level, fire and humans. Quat. Sci. Rev. 122, 51–62. doi:10.1016/j.quascirev.2015.05.009

Behling, H., 2001. Late Quaternary enviornmental changes in the Lagoa da Curuca region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. Veg. Hist. Archaeobot. 10, 175–183. doi:10.1007/PL00006929

Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. J. Paleolimnol. 21, 461–476. doi:10.1023/A:1008051720473

Behling, H., Hooghiemstra, H., 1998. Late quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 139, 251–267. doi:10.1016/S0031-0182(97)00139-9

Blaauw, M., Christeny, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. doi:10.1214/11-BA618

Carreira, L.M.M. & Barth, O.M., 2003. Atlas de pólen da vegetação de canga da Serra de Carajás, Pará, Brasil. Illustrated ed. Museu Paraense Emílio Goeldi, Belém, Pará.

Colinvaux, P.A., De Oliveira, P.E., Moreno, E., 1999. Amazon Pollen Manual and Atlas - Manual e Atlas Palinológico da Amazônia. Hardwood Academic, Amsterdam.

De Toledo, M.B., Bush, M.B., 2007. A mid-Holocene environmental change in Amazonian savannas. J. Biogeogr. 34, 1313–1326. doi:10.1111/j.1365-2699.2006.01606.x

Faegri, K. & Iversen, J., 1989. Textbook of Pollen Analyses, 4th ed. Wiley, New York.

Guimarães, J.T.F., Cohen, M.C.L., França, M.C., Pessenda, L.C.R., de Jesus Souza, E., Nogueira, A.C.R., Alves, R., 2013. Recent effects of tidal and hydro-meteorological changes on coastal plains near the mouth of the Amazon River. Earth Surf. Process. Landforms 38, n/a–n/a. doi:10.1002/esp.3396

Guimaraes, J.T.F., Cohen, M.C.L., Pessenda, L.C.R., Franca, M.C., Smith, C.B., Nogueira, a. C.R., 2012. Mid- and late-Holocene sedimentary process and palaeovegetation changes near the mouth of the Amazon River. The Holocene 22, 359–370. doi:10.1177/0959683611423693

Hermanowski, B., Da Costa, M.L., Behling, H., 2014. Possible linkages of palaeofires in southeast Amazonia to a changing climate since the Last Glacial Maximum. Veg. Hist. Archaeobot. 24, 279–292. doi:10.1007/s00334-014-0472-0

Hermanowski, B., da Costa, M.L., Behling, H., 2012. Environmental changes in southeastern Amazonia during the last 25,000yr revealed from a paleoecological record. Quat. Res. 77, 138–148. doi:10.1016/j.yqres.2011.10.009

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2015. Cluster Analysis Basics and Extensions. R package version 2.0.1. CRAN.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-Garćia, S., Hooghiemstra, H., Ledru, M.P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev. Palaeobot. Palynol. 121, 1–75. doi:10.1016/S0034-6667(02)00082-9

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., O’Hara, R., 2016. Vegan: community ecology package. R Packag. 2.3-3. doi:10.4135/9781412971874.n145

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Ko¨ppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644. doi:citeulike-article-id:8144782

Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. t., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. Science (80-.). 323, 1344–1347. doi:10.1126/science.1164033

Reimer, P., 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. Radiocarbon 55, 1869–1887. doi:10.2458/azu_js_rc.55.16947

Roubik, D.W., Moreno P.J.E., 1991. Pollen and spores of Barro Colorado Island. Monographs in Systematic Botany. Missouri Botanical Garden.

Rull, V., 1998. Biogeographical and evolutionary considerations of Mauritia (Arecaceae), based on palynological evidence. Rev. Palaeobot. Palynol. 100, 109–122. doi:10.1016/S0034-6667(97)00060-2

Rull, V., Montoya, E., 2014. Mauritia flexuosa palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. Quat. Sci. Rev. 99, 17–33. doi:10.1016/j.quascirev.2014.06.007

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores. 13, 615–621.

Wanner, H., Beer, J., Butikofer, J., Crowley, T., Cubasch, U., Fluckiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J., 2008. Mid- to Late Holocene climate change: an overview. Quat. Sci. Rev. 27, 1791–1828. doi:10.1016/j.quascirev.2008.06.013

VI. Synthesis

1.2 Research outcomes

The late Quaternary environmental history of eastern Amazonia was investigated by multi-proxy analyses of three new sediment cores. At local scale the sea level oscillation, mangrove dynamics and forest-savanna interaction were addressed in chapter II and IV. Large scale reviews on expansion of non-analogue forests at the Pleistocene-Holocene boundary and episodic expansion of *Mauritia* communities were discussed in Chapter III and V. As a general outcome, the thesis suggests that environmental changes in eastern Amazonia are mainly driven by natural forces such as large scale climate dynamics and edaphic factors. But the role of human and fire cannot be excluded. The outcomes of this thesis are summarized as following:

1.1 The northern South American coastal savanna belt during the Holocene

Savanna expansion during the early Holocene. Savanna has been present in the northern South American coastal savanna belt since the beginning of the Holocene. During the early to mid-Holocene savanna expanded in the coastal plain of Amapá (site Curiaú (CUR)). A similar expansion of open vegetation occurred in other regions of tropical South America as shown by the records from savanna of Llanos Orientales in northwestern Amazonia such as the Laguna Loma Linda (Behling and Hooghiemstra, 1998), Laguna Angel, Laguna Sardinas (Behling and Hooghiemstra, 1998), Laguna El Pinal (Behling and Hooghiemstra, 1999) and Las Margaritas (Velez et al., 2005) and the records from eastern Amazonia such as Lagoa do Caçó (Pessenda et al., 2005). This savanna expansion is interpreted as prevalence of drier climate. At the same time the water level of Lake Valencia on the northern most region of the continent was quite high implying a wetter climatic conditions (Bradbury et al., 1981; Curtis et al., 1999). This latitudinal difference in moisture availability is attributed to a more northerly position of the ITCZ (Inter Tropical Convergence Zone) during the early to mid-Holocene that caused a long dry period in most regions of Amazonia. This long dry season is more likely the trigger of the savanna expansion.

