ZENTRUM

FÜR BIODIVERSITÄT UND NACHHALTIGE LANDNUTZUNG

SEKTION

BIODIVERSITÄT, ÖKOLOGIE UND NATURSCHUTZ

- CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND USE -
SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

Development and dynamics of the Atlantic rainforest during the Late Quaternary and its connections with the climate system

Dissertation zur Erlangung des Doktorgrades der

Mathematisch-Naturwissenschaftlichen Fakultäten der

Georg-August-Universität Göttingen

vorgelegt von

M.Sc.

Martins Rodrigues, Jackson

aus

Muriaé

Göttingen, June 2016

Referentin/Referent: Prof. Dr. Hermann Behling

Korreferentin/Korreferent: Dr. Thomas Giesecke

27.06.2016

Atlantic rainforest fauna and flora. Source: SOS Mata Atlântica

Contents

Acknowledgements

I am grateful to all people have somehow contributed to my work and life in Germany during the past years making it a pleasant time as a scientist and non-scientific person and helped me to finish my work.

My special thanks go to my supervisors, Professor Hermann Behling, who helped me to discover the scientific fields of palynology and palaeoecology and Dr. Thomas Giesecke, who challenge me, encouraged me, supported me and at the same time, gave me the freedom and directions I needed to develop new ideas, concepts and strategies for development of my own scientific work. I also would like to thank my third supervisor Professor Dirk Gansert for all support.

I would like to thank the institutions DAAD for the funding of the research "Development and dynamics of the Atlantic rainforest during the Late Quaternary and its connections with the climate system", IBGE and SOS Mata Atlântica that shared vegetation maps Atlantic rainforest.

Thanks also to the entire staff of the Department of Palynology and Climate Dynamics. It was a great time, I appreciated the scientific and social company of each one of you. In this context I especially want to thank Inke Achterberg, Siria Biagioni, Jörg Christiansen, Sonia Fontana, Thomas Giesecke, Vivian Jeske-Pieruschka, Isabelle Matthias, Paula Rodríguez, Malte Semmler, Anggi Hapsari, Christina Ani, Fang Gu, Lisa Schüler, Lyudmila Shumilovskikh and Sina Alizadeh, Farooq Jan who always maintained the good spirit, gave room for scientific enthusiasm and were nice company at work-related and non-work related social events.

Behling family is thanked for warm and lovely time dedicated to me.

I especially thank Nele Jantz and Carolina Guarinello for sharing the office, lots of fruitful discussions about everything. Apart from my scientific work I would especially like to thank my friends Mauricio Pacheco, Jenni Otti, Ramon Vidal, Alinne Ambrósio, Elaine, Jens, Victor, Helge Roose, Sina, Elmira, Vivian and Marius for being there for

me at all times and enriched my life with their friendship and company during the past years and helped me to gather strength and discover and enjoy life in many different ways.

Lastly, I would like to thank my family – my parents Lideir and Amir. They support and encourage me at all times of my life, each one in his/her own way, and made me feel loved and at home, no matter how far I may be in terms of space. Specially thank my wife/life, without her support nothing could be done, this thesis belongs 50% or more to her. I love you!

In memory of my stepfather Amir Silveira de Lima.

Thank you!

Summary

The Atlantic rainforest harbour an outstandingly high biodiversirty. Many different environmental factors (climate, soil, geomorphology, ocean and etc) interact in a very large space creating complex ecosystems with high endemism. Altough, its richness, the Altnatic rainforest is highly endangered due to increasing human impact through the intensification of land-use and consequent broad landscape replacement. Many palaecological studies have been developed during the last decades providing important background of diverse location around Atlantic rainforest, however little is known about regional palaeoecological history and landscape dynamics. In this study, we present palynological analyses carried out in a compilation of several pollen records from Alantic rainforest ecosystems and surrounding regions that help to unveil patterns and processes in present and past vegetation change during the Late Quaternary.

A palaeoecological study of 3 time periods (3000 yrs BP, pre-colonization and modern) of 27 pollen records of Atlantic rainforest and associated ecosystems reveals marked vegetation changes as consequence of climate and human impacts during the Late Holocene. The samples concerning the pre-colonization period was used as standard for comparison once it represents the natural vegetation conditions once climate was similar to today and there was no human impact on it. Handling multivariate techniques associated to pollen abundaces threshold, the pre-colonization period was classified into 7 groups. Moreover, it was noticed a clear differentiation between grassland and forested vegetation and between tropical and subtropical vegetation types. The comparison of pre-colonization with the other two time slices revealed that using Poaceae threshold most of sites from 3,000 BP and modern assemblages maintained their classification. Furthermore, combining with other taxa abundance, the number of sites with the same classification became reduced. Using square chord dissimilarity as a quantitative of change indicator, the change prompted by human actions within 500 years of colonization and 3,000 years of natural changes were equivalent. Comparing pre-colonization with surface samples, it is noticed that modern pollen still able to represent important environmental gradients however, their use as modern analogue requires careful treatment.

Oonce fossil pollen are the best indicators to track past vegetation changes, we carried out a parallel analysis of 19 pollen records to unveil the regional vegetation history

allowing inferences about synchronoicity. The accumulated probability distributions show potential synchronous vegetation at 8900, 5900, 2800, 1200 and 550 cal yrs BP. The southern sites experienced more cycles of changes than others, mainly during the late Holocene. The main variations on pollen spectra were captured by both PC and rate of change analysis, that well represented the main periods of change. In general, the early Holocene was a stable period, after the mid-Holocene the changes have started and intensified around 2800 cal yrs BP with other pulses later on agreeing with other researches carried out at other regions of South America indicating connections with continental climate patterns associated to South American monsoon.

The application of unconstrained cluster analysis and pollen abundance threshold to 16 pollen samples from southern andsoutheastern Brazil, revealed that although no large temporal pattern is noticed, the used of appropriate technique can give a broad perspective of vegetation type atspecific time. Moreover, the clear differentiation of vegetation among different times was successfully achived revealing the major variation of vegetation between open and forested landscapes.

Chapter 1

1.1 Introduction

1.1.1 Background: Scientific Investigation of elements of the Atlantic rainforest

The Atlantic rainforest, also known as Mata Atlântica, is one of the largest tropical forests of America. It covered originally an area of approximately 1,227,000 Km^2 between latitudes 3 and 33º S and longitudes 35 and 57º E along Brazilian coast reaching inland regions of 17 Brazilian states and territories of Argentina and Paraguay (Figure 1). Due to its large extension, the Atlantic rainforest encompasses a wide variation of physiographic elements such as different climates and soils associated with a complex geomorphology. Furthermore, it is one of the five most important biodiversity hotspots in the world, defined by high species endemism and species/area ratio harboring more than 8,000 plant and 567 endemic vertebrate species in an area of about 91,340 km² remaining primary vegetation (Myers et al. 2000).