Mid-Holocene forest expansion. The record CUR shows a mid-Holocene forest expansion that has an intermediate status compared to the sites from Llanos Orientales in Colombia (Laguna Angel and Sardinas (Behling and Hooghiemstra, 1998), Lagunas Chenevo (Berrio et al., 2002), Las Margaritas (Velez et al., 2005) and Laguna Loma Linda (Behling and Hooghiemstra, 1998)) and the sites from eastern Amazonia near the mouth of the Amazon River such as Lagoa da Curuça (Behling, 2001), Lago Crispim (Behling and Lima Da Costa, 2001) and Lagoa do Caçó (Pessenda et al., 2005). Precipitation at sites from Llanos Orientales is mainly affected by the shift in ITCZ position; however sites on the southern side of Amazon River mouth receive the rainfall mainly from SACZ (South

Atlantic Convergence Zone). It is suggested that during the austral summer of the mid-Holocene, the combined northward shift of SACZ and southward shift of ITCZ led to merge of these two systems near equator causing higher precipitation and forest expansion in northeastern Amazonia (Silva Dias et al., 2009).

Mid- to late Holocene unstable forest establishment. During the mid- to late Holocene, the gallery forests in the coastal savanna of Amapá experienced two periods of contraction between 5,600-3,300 and 2,300-1,000 cal yr BP and a period of expansion between 3,300 and 2,300 cal yr BP. A similar unstable condition has been also recorded in the water level of Las Margaritas (Velez et al., 2005) in Colombia. This oscillation of forest area can be attributed to the varying intensity of ENSO. For example studies suggested that the ENSO activities were less intense between 3800 and 2800 cal yr BP that is almost coincident with the period of forest expansion at the site CUR.

During the late Holocene, orbital forcing pushed the Northern Hemisphere summer position of the ITCZ farther south compared to its position during the mid-Holocene. This led to summertime cooling of the Northern Hemisphere and triggered changes in temperature gradients in the world Oceans. These changes may have caused an intensified ENSO that in turn exacerbated inter-annual variability of the SACZ movement. The warm phase of ENSO or El Niño is the main reason for decreased rainfall near the equator between December and February which prolongs dry season over this region from 3 to up to 6 months.

Soil and geomorphology. Although the occurrence of ferruginous and aluminous horizons at soil depths of 1-3 m might play a role to maintain the costal savanna belt, the vegetation history of the area that shows intervals of forest expansion on the same soil, rejects the effect of soil properties as the main factor of savanna establishment on the coastal belt of northern South America.

Fire and humans. Due to the high concentration of charcoal particles in the record CUR, it can be concluded that the savanna burning is definitely a factor that hampered the forest expansion during the Holocene. However the lack of evidence for big-game hunting near the study site on one hand and the synchrony between higher frequency of fire events and the periods with the seasonal climate (with longer dry season) on the other hand, suggest that the fire regime was mainly under the influence of climate though the role of human cannot be completely excluded.

1.2 Atlantic sea level oscillation and dynamics of mangrove population.

The diverse coastal settings and tectonic activity of the coastal zone of the western Atlantic Ocean result in different local sea levels ranging from ca. 40 m in Barbados (Fairbanks, 1989) to only ca. 3 m below the current sea level in southeastern coast of Brazil, state of Rio de Janeiro (Castro et al., 2014) at ca. 10,000 yr B.P. Palynological studies from CUR and Lagoa da Curuça (Behling, 2001) which are located on two sides of the Amazon delta are in agreement with the result from Rio de Janeiro. From these records it can be concluded that the mangroves existed in a distance of 2-3 km from these two sites during the early Holocene.

Due to the rapid sea level rise, the low water discharge of Amazon River and the absence of the sediments deposits on the river banks, brackish water transgressed into the palaeo-channels on the coastal plain of Amapá at the early Holocene. These hydrological changes facilitated the establishment of mangrove. Consequently the higher sea level caused the higher water table along the network of palaeo-channels which in turn favored the development of inundated *várzea* forests and swamp forest vegetation. After 10,000 cal yr BP some channels were abandoned perhaps because of high sedimentation rate between 11,000 and 10,000 cal yr BP and channel shifting. These abandoned channels constituted the shallow water bodies in the depressions which were suitable for the expansion of the *Mauritia* palm swamps. After 7,000 cal yr BP, higher precipitation in Amazon basin caused higher input of fresh water and disruption of mangrove belt.

1.3 The forest with no modern analogue

The study on the record CUR (chapter II) and a review on 7 other records from Amazonia and surrounding (chapter III) reveal that forests with no modern analogues expanded in tropical South America at the Pleistocene-Holocene boundary. The floral composition of these forests with some local differences is composed of *Micropholis*, *Podocarpus*, Ericaceae, *Humiria* and/or higher amount of *Ilex, Hedyosmum, Myrsine (Rapanea)*. In addition to the sites reviewed in our study, hill of six lakes in western part of Amazon rainforest (Bush et al., 2004; Colinvaux et al., 1996), Lagoa do Caçó (Pessenda et al., 2005) in eastern Amazonia and cerrãdo of the Huanchaca Mesetta in northeast Bolivia (Maezumi et al., 2015) show such late Pleistocene-early Holocene forest expansion. The age probability distributions of the sediment samples showing signals of such forests indicate that this forest expanded between 13000-10000 cal yr BP that is the time for transition from Late Glacial to Holocene (LG-H).

The maxima of percentages and influxes of arboreal pollen during the LG-HT suggest favorable climatic conditions either for forest expansion or for the predominance of specific tree taxa. These LG-HT percentages and influxes of arboreal pollen are higher than these values during the glacial times and in most of the studied records they are comparable with those during the wetter late Holocene. However the climatic conditions of the LG-HT is suggested to be much drier than the late Holocene and therefore forest expansion during such dry period looks contradictory. To explain these contradictions three scenarios are proposed:

i) According to the new palaeo-precipitation studies from Andes, the LG-HT was not the driest period since the Late Glacial, but it was almost as wet as the late Holocene. According to this scenario forest expansion during the LG-HT is not unexpected.

ii) The second scenario assumes that the LG-HT was very dry but the effect of its particular climatic conditions on the activities of the enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) is the reason for expansion of a specific forest. During the LG-HT, the lower insolation and mean annual temperature (compared to the late Holocene) might reduce the water stress for the trees and increase the CO_2 solubility in the leaves and CO_2/O_2 specificity in the Enzyme. In addition the increasing atmospheric CO_2 might guarantee its efficient diffusion into the leaves and turn the Rubisco activity in favor of carboxylation. As a result, in addition to the better photosynthesis and net primary production, the water use efficiency of plants improved and they could overcome the suggested dryness.

iii) The third scenario suggests that the LG-HT was just an optimum condition for predominance of strong pollen producers such as Moraceae, Melastomataceae, *Alchornea* and *Celtis*. In studies on relationship between pollen rain and modern vegetation cover, pollen grains of these trees constitute a large proportion of pollen assemblage captured by pollen traps. Based on this inference the maxima in arboreal pollen during the LG-HT might be due to dominance of higher pollen producing taxa rather than increased forest area.