In Brazil, the Atlantic rainforest is defined by federal law number 11,428/2006 which determines that all ecosystems associated to closed evergreen forest, Araucaria forest, deciduous and semi-deciduous forest, mangroves and different grasslands as portrayed on map of IBGE (Instituto Brasileiro de Geografia e Estatística – Brazilian Institute for Geography and Statistics) compose the Atlantic rainforest biome (Figure 1).

Atlantic Rainforest
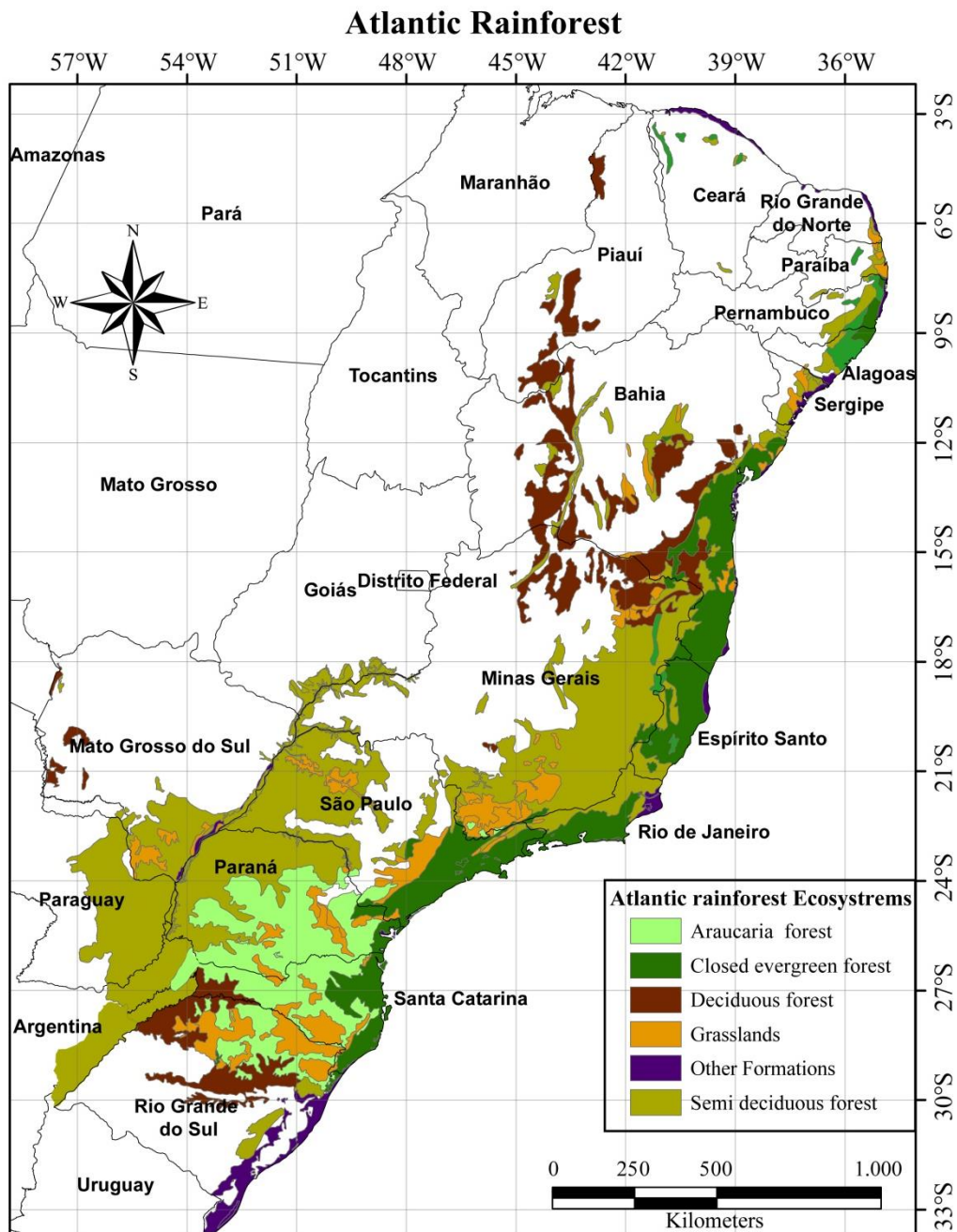
Figure 1: Atlantic rainforest and associated ecosystems

Nevertheless, despite the rich biodiversity, studies revealed that Brazil has one of the highest deforestation rates in the world mainly caused by fire, agriculture, overgrazing and urban expansion (Tollefson 2015). The landscape replacement registered a loss of approximately 24% of the total vegetation net between the years 2000 - 2005 (FAO 2006) mainly caused by human actions.

In fact, the human impacts on Brazilian vegetation has begun when first humans arrived in South America probably at the end of the Pleistocene. They may have altered the vegetation with the use of fire since then, with the addition of agriculture since

about 4000 years ago (Denevan 1992; Dean 1995; Dillehay et al. 2008). Archaeological sites located in the northeast of the Rio Grande do Sul State, documented human occupation since 10000 yrs BP with evidences of local impacts such as accumulation of phosphates and gravels (Dias and Neubauer 2010; Hadler et al. 2012).

Despite the local impacts caused by Amerindians for millennia, the strongest most and the most spread impact and use of the natural resources has started in the 16th century when European settlers arrived and implemented intensive wood extraction, plantation, gold mining and grazing (Dean 1995; De Câmara 2003; Fonseca et al. 2004). Later, during the 20th century, changes of the Brazilian landscapes were intensified as result of population growth, industrialization and urbanization which led to an increase of forest replacement by agriculture which is currently the predominant land use (Young 2005; De Câmara 2003; Tabarelli et al. 2010). These impacts have been being predominantly at Atlantic rainforest region, where nowadays 70% of Brazilian human population lives in and the original vegetation remaining covers only 7% of the past original area (IBGE 2010; SOS Mata Atlântica 2013).

Currently most of the remaining Atlantic rainforest exists in small isolated fragments (Ranta et al., 1998; Tabarelli et al., 2006) while the large preserved forests are usually located at areas of difficult access such as sharp slopes or conservation parks (Silva et al. 2007; Jescke-Pieruscka 2012). These fragments have been used to support studies and conservation strategies for local regions, compromising however, for large areas due the reduced data availability (Ribeiro et al. 2009; Metzeger et al. 2008). In this context, it is important to conduct studies that explore the available vegetation information in order to achieve answers about the ways the environment respond to changes caused by natural or human forcing.

For this reason, Brazilian and German palynologists have been cooperating in palaeocological studies of the Atlantic rainforest biome for more than 2 decades. Since 2012, this work, funded by Deutscher Akademischer Austauschdienst (DAAD), has been developed aiming to reveal the patterns of palaeoecological plant dynamics in response to climate, land use changes through space and time. Therefore, to reach the goals of this study we have integrated several pollen records collected by group of palynologists from the Department of Palynology and Climate Dynamics of the Georg-August University Göttingen, under responsibility of Professor Dr. Hermann Behling, in the project "Development and dynamics of the Atlantic rainforest vegetation during the late Quaternary".