The Late Glacial – Holocene transition vegetation history and climate dynamics discussed in chapter III reveal new insight into the future of Amazon forests under the post-industrial climate change. The atmospheric CO2 starts to increase markedly at ca. 12,800 cal yr BP and continues until ca. 11,200 cal yr BP. Afterward it increases with a lower rate until ca. 10,000 cal yr BP and then it starts to decrease. The temperature rise however continues until 9500 cal yr BP. Therefore around 10,000 cal yr BP, the patterns of rise in temperature and CO2 levels became uncoupled and the temperature increases without increase in CO2 levels. At this stage the maxima in influxes and percentages of arboreal pollen decline in most of our records.

Although the approximate maximum summer insulation and the ca. 3 °C higher temperature in the modern time compared to LG-HT cause water use defficiency in plants, the higher concentration of atmospheric CO_2 compared to LG-HT may still help the efficient water use. During the LG-HT the temperature might increase by ca. 3 °C degree, whereas the CO_2 concentration raised only 30 ppm. However, during the postindustrial period for a temperature increase of around 0.8 °C the CO_2 concentration raised by ca. 120 ppm (Edenhofer et al., 2014), therefore the post-industrial increase in CO_2 levels is much higher than temperature rise. Thus, according to the knowledge from LG-HT vegetation and climate history, either higher productivity or change in plant composition of forests is expected in the future. Multi-decadal studies on forests dynamics have also suggested accelerated growth of Amazonian trees (Lewis et al., 2004; Phillips et al., 2009) that can be attributed to a raised CO_2 concentration during the last decades (Lewis et al., 2004; Lloyd and Farquhar, 2008).

Nonetheless the higher tree growth can be expected provided that the moisture levels do not drop below critical values as occurred in 2005 (Lewis et al., 2004).

1.4 Environmental change in Serra Sul dos Carajás since the mid-Holocene

Forest-savanna boundary shifts. The palynological results of the record BRT indicates that the vegetation composition of the forest around the plateau was relatively stable during the last 6600 cal yr BP with continuous dominance of the local forest vegetation. A slight increase in pollen percentages of forest trees and decrease in percentages of shrubs and herbs may suggest that forest borders shifted toward savanna and therefore the distance between the site BRT and savanna became longer. This in turn may imply better climatic conditions such as less seasonality in the rainfall regime.

Conversely pollen diagrams of the sites from savanna on top of the plateau (LDC, PDM, CSS) show a marked shift in percentages of non-arboreal and arboreal pollen. Since the mid-Holocene the records show very strong signals of savanna that was replaced by signals from arboreal pollen after 2500 cal yr BP. Therefore, in LDC, PDM and CSS the signal of arboreal vegetation that comes from surrounding forests reached its maximum approximately 3400-4000 years later compared to BRT.

The records from savanna of Serra Sul dos Carajás reveal a seasonal climate with dry seasons longer than today between the mid and the late Holocene. These long dry seasons were alternated with short wet seasons with enough precipitation to support swamp formation in the site PDM. At this time forests existed on the slopes around the savanna but away from their modern boundaries and with less density. The presence of pioneering taxa such as *Celtis* implies the failed attempts for forest reestablishment on the savanna area during this period. During the late Holocene after ca. 4000 cal yr BP, the signal from tropical forests increased in the records from savanna that implies replacement of forest borders toward the savanna. During this period the abundance of pioneers such as *Piper*, *Celtis* and *Trema* increased that suggests a gradual successive expansion of tropical forests from the slopes toward the savanna. Considering the fact that the site BRT is located near the modern forest borders and almost at the same elevation, it can be concluded that the forest boundary shift was a slow horizontal movement. Therefore the possibility of interference from some limiting factors that slowed down forest expansion is suggested.

Limiting factors for forest-savanna boundary shifts. The following factors might delay the forest boundary shifts toward the savanna during the mid- to late Holocene:

- **Micro-climates.** Because signal of forest taxa has been always present in the records LDC, PDM and CSS even during the drier periods since the mid-Holocene, it can be concluded that a fringe of forest has been present around the whole plateau not only around BRT. Therefore the occurrence of a microclimate that could support forest establishment only around the site BRT cannot be accepted.

- **Climate.** This factor makes differences in vegetation history in a large regional to continental scales or through altitudinal gradients. Nonetheless the sites investigated in this study are close together and almost at the same elevation. Then the difference in climate could not be the reason for delay in forest expansion.
- **Fire and human**. Presence of charcoal together with pollen of pioneering taxa indicates a continuous succession for forest reestablishment and fire-forest interaction. Therefore natural or manmade fire may play a role to delay forest expansion.
- **Ferruginous soil**. Our results obtained from measurement of extractable Fe and remote sensing show that there is a negative correlation between forest establishment and amount of soil extractable Fe in space and time. This suggests that ferruginous soil is the main limiting factor for forest expansion. However based on the results of a new study on the relation between soil and vegetation in Serra Sul dos Carajás the amount of extractable Fe in the record BRT has been always in tolerable range for forest trees. Besides this study proposed that because most of the Fe in soil is present as Fe^{3+}, that is insoluble and non-available, the high levels of extractable Fe cannot be the reason for vegetation differences on the plateau.
- **Soil depth**. According to the same study on the relation between soil and vegetation in Serra Sul dos Carajás the soil depth is the main driver of variation in vegetation communities on the plateau of Serra Sul dos Carajás. This conclusion can explain the reason for slow forest expansion on the plateau. The surface of the forest hollow where the site BRT is located was covered by a hard lateritic substrate at ca. 6600 cal yr BP. Since that time a soil layer of 93 cm has formed that is still not sufficient for upland forests establishment. This data suggest that the 4000 years delay in forest expansion might be spent on the slow process of soil formation.

Driving forces for forest-savanna boundary shift. The establishment of forest during the last 6 millennia is well known in several records from tropical South America. For example Lagunas Chenevo (Berrio et al., 2002), Laguna Loma Linda (Behling and Hooghiemstra, 1998), Laguna Angel, Laguna Sardinas (Behling and Hooghiemstra, 1998), Laguna El Pinal (Behling and Hooghiemstra, 1999) and Las Margaritas (Velez et al., 2005) and cerrãdo of the Huanchaca Mesetta, northeast Bolivia (Maezumi et al., 2015) show the late Holocene forest expansion. The mostly accepted reason for the change to wetter climatic conditions during the late Holocene in Amazonia is orbital scale southward shift of the ITCZ. In Serra Sul dos Carajás, the ITCZ brought humidity which was necessary for soil formation and forest expansion.