1.2 Geographical features of the study region

1.2.1 Climate

The Atlantic rainforest presents non-zonal characteristics once it stretches over large longitudes and short latitudes. It covers different climates patters and geomorphological structures being considered vegetation on climatic climax due its high correspondence with climate (Coutinho 2006).

The climate of Atlantic rainforest varies between tropical and subtropical. The tropical climate is typically moist and warm with precipitation rates of around 2000 mm/year and temperature ranging from 10 to 26º C with strong seasonal variation. The subtropical climate is characterized by moist conditions and mild temperatures where the annual precipitation varies between 1.250 and 2.000 mm/year being well distributed along the year while annual mean temperatures varies between 14 and 19º C.

Based on climate classification proposed by Köppen (1936), both tropical and subtropical climate of Atlantic rainforest correspond to group A and C, respectively (Figure 2a). Both classifications for the Atlantic rainforest area can be arranged into 4 subcategories each (Af, Am, As and Aw for tropical and Cfa, Cfb, Cwa and Cwb for subtropical).

Regarding the tropical climate divisions, the subgroup Af, which stretches along the southeast and northeast coast, is characterized by high temperatures, average 24 ºC and 27º C during winter and summer (Figures 2c, d), respectively. Its precipitation annual rates can be higher than 3000 mm (Figure 2b), comparable to equatorial regions, without drought period. The climate Am, encompasses seasonal temperatures averages are similar to Af, while the precipitation rates that are smaller with a short drought period. The As climate classification occurs at regions up to 600 km apart from the Atlantic Coast, extending from southeast to northeast at altitudes lower than 950 m a.s.l. It is characterized by winter rainfall rates varying between 700 and 1500 mm/year and dry summer. The climate Aw is marked by a seasonal precipitation variation with wet summer and dry winter. Moreover, due its occurrence at different locations, Aw is identified in wide range of strong E–W humidity gradient between 750and 1800 mm/year, being higher near to coast. This climatic group is characterized by high temperatures, once during the winter average temperature are higher than 18º C and while during the summer temperatures can reach up to 40º C (Antunes 1986).

The subtropical climate, subdivision C, is characterized by cold winter (near to 0º C) and warm summer when mean temperatures are higher than 22º C, moreover during the driest month there are at least 30 mm of precipitation. Moreover, it occurs mainly at southern Brazil, distributed surrounding the Araucaria plateau along the coast, Brazilian board with Argentina and Paraguay and southeast of São Paulo state (Gollfari et al. 1978). The regions classified as Cfb are characterized by annual precipitation rates higher than 1500 mm uniformly distributed during the year. The summer presents mild mean temperatures of 22° C and during the winter the temperatures can reach few negative degrees when frosts are frequent for a period between 10 and 25 days. This climate type predominantly occurs at southern plateaus (Araucaria plateaus) and along crests of mountain chains toward north reaching the hilltops on Espírito Santo state. The climate Cwa is marked by dry winter with temperatures lower than 18º C and warm summer when temperatures are usually higher than 22º C. It occurs mainly at eastern highlands of Minas Gerais state and small areas of Rio de Janeiro and São Paulo (Ventura 1964; Antunes 1986). The climate Cwb, occurs at high altitudes of Canastra, Mantiqueira and Espinhaço mountains in Minas Gerais and at Serra do Órgãos in Rio de Janeiro state (Antunes 1986). Its main climatic features are dry winter and moderate summer when temperature barely overcomes 22º C.
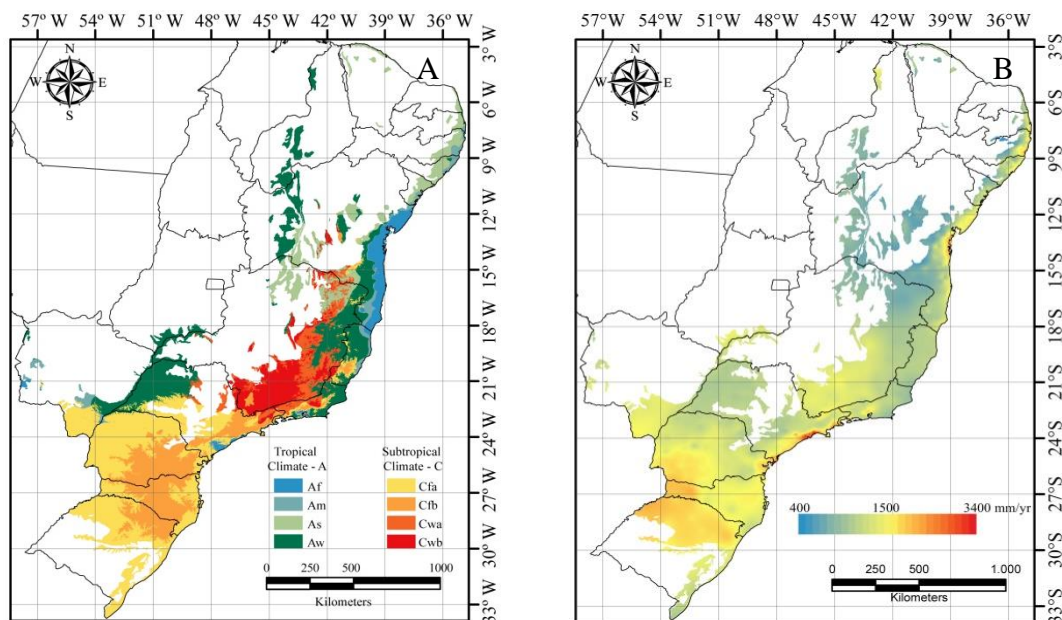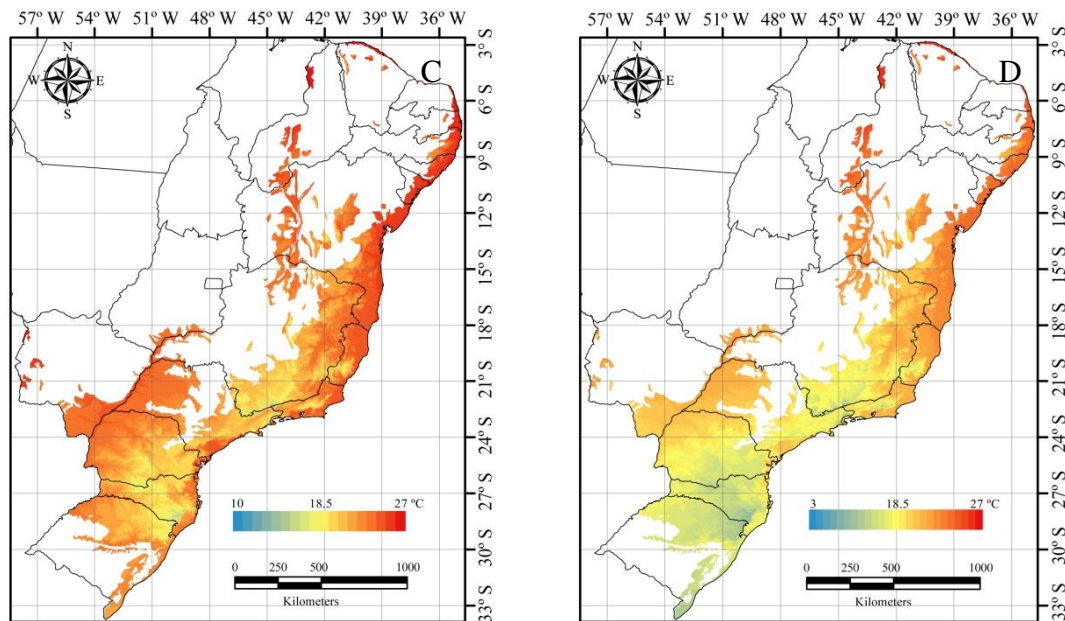
Figure 2: a) Climate classification according to the Köppen criteria of Atlantic rainforest, adapted from Alvarez et al. (2014); b) Total annual precipitation of Atlantic rainforest adapted from Alvarez et al., (2014); c) Summer (December, January and February) mean air temperature of Atlantic rainforest adapted from Alvarez et al, (2013); d) Winter (June, July and August) mean air temperature of Atlantic rainforest adapted from Alvarez et al, (2013).

1.2.2 *Air masses acting in Atlantic rainforest*

The distribution of climatic elements over Atlantic rainforest is determined by interaction of 5 different air masses that act over entire Brazilian territory (Atlantic equatorial mass – AE, equatorial continental – Ec, tropical continental– Tc, tropical atlantic – Ta and polar atlantic mass – Pa) (Figure 3) and cause the seasonal variation in Southern and Southeastern Brazil. These air masses are responsible for either dry or wet conditions as well as high or low temperatures.

The continental tropical mass (Tc) is formed at Central South America, region known as Chaco depression. Chaco depression is a low pressure region which acts attracting seasonal winds. In summer is dominated by moist and warm conditions from Amazonia while during the winter, it is marked by cold and dry condition due to influence of polar air mass.

The air mass Ce is warm and moist due its origin over equatorial region of Amazonia forest. There, occurs an intense solar radiation entire year and concentration of high amounts of moisture that converge from westerlies forming the ITCZ (Intertropical

convergence zone) and that is produced by forest evapotranspiration. During the summer, the Ce is carried out toward southeastern Brazil by low level jets combined with deflection caused by Andes causing both high temperatures and precipitation rates at south and mainly at southeastern Brazil. In the winter, Ce has its influence restricted to northern South America causing non-significant influences on Southeast and South of Brazil.

The Pa is a cold and dry air mass formed at polar zone that shifts toward north passing on Atlantic Ocean at Argentinian Patagonia coast where acquires moisture, thus becoming wet. During the summer, it migrates through south Brazil, where it leaves high amounts of humidity mainly at Araucaria plateaus, until southeastern Brazil where it collides with warm and moist air masses Ce and Ta causing tropical storms with high precipitation rates. In the winter it migration causes precipitation and drought at south and southeast Brazil, respectively reducing the temperatures at both regions.

Tropical Atlantic Mass (Ta) is a warm and moist air mass that originates at tropical south Atlantic Ocean around tropic of Capricorn. It is responsible for high moisture income along the coast in south and southern regions during the summer and during the winter its action are more intense at northeastern Brazil.

In Southeastern and Southern regions occur the intense interaction of the other Ae, Tc and Ta that collide and cause high rainfall rates, tropical storms are also common. During the winter, the 4 air masses become weaker than Atlantic polar (Ap) which advance over Brazilian territory reducing significantly the temperatures main at southern plateaus and southeastern high altitudes.

The Atlantic equatorial mass (Ae) is characterized by moist conditions due to its formation on the Atlantic Ocean. Its position shifts seasonally being during the winter positioned at northern hemisphere bringing moisture to Amazonia forest while in the summer, due to its position southern, the moisture goes mostly to northeast Brazil coast where there is the occurrence of Atlantic rainforest.

During the summer the masses Ce, Ae, Tc and Ta are responsible for high temperatures and precipitation at south and southeast of Brazil. The northeastern coast Ce is responsible for bringing moisture from the equatorial ocean causing elevated precipitation rates.
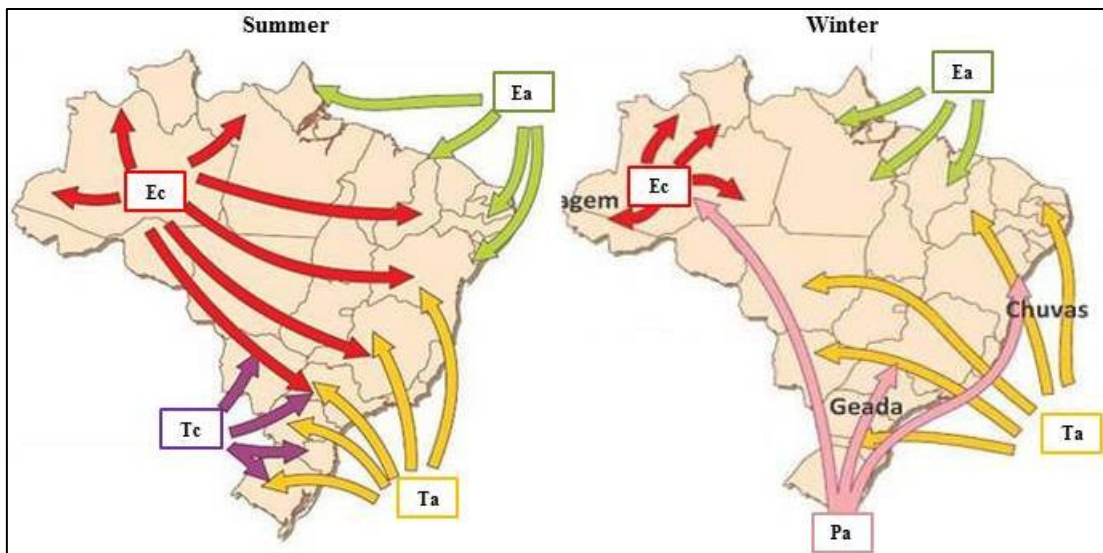
Figure 3: Air masses that act on Brazil causing influences on Atlantic rainforest biome. Adapted from the internet.

1.2.3   *Geomorphology and soils*

The geomorphology of Atlantic rainforest covers diverse elevations (Figure 4) and formations from northeastern tertiary plateaus to basaltic escarpments of mountain chains of southeast and south of Brazil with steep slopes and isolated inselbergs (Ab'Saber 2003). The most common soil types are oxisol and ultisol that are results of years of intense chemical weathering and continuous leaching (Baptista 2009).