1.5 Episodic expansion of *Mauritia.*

Some records from tropical savannas contain abundant charcoal particles during the wet late Holocene period. High frequency of fire during a wet period may imply the anthropogenic origin for fire events.

Synchronous with more frequent fires the *Mauritia* pollen shows higher percentages in the records. These observations led to the hypotheses that the late Holocene expansion of *Mauritia* might be due to the human activities. However, the preliminary results of the review on the origin of episodic expansion in *Mauritia* communities (chapter V) indicate that the increased population of this palm is neither a late Holocene event nor fire dependent. The *Mauritia* communities have occurred since the early Holocene in the northern South American coastal savanna belt as it has been recorded in CUR. Therefor the former belief about anthropogenic origin for expansion of *Mauritia* population during the late Holocene is contentious.

2. Concluding remarks and prospective

The following conclusions can be made by this thesis:

1. A forest with no modern analogue expanded in the Amazonia and in gallery forests in the surrounding savannas between ca. 13,000-10,000 cal yr BP under a specific climatic condition that was suitable either for forest expansion or for predominance of specific arboreal taxa. Since the signals from arboreal taxa during the LG-HT are comparable with those during the wetter late Holocene, the suggested dry climate during LG-HT is questionable.
2. The vegetation history and climatic conditions of the LG-HT can provide an insight into the future of Amazon rainforest under post-industrial climatic conditions. The modern climate is suggested to be wetter than the LG-HT with much higher concentration of atmospheric CO_2. These two factors may offset the effect of warmer modern climate compared to LG-HT that may cause higher evapotranspiration and water stress. Therefore the forest expansion is expected under the modern climatic conditions. However this hypothesis needs more palaeo-temperature and palaeo-precipitation data to be proved.
3. Savanna had been continuously the important constituent of the landscape in the coastal area of Amapá State at least since the beginning of the Holocene (11,500 cal yr BP).
4. The climate of eastern Amazonia near equator has been under influence of ITCZ, SACZ and ENSO. At the beginning of the Holocene the northern position of ITCZ caused longer dry season and savanna expansion in the area. During the mid-Holocene the southward movement of ITCZ and northward shift of SACZ led these two convection systems to merge and bring more rainfall that caused forest expansion in the area. The late Holocene was coincident with the higher ENSO activities that caused episodic expansion of the forest.
5. Changes in Atlantic sea level and the Amazon River discharge are the main factors controlling the mangrove development and vegetation changes (*Mauritia* swamp versus swamp forest) in the network of palaeo-channels and palaeo-lakes in coastal savanna belt of northern South America during the Holocene. More records which can at last cover the last 12,000 years are needed from coastal savanna belt to reconstruct the early Holocene sea level rise and its effect on the coastal vegetation.

6. The incidence of wetter climatic conditions in eastern Amazonia, more likely due to the southward shift of ITCZ promoted the forest incursion into the savanna region during the late Holocene. In Serra Sul dos Carajás the well-established forests on the slopes around the plateau started to expand toward the savanna and reached their modern borders through a long period of 3400-4000 years. Among the different factors that may delay the forest expansion, the soil depth and fire may play the key role.
7. Human activities together with natural and manmade fire definitely played an important role to maintain the savannas of eastern Amazonia especially during the late Holocene. However, the synchrony of marked changes in vegetation with climatic events proposes that the vegetation dynamics in eastern Amazonia is more under influence of climate.
8. The geomorphology and soil properties may interact with and slow than the changes promoted by climatic factors.

The eastern Amazonia is a very huge area and our knowledge about its vegetation and climate history is poor. In this regard multi-proxy studies on sediment cores and using independent palaeo-climate proxies such as cave speleothems are essential. The modern vegetation-pollen rain study that affords an efficient way of more precise vegetation reconstruction is also missing from the area. Remote sensing studies combined with field work must be integrated into the palaeoecological studies especially for the savanna of eastern Amazonia to detect the effect of soil properties and savanna burns in a larger scale.

References

Behling, H., 2001. Late Quaternary enviornmental changes in the Lagoa da Curuca region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. Veg. Hist. Archaeobot. 10, 175–183. doi:10.1007/PL00006929

Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. J. Paleolimnol. 21, 461–476. doi:10.1023/A:1008051720473

Behling, H., Hooghiemstra, H., 1998. Late quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 139, 251–267. doi:10.1016/S0031-0182(97)00139-9

Behling, H., Lima Da Costa, M., 2001. Holocene vegetational and coastal environmental changes from the Lago Crispim record in northeastern Par?? State, eastern Amazonia. Rev. Palaeobot. Palynol. 114, 145–155. doi:10.1016/S0034-6667(01)00044-6

Berrio, J.C., Hooghiemstra, H., Behling, H., Botero, P., Van der Borg, K., 2002. Late-Quaternary savanna history of the Colombian Llanos Orientales from Lagunas Chenevo and Mozambique: a transect synthesis. The Holocene 12, 35–48. doi:10.1191/0959683602h1518rp

Bradbury, J.P., Leyden, B., Salgado-Labouriau, M., Lewis Jr., W.M., Schubert, C., Binford, M.W., Frey, D.G., Whitehead, D.R., Weibezahn, F.H., 1981. Late quaternary environmental history of Lake Valencia, Venezuela. Science (80-.). 214, 1299–1305. doi:214/4527/1299 [pii]\r10.1126/science.214.4527.1299

Castro, J., Suguio, K., Nacional, M., Castro, J., Suguio, K., Nacional, M., 2014. Sea-level fluctuations and coastal evolution in the state of Rio de Janeiro , southeastern Brazil. An. da Acad. … 86, 671–683. doi:10.1590/0001-3765201420140007

Curtis, J.H., Hodell, D. a., Brenner, M., 1999. Climate change in the Lake Valencia Basin, Venezuela, |12600 yr BP to present. The Holocene 9, 609–619. doi:10.1191/095968399669724431

Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Minx, J.C., Farahani, E., Susanne, K., Seyboth, K., Adler, A., Baum, I., Brunner, S., Eickemeier, P., Kriemann, B., Savolainen, J., Schlomer, S., von Stechow, C., Zwickel, T., 2014. Climate Change 2014: Mitigation of Climate Change, Working Group III Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. doi:10.1017/CBO9781107415416

Fairbanks, R.G., 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature. doi:10.1038/342637a0

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Lezama, A.T., Martínez, R.V., Brown, S., Chave, J., Kuebler, C., Vargas, P.N., Vinceti, B., 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 359, 421–36. doi:10.1098/rstb.2003.1431

Lloyd, J., Farquhar, G.D., 2008. Effects of rising temperatures and [CO2] on the physiology of tropical forest trees. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 363, 1811–7. doi:10.1098/rstb.2007.0032

Maezumi, S.Y., Power, M.J., Mayle, F.E., McLauchlan, K.K., Iriarte, J., 2015. Effects of past climate variability on fire and vegetation in the cerr??do savanna of the Huanchaca Mesetta, NE Bolivia. Clim. Past 11, 835–853. doi:10.5194/cp-11-835-2015

Pessenda, L.C.R., Ledru, M.P., Gouveia, S.E.M., Aravena, R., Ribeiro, a. S., Bendassolli, J. a., Boulet, R., 2005. Holocene palaeoenvironmental reconstruction in northeastern Brazil inferred from pollen, charcoal and carbon isotope records. The Holocene 15, 812–820. doi:10.1191/0959683605hl855ra

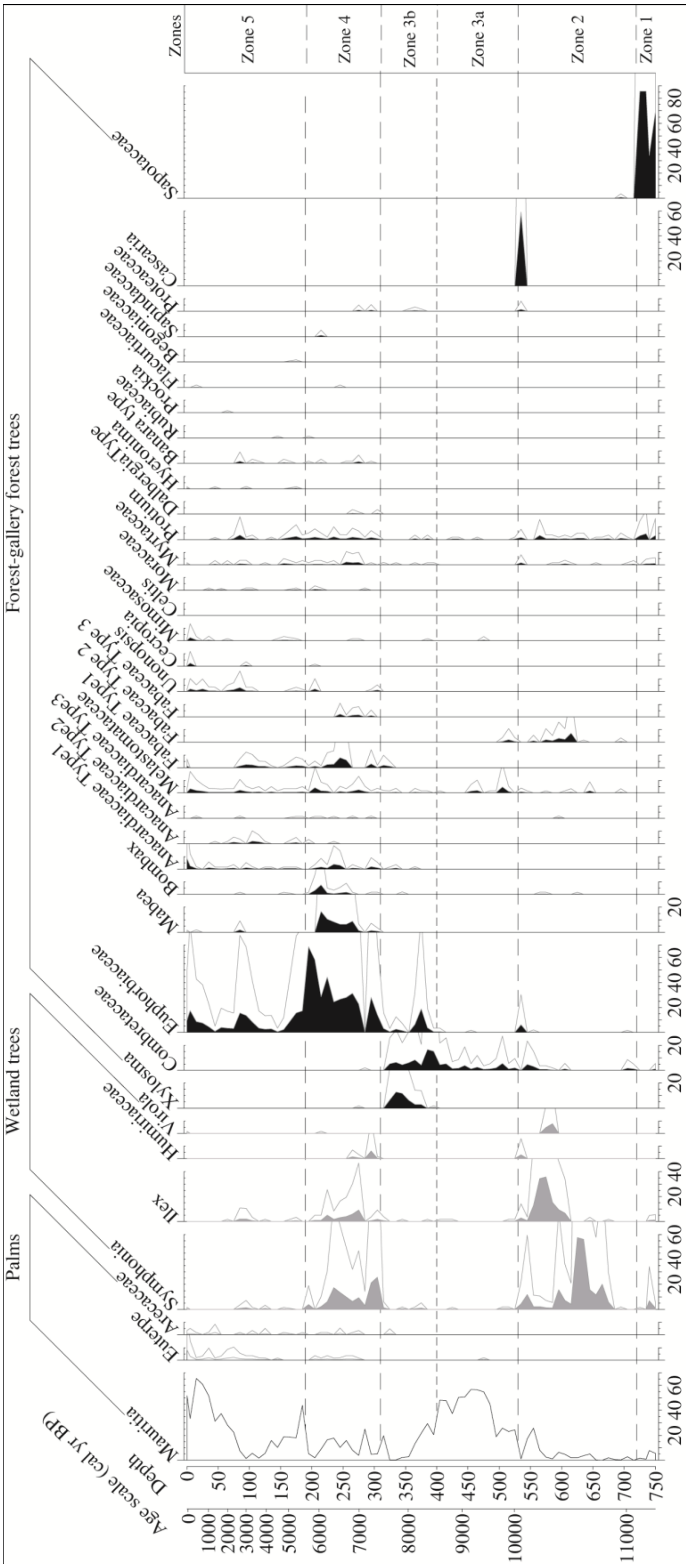
Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. t., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. Science (80-.). 323, 1344–1347. doi:10.1126/science.1164033

Silva Dias, P.L., Turcq, B., Silva Dias, M.A.F., Braconnot, P., Jorgetti, T., 2009. Mid-Holocene Climate of Tropical South America: A Model-Data Approach, in: Past Climate Variability in South America and Surrounding Regions. pp. 259–281. doi:10.1007/978-90-481-2672-9