The Atlantic rainforest originally extends along narrow lowland portions of northeast, southeast and south coast varying between 10 and 50, being delimited by the ocean at east and cliffs at west. These cliffs are formed by clay and sandstones that spread over hills and high plateaus that in the past were covered by tropical forest and has been successively replaced by cattle grazing, sugar cane, monoculture of *Eucalyptus* and others (Ross 2006).

At lowlands of southern Bahia state, located between the coastal line and inland plateaus, the vegetation acquire orographic features once there are an increase of water availability caused by moisture that comes from the ocean and drops on plateau slopes. The moisture at this region can reach western locations of plateau where due to temperatures lower than in the coast, the vegetation receives the local name of cold forest (Ab'Sáber 2003). From southeast of Bahia toward northeast of Minas Gerais state the Atlantic rainforest spreads throughout the valleys and small patches where there are enough moisture to support the vegetation forms that reach the Serra do Espinhaço

Mountain chain which extents from central Minas Gerais, passing by Bahia reaching Piauí states. At southeast of Minas Gerais the forests are continuous over geomorphological formation known as *Mares de Morros* (Sea of Mountains) connecting with Serra da Mantiqueira in Rio de Janeiro, reaching in both states 600 km toward inland.

From São Paulo state, the Atlantic rainforest spreads over all plateaus toward south where there is the presence of basaltic soil, except in the central part of state where penetration of Cerrado vegetation occurs. From Paraná state the typical high temperatures of tropical climate conditions become weak, but the constant high moisture values associated with rich basaltic soils propitiate the development of Araucaria forest at highlands of southern plateaus of Serra Geral.

The differentiation and occurrence of Atlantic rainforest over large area mainly at southern Brazil, beyond the coastal line, is due to a combination of variables that support different forest types. Along the borders between Brazil, Argentina and Paraguay the fertile soils resulted from basalt decomposition together with moisture brought by air masses, gave ecological support for tropical semi-deciduous forest establishment. At Serra Geral plateau at southern Brazil, the high moisture availability combined with oxisols propitiates the establishment of Araucaria Forest.
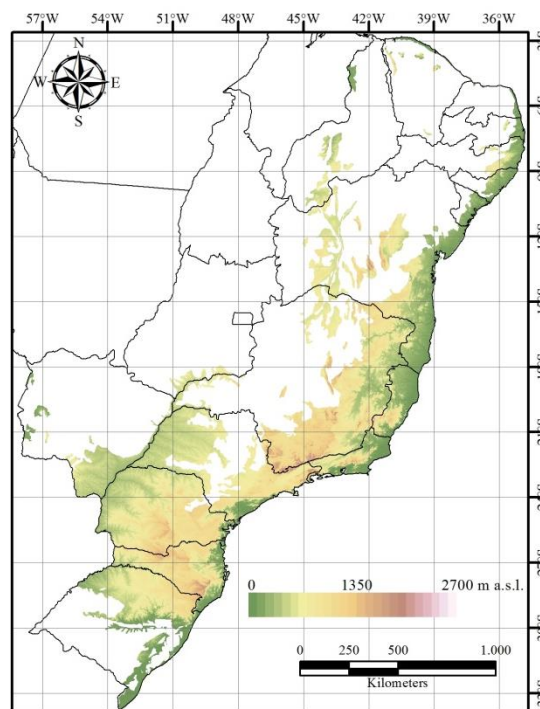
Figure 4: Digital elevation model of Altnatic rainforest adapted from Alvarez et al., (2013).

1.3   Vegetation and physiognomies

In the Atlantic Rainforest occur different vegetation formations that range from grasslands and extensive shrub-land to different tropical forest types in southern and southeastern Brazil including the Misiones Province (Argentina) and southeastern Paraguay (Fig. 1). They are best known as closed evergreen forest, deciduous forest, semi-deciduous forest, grasslands (campos and campos de altitude), Araucaria forest and other formations. These distinct vegetation types cover large areas of the inland and coastal mountains where mainly orographic precipitation and temperatures determine the vegetation composition.

1.3.1   Closed Evergreen Forest

The closed evergreen forest occurs along the tropical coast between 0 and 1,000 m elevation with annual average temperatures of 25°C without drought period with annual rainfall average of 1,500 mm well distributed over the year. These conditions are often connected to orographic precipitation caused by mountain chains (Serra do Mar and Serra da Mantiqueira) that stretch along the coast.

The closed evergreen forest take place at different soil types originated from several rocks such as granites, gneiss and sandstone with volcanic spill (Veloso et al. 1991). Its plant composition is rich in phanerophytes with tall trees that can reach 50 m and lianas, epiphytes, ferns and species such as *Tabebuia cassinoides*, Bignoniaceae, Piperaceae, *Alchornea iricurana*, Euphorbiaceae, *Cecropia sp.*, Moraceae and *Sloanea sp.* (Veloso et al. 1991).

The closed evergreen forest is subdivided into 5 categories, organized following topographical hierarchy reflecting ecotypes variations: Closed evergreen alluvial, closed evergreen lowland, closed evergreen submontane, closed evergreen montane and closed evergreen high montane (Figure 5).

5 - High Montane   4 - Montane   3 - Low Montane   2 - Low Land   1 - Alluvial
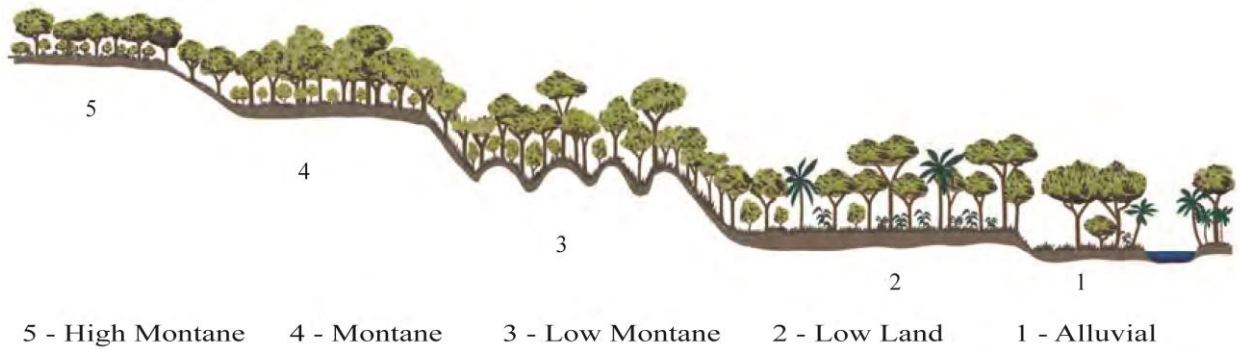
Figure 5: Closed evergreen forest profile (Veloso et al. 1991).