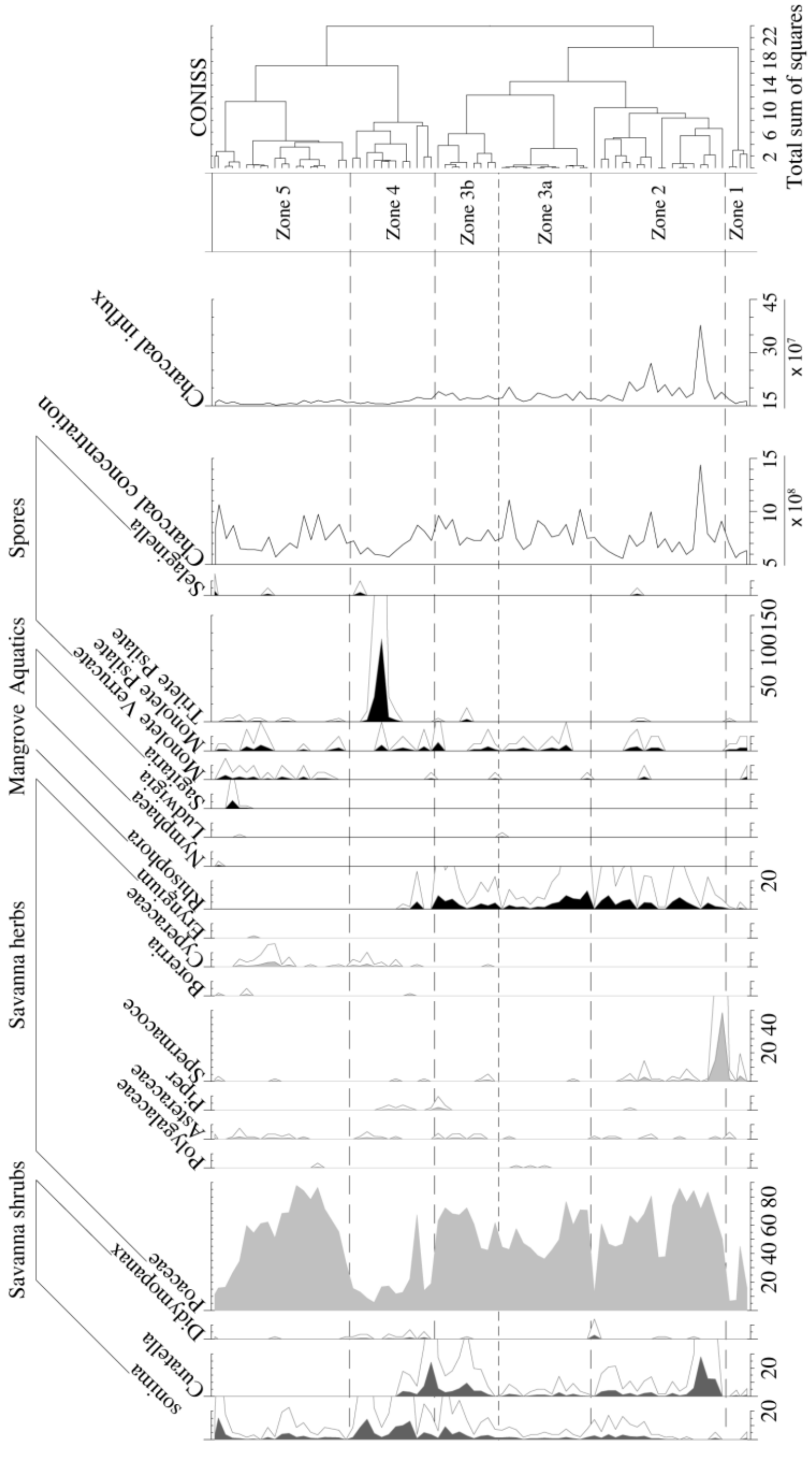
Velez, M.I., Wille, M., Hooghiemstra, H., Metcalfe, S., 2005. Integrated diatom-pollen based Holocene environmental reconstruction of lake Las Margaritas, eastern savannas of Colombia. The Holocene 8, 1184–1198. doi:10.1191/0959683605hl890rp

Appendix

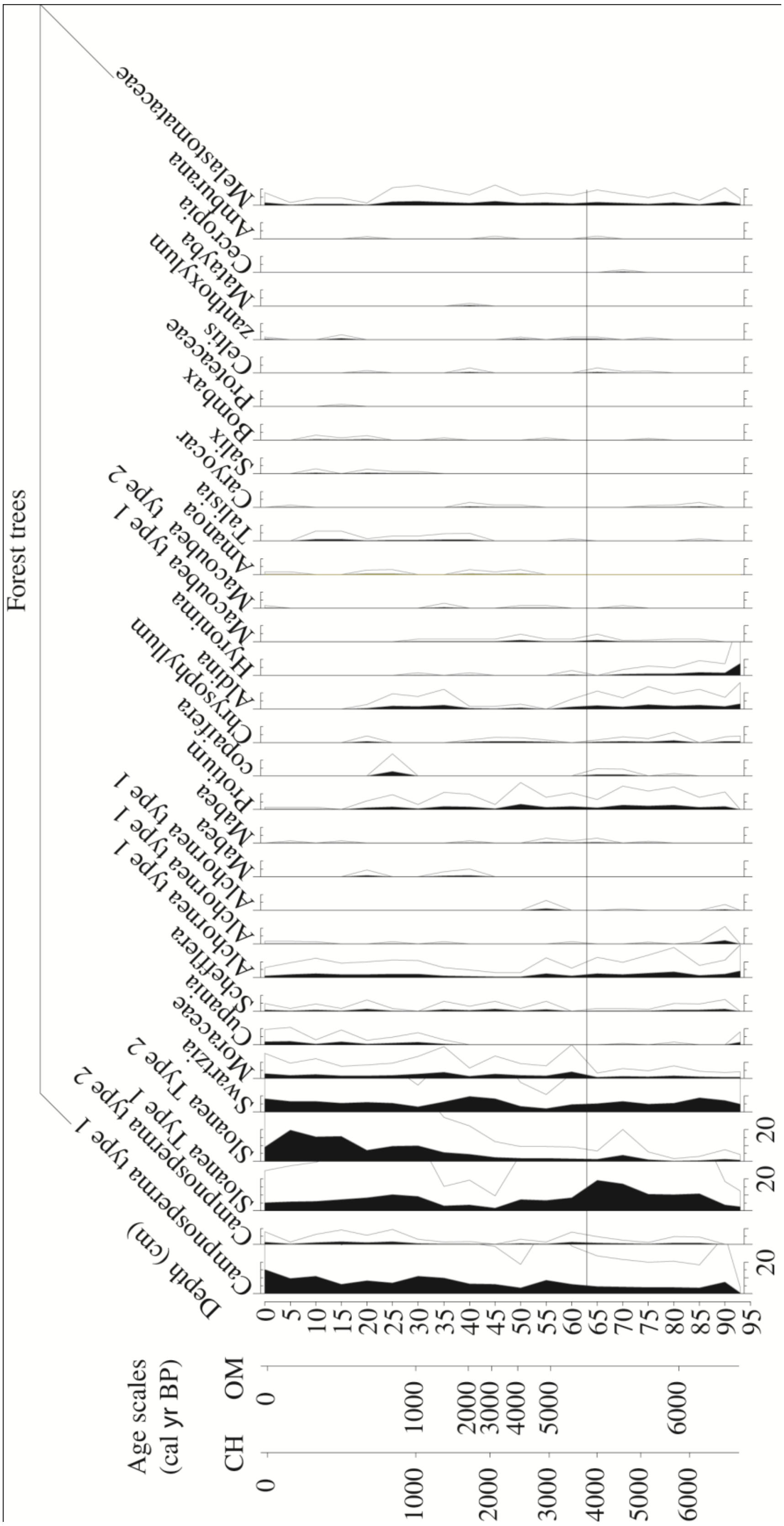
Appendix I. Complete pollen diagram of the record Curiaú



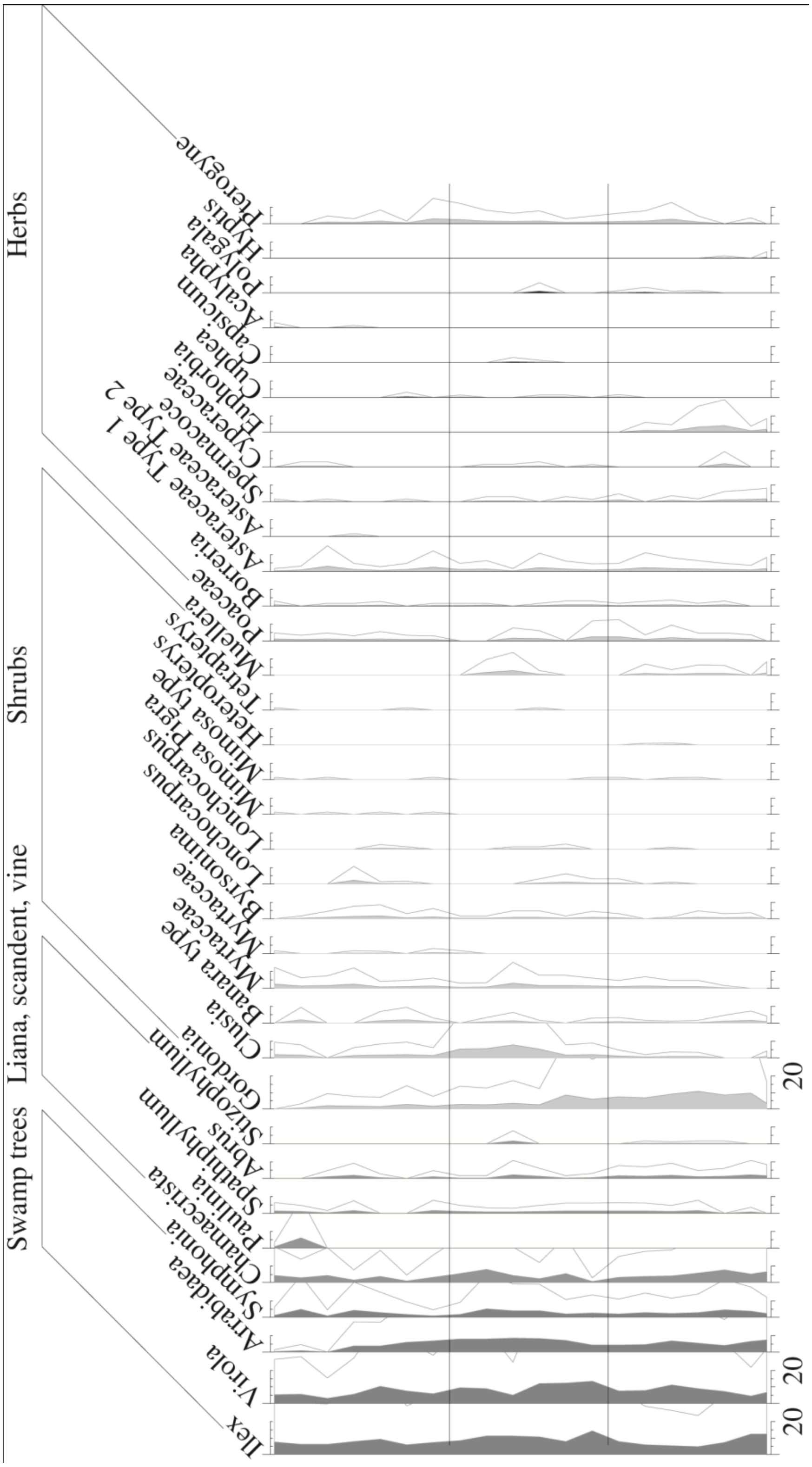
Appendix I. Continued



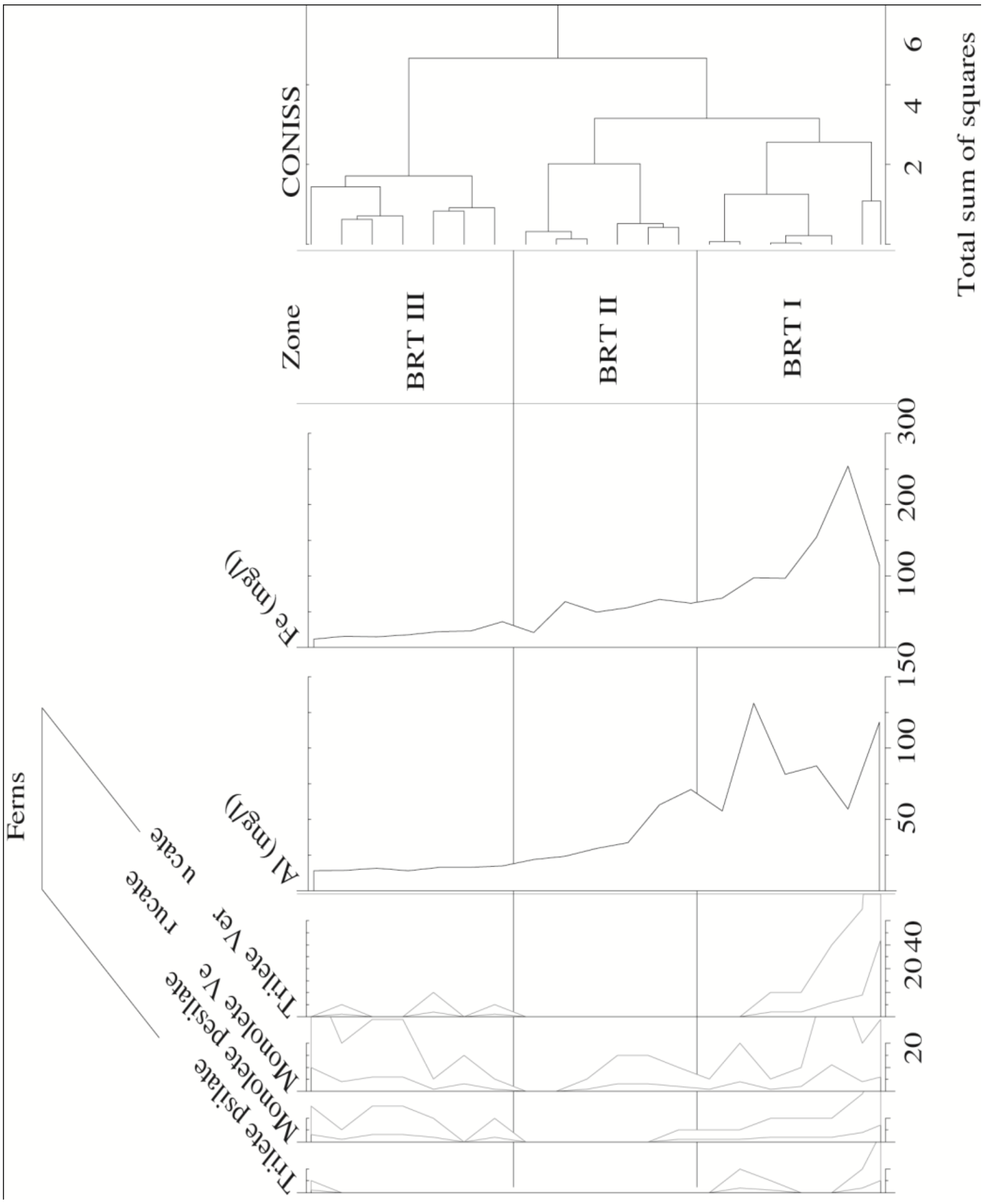
Appendix II. Complete pollen diagram of the record Buriti



Appendix II. Continued



Appendix II. Continued



Curriculum Vitae

Kamaleddin Alizadeh
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Educational Background

(2013- 2017)
PhD student, Department of palynology and climate dynamics,
Georg-August-Universität Göttingen.