1.3.2   *Araucaria forest*

These distinct vegetation types cover large areas of the inland and coastal mountains where mainly orographic precipitation and temperatures determine the vegetation composition. Araucaria forests encompass 4 different formations (Alluvial, Sub Montane, Montane and High Montane) (Figure 6) that spread along different elevations between 400 and 1,400 m a.s.l. in southern Brazil and in smaller areas at altitudes between 1,400 and 1,800 m in southeastern Brazil. These forests are marked by rainfall rates over 2,000 mm and annual average temperatures around 15 °C. In the summer maximum temperatures can reach 30 °C and the lowest recorded temperature in winter is -10 °C (Nimer 1989; Veloso et al. 1991). The most representative taxa of Araucaria forest are *Araucaria angustifolia*, *Podocarpus lambertii*, *Ilex paraguariensis*, *Mimosa scabrella* and *Drymis brasilensis* (Hueck 1953; Rambo 1956 a, b; Hueck 1966; Higuchi et al. 2012).

4 - High Montane   3 - Montane   2 - SubMontane   1 - Alluvial
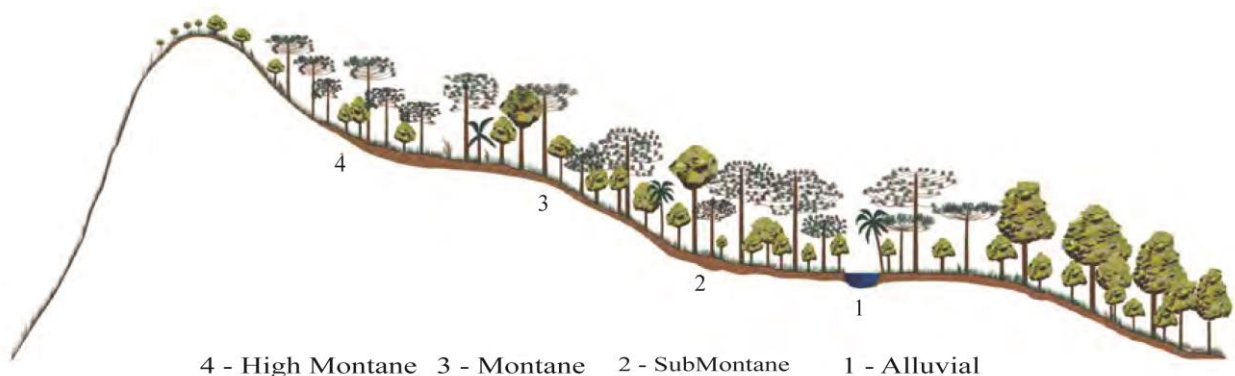
Figure 6: Araucaria forest profile (Veloso et al., 1991)

1.3.3   *Semi Deciduous Forest*

Semi-deciduous forests at tropical zones are characterized by two well defined seasons, one rainy season with rainfall ranging between 1,250 and 2,000 mm, followed by a long drought period when plants loose between 20 and 50% of their leaves. These forests occur discontinuously throughout the Brazilian territory, at subtropical zones there is no drought period, however due to a cold period the vegetation has a physiological rest with loss of leaves.

At tropical regions this vegetation is composed by mesofanerophytes covering dystrophic sand soils. At subtropical regions it is formed by macrophanerophytes that spread over eutrophic basaltic soils. This vegetation is dominated by Amazonian genus such as *Parapiptadenia, Peltophorum*, *Carininiana*, *Lecythis*, *Tabebuia* and *Astronium* (Nimer 1989; Veloso et al. 1991; IBGE 1995).

As observed in other vegetation types, semi deciduous forest has also 4 sub classifications (alluvial, low land, Sub Montane and Montane) that are accessed based on elevation associated with vegetation formation (Figure 7).

4 - Montane   3 - Sub Montane   2 - Low Land   1 - Alluvial
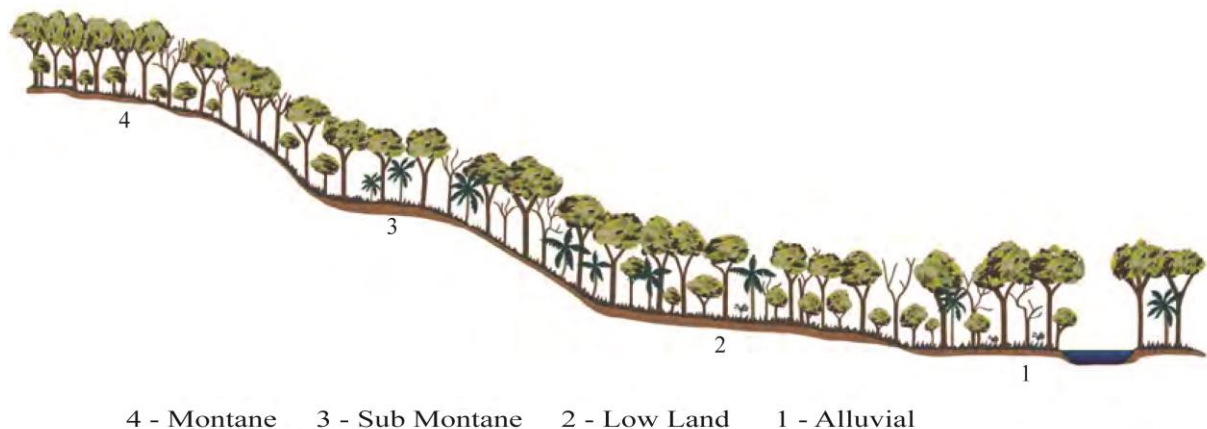
Figure 7: Semi deciduous forest profile (Veloso et al., 1991)

1.3.4 Deciduous Forest

Deciduous forest is an ecosystem present in small patches between different vegetation types, mainly between dry and moist vegetation, mainly characterized by trees that lose 50% of their leaves during stress periods. At tropical regions it occurs at locations characterized by a rainy season followed by a dry period while, at subtropical locations no drought period is identified but due to low temperatures (annual average of 15º C) determines a physiological rest. The deciduous forest is dominated at both

12

regions, tropical and subtropical, by the same genus such as *Peltophorum*, *Anadenanthera*, *Apuleia*. Inside the deciduous forest it identified 4 different formations (Alluvia, low land, Sub Montane and Montane).

4 - Montane   3 - Low Montane   2 - Low Land   1 - Alluvial
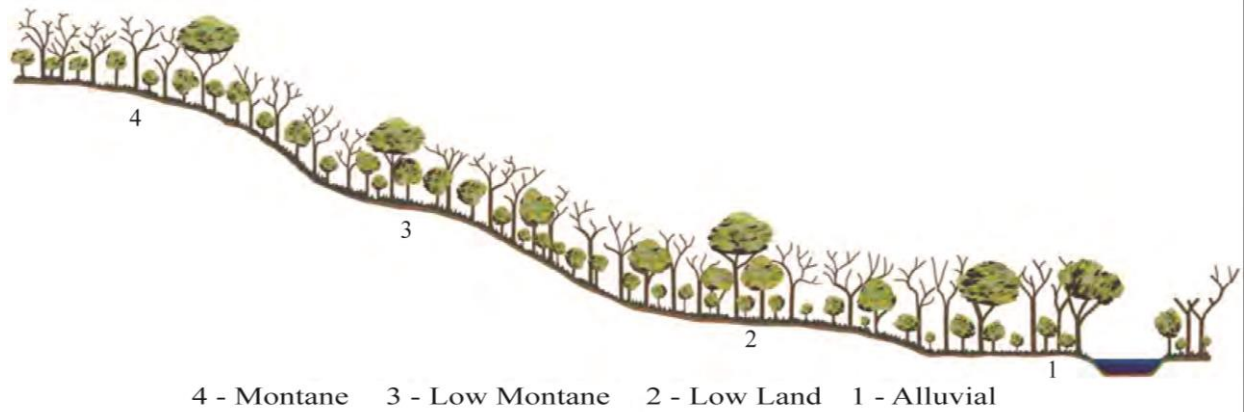
Figure 8: Deciduous forest profile (Veloso et al., 1991)

1.3.5 *Grasslands*

The vegetation type here considered as grasslands encompasses 2 types of open landscapes, campos de altitude and campos (Figures 9 a, b) that occurs mainly at Brazilian southeastern high lands and southern flatlands, respectively. Grasslands formations are characterized by dominance of Poaceae such as *Andropogon lateralis*, *Axonopus siccus*, *Paspalum maculosum* and Asteraceae such as *Acmella bellidioides*, *Baccharis milleflora* and *Calea phyllolepis* (Boldrini 2009; Veloso et al. 1991).

These formations spread over large areas in the lowlands and highlands of southern Brazil, where temperatures can reach 35° C in summer and the presence of frost is common during the winter. The annual rainfall varies between 1,500 and 2,000 mm without drought periods. In southeastern Brazil such vegetation occurs on escarpments, plateaus and mountain tops above 1,500 m at Serra da Mantiqueira and Serra do Mar with an annual precipitation around 1,800 mm and mean temperatures between 16 and 22° C (Nimer 1989; Safford 1999; Overbeck et al. 2007).

Figure 9: A) Campos ecosystem and B) Campos de Altitude ecosystem. Source: ICMBIO.

1.3.6 Other Formations

The other formation groups are formed by 2 different vegetation types, restingas and mangroves that occur mainly at low coastal lands under direct influence of ocean waters (Veloso et al. 1991).

1.3.7 Restingas

Restingas are geopgraphical areas formed by sand deposition along the coast that are caracterized by sparse vegetation at dunes. There are high abundance of genus *Remirea* and *Salicornia* at low beaches. At higher lands, influenced by tides, occur plant types such as *Ipomoea pescaprae* and *Canavalia rosea* and genus *Paspalum* e *Hidrocotyle* while pioneer formations at the highest lands are characterized by genus *Acicarpha, Achyrocline, Polygala, Spartina, Vigna* and others. The specie *Allagoptera arenaria* is the most common, once it occurs from Sergipe to Rio de Janeiro states (Veloso et al. 1991).

At dunes the woody vegetation communities are dominated by nano-phanerophytes and *Schinus terebinthifolius* and *Lythrea brasiliensis* and in lower frequency *Erythroxylum, Myrcia, Eugenia* and others (Veloso et al. 1991).

Figure 10: Restinga ecosystem. Source: ICMBIO

1.3.8   Mangroves

Mangroves are characteized by marine alluvial vegetation formed by microphenrophytes adapted to high salt concentrations. The vegetation is rich of *Rhizophora mangle*, *Avicennia sp.,* which species varies according to latitude, and Laguncularia racemose that establishes at high places. However at some plant communities, one of these plant types are not present, as observed at Maranhão state where it is common mangroves composed only by *Rhizofora* or composed only by *Avicennia,* observed Amapá state. Moreover, the genus is only present at mainlands and salted flatlands of rivers and bays. At some of these flatlands, where ocean waters are dammed the brackfish water are dominated by *Spartina alterniflora* and *Blutaparon portulacoides* (Veloso et al. 1991).
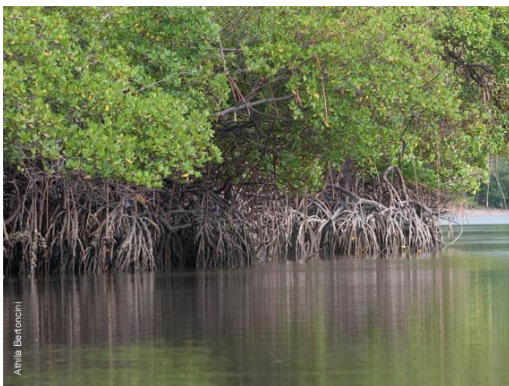
Figure 11: Mangrove ecosystem. Source: MMA (Ministério do Meio Ambiente)

1.4 Palynological and palaeoecological findings at Atlantic rainforest

1.4.1 *Vegetation and climate history of the Atlantic rainforest*
Pleistocene - Holocene (ca. 40,000 yrs BP to ca. 11,500 yrs BP)

A compilation of 14 pollen records from south and southeast Brazil carried out by Behling (2002), revealed that during the Late Glacial these landscapes were dominated by grasses and seasonal dry forest, respectively, as a consequence of likely low temperatures, that may reach -10° C, and long dry seasons.

Palynologycal study at Serra da Boa Vista in Santa Catarina state dated up to 14,000 cal yrs BP showed large dominance of campos taxa with few and sparse Araucaria forest elements mainly preserved in deep valleys until around 10,000 cal yrs BP while other pollen records of Serra do Rio Rastro and Morro da Igreja presented that such of characteristics persisted until around 1,000 cal yrs BP.

Analysis of pollen record of Volta Velha site showed that campos and cold-adapted forests vegetation dominated Atlantic coast of Paraná state, southern Brazil, due to a cooling of about 5 - 7° C for the Last Glacial Maximum (LGM). These characteristics changed in beginning of the Holocene, around 12,300 cal yrs BP when typical tropical forest replaced open glacial grasslands (Behling and Negrelle 2001).

At Rio Grande do Sul state, other pollen records corroborate the large dominance of campos vegetation on southern Brazil landscapes during the glacial extending into the Holocene. The pollen record of Cambará do Sul shows that campos vegetation rich of Poaceae, Asteraceae and Apiaceae with few shrubs dominated the northeast of Rio Grande do Sul state from 42,800 until 10,000 cal yrs BP (Behling et al. 2004). The same vegetation pattern was observed at Serra do Tabuleiro and Rincão das Cabritas (Jeske-Pieruschka and Behling 2011; Jeske-Pieruschka et al. 2012) once graminoids dominated the landscape since 40,000 cal yrs BP until the Late Holocene when Araucaria forest, which taxa has progressively increased since the mid-Holocene, replaced abruptly the open landscape as a consequence of climate shift from dry to wetter conditions.

The late glacial vegetation and climate at southeastern Brazil presented patterns similar to observed South Brazil. The palynologycal records from Botucatu and Catas Altas indicate that between 48,000 and 18,000 yrs BP the landscape was composed basically by campos with scattered trees and shrubs due to dry and cold climate conditions. At Morro Itapeva, near to Campos do Jordão in São Paulo state, Behling

(1997) showed that between 35,000 and 17,000 yrs BP the same pattern occurred. From 17,000 until 10,000 yrs BP few elements of Araucaria and evergreen forests expanded toward mountains, but still rare on landscape and were more abundant at low lands.

1.4.2 Early to Late Holocene (ca. 11,500 yrs BP to ca. 3,000 yrs BP)

The history of Brazilian vegetation reported by several studies that explored pollen, charcoal and others palaeoecological records show with high confidence local abrupt, smooth or stepwise vegetation changes during the Holocene (e.g. Behling et al. 2004, Pessenda et al. 2005 and Enters et al. 2010).

The Holocene in South America has been a period intensely dynamic with strong variation on vegetation cover. Although the human impacts are relevant aspects of South American vegetation history, they are diffuse and can barely be interpreted together for millennia periods, since their large scale influences occurred mainly in the last centuries of human colonization (Jomelli et al. 2008 and Rodrigues et al. 2016). Apart from human impacts, there is an agreement that the climate was the main driver of the changes noticed along the Holocene.

In general, palaeoecological inquires (e.g. Absy et al. 1991, Siffedine et al. 2001 and Cordeiro et al. 2008; Jeske-Pieruschka et al. 2012) sustain that the vegetation in South America during early Holocene was steady due to climate stability, thereafter the most pronounced changes occurred from the mid-Holocene onward with several vegetation turnovers driven mainly by climatic fluctuations

The pollen records of Morro da Igreja (Behling 1995) and Serra da Boa Vista (Behling and Negrelle 1998) showed that large areas of southern Brazil landscapes were dominated by campos vegetation mainly taxa of Poaceae and Asteraceae from the early to mid-Holocene. Such of vegetation may indicate a dry and warm climate condition when drought periods may last for 3 months (Behling 1997).

The second half of the Holocene was very dynamic with broad and progressive vegetation changes. Moreover, pollen taxa from trees and shrubs slowly increase, resulting often in an abrupt expansion between 4000 and 1000 cal yrs BP. Such a pattern was identified by Leonhardt and Lorscheitter (2010), who analyzed a sediment core of southern Brazil and suggested that forest expansion was related to gradual moisture increasing between 6500 and 4000 uncal yrs BP. In addition, at southern

coastal a wet climate since 4000 uncal yrs BP was recorded by Cordeiro and Lorscheitter (1994). The expansion of Araucaria forest is the most pronounced indicator for environment changes, once between 4000 and 3000 cal yrs BP, its main taxa (e.g *Araucaria angustifolia*, *Podocarpus* type, *Ilex* type and other) expanded through the water sources forming diverse gallery forests replacing partially the areas covered by grasses (Behling et al. 2004; Jescke-Pieruschka et al. 2012). Associated to Araucaria forest, the expansion of other populations such as *Myrsine*, *Mimosa scabrella*, Myrtaceae was also noticed (Jescke-Pieruschka and Behling 2011) mainly out of subtropical regions where these taxa are more common.

The analysis of record of Lago Pires at Minas Gerais state, performed by Behling (1995), indicate the presence of cerrado since the beginning of the Holocene until approximately 5500 years BP which may indicate a dry season of up to 6 months. Thereafter, semi-deciduoius forest expanded replacing the Cerrado vegetation. Such of vegetation changes were also observed at Lake Silvana (Rodrigues Filho et al. 2002), Lake Olhos D'água (De Oliveira 1992) and Lake Santa (Parizzi et al.1998) where large areas of Cerrado dominated the landscape in the early and mid Holocene as a consequence of a drought of 5-6 months. For the Atlantic rainforest in southern and southeastern Brazil, Pessenda et al. (2004), analyzing soil organic matter (SOM) and coal sediments of the states of São Paulo and Minas Gerais, identified drier climates during the mid-Holocene when compared to current conditions. Conversely, Mahiques et al. (2009) analyzed a multi-proxy of a sediment core from southeastern Brazilian shelf for the last 8000 years and observed high terrigenous sediment input after 3000 cal yrs BP caused by strong southwesterly winds and high humidity in SE South America linked to development of monsoon system.

At the beginning of the Holocene, the rainforest which developed near the Morro da Itapeva in the State of Rio de Janeiro, reflected a warm and humid climate in its eastern hillside, while at the plateau *Araucaria* and *Podocarpus* were rare, which increased later indicating a progressive increase of moisture in the mountain (Behling 1997a; Behling 2007).

A pollen compilation from southeastern and southern Brazil investigated by Behling (1998) showed that during the early and mid-Holocene the highlands were dominated by Campos vegetation suggesting a warm and dry climate, and during the late Holocene a very humid climate establishes allowing the Araucaria and tropical forests expansion mainly around at 1000 uncal yrs BP. For the same region, Ledru et al.,

(1998) analyzed 11 pollen diagrams covering the last 10000 years and observed three different stages on palaeovegetation historyof southeastern Brazil vegetation. Between 10000 and 7000 yrs BP (12000 – 8000 cal yrs BP), arid conditions was predominant and in consequence the landscapes were mainly dominated by non-arboreal pollen, whereas the arboreal elements were more evident at sites located at valleys. Later, between 7000 and 4000 yrs BP (8000 – 4500 cal yrs BP), in consequence of moister climate, occurred the expansion of swamp vegetation and gallery forests and thereafter, from 4000 yrs BP (4500 cal yrs BP) to the present, the humidity still increasing resulting in a broad vegetation development mainly represented by cerrado, semi-deciduous and Araucaria forest.

At both sites Lake Silvana (Rodigues-Filho et al. 2002) and Caparaó (Veríssimo et al. 2012) a slightly increase on moisture at around 8900 cal yrs BP may have caused the expansion of vegetation typically from cerrado and semi-deciduous forest replacing arid grass composition as evidenced by sharp decrease of Poaceae at Lake Silvana and increasing of *Symplocos* at Caparaó. Later on at Lake Silvana the vegetation composition remained stable while at Caparaó occurred a gradual increase of tropical forest indicators until 2700 cal yrs BP when taxa *Luehea* was the most promeminent reversin after 1200 yrs BP. Similarly, around 8500 cal yrs BP at Serra do Salitre, located deeply in cerrado ecosystem, Ledru (1993) also noticed