(2008- 2010)
M.Sc. Degree of Science in Plant Science, School of Biology,
University College of Science and Agriculture,
Payam-e-Nour University, Tehran branch. (GPA=18.55 out of 20)

(2002- 2007)
Bachelor of Science in Zoology, School of Biology,
University College of Science, University of Tehran. (GPA=15.43 out of 20)

Scholarships and grants:

- Erasmus Mundus scholarship for 3 years to accomplish PhD in Goettingen.

Workshop

- Multivariate analysis of data in R. Thomas Giesecke. Goettingen, Summer semesters 2014 and 2015.

Publications

- Khansari, E., Zarre, Sh., **Alizadeh, K.,** Attar, F., Aghabeigi, F., Salmaki, Y., 2012. Pollen morphology of Campanula (Campanulaceae) and allied genera in Iran with special focus on its systematic implication. ***Flora*** 207 (3) 203–211.
- **Alizadeh, K.,** Cohen, M., Beling, H., 2015. Origin and dynamics of the northern South American coastal savanna belt during the Holocene – the role of climate, sea-level, fire and humans. ***Quaternary Science Reviews*** 122 (15): 51–62.
- Talebi, T., Ramezani, E., Djamali, M., Alizadeh, H., Naqinezhad, A., **Alizadeh, K.,** Ponel V. 2015. The Late-Holocene climate change, vegetation dynamics, lake-level changes and anthropogenic impacts in the Lake Urmia region, NW Iran. ***Quaternary International***, 480: 40-51.
- **Alizadeh, K.,** Rodrigues, J, M., Behling, H. 2016. Contradictions between vegetation history and reconstructed climate in Amazonia during the Late Glacial-Holocene transition. ***Climate of the Past*** (Under revision).
- **Alizadeh, K.,** Matthias, I., Rodríguez-Zorro, P. A., Hermanowski, B., da Costa, M. L., Behling H. 2016. Forest-savanna boundary shift on the plateau of Serra Sul dos Carajás (southeastern Amazonia) since the mid-Holocene; driving forces and limiting factors. ***Quaternary International*** (Under revision).

Poster and oral presentation

- **Alizadeh, K.,** Cohen, M., Behling, H. Why does an unexpected savanna belt occur in coastal area of northern South America? Annual Conference of the Society for Tropical Ecology (GTOe), 7th-10th April 2015, Zurich. Switzerland. **(Talk and poster)**
- Rodríguez-Zorro, P. A., **Alizadeh, K.,** Cohen, M., Beling, H. Long term vegetation-climate interaction in coastal savanna of northern South America. XIX INQUA Congress, 26th Jul – 2nd Aug, 2015, Nagoya, Japan. (**Poster**)
- **Alizadeh, K.,** Cohen, M., Behling, H. Long term vegetation-climate interaction in coastal savanna of northern South America. GFOe Annual meeting. 31st Aug- 4th Sep 2015, Goettingen, Germany. **(Poster)**
- **Alizadeh, K.,** Rodríguez-Zorro, P. A., Hermanowski, B., Costa, M., Behling, H. Comparison between long-term south eastern Amazonian upland and lowland rainforest dynamics during the Holocene. GFOe Annual meeting. 31st Aug- 4th Sep 2015, Goettingen, Germany. **(Poster)**
- **Alizadeh, K.,** Matthias, I., Rodríguez-Zorro, P. A., Hermanowski, B., Costa, M., Behling, H. Reconstruction of 7000 years environmental changes in Serra Sul dos Carajás southeastern Amazonia using palynology and remote sensing: a new approach. Annual Conference of the Society for Tropical Ecology (GTOe), 23rd-26th Feb 2016, Goettingen, Germany. **(Talk)**

- **Alizadeh, K.,** Rodrigues, J., Behling, H. The Amazon rainforest expansion at the boundary of Holocene and Pleistocene. Annual Conference of the Society for Tropical Ecology (GTOe), 23rd-26th Feb 2016, Goettingen, Germany. **(Poster)**
- Talebi, T., Ramezani, E., Djamali, M., **Alizadeh, H.,** Naqinezhad, A., Alizadeh, K., Andrieu-Ponel, V. Holocene climate change, vegetation dynamics, lake-level changes and anthropogenic impacts in the Lake Urmia region, NW Iran. European pollen Database annual meeting, 1st-3rd June 2016, Aixen-Provence, France. **(Poster)**
- **Alizadeh, K.,** Akbari Azirani, T., Ramezani Kakroudi, E., Behling, H. Pollen assemblages of honey from different landscapes of Iran. European pollen Database annual meeting, 1st-3rd June 2016, Aix-en-Provence, France. **(Poster)**
- **Alizadeh, K.,** Rodrigues, J, M., Behling, H. Contradictions between vegetation history and reconstructed climate in Amazonia during the Late Glacial-Holocene transition. International Palynology Congress (IPC), 23-28 Oct 2016, Salvador, Brazil. **(Talk and poster)**
- **Alizadeh, K.,** Behling, K., Coroian, C. O., Fenesan, M. P., González Porto, A. V., Fagúndez, G. A., Telleria, M. C., Vásquez Quitral, P. A., da Silva, C. I., Martinez, E. S. The South American Honey Monitoring (SAHM) project. International Palynology Congress (IPC), 23-28 Oct 2016, Salvador, Brazil. **(Talk and poster)**

Event organization

Behling, H., **Alizadeh, K**,. Rodríguez-Zorro, P. A., Biagioni, Siria. Long-term vegetation, climate, fire dynamics and human impact in tropical and subtropical ecosystems. XIV International Palynological Congress, 23rd-28th Oct 2016, Salvador, Brazil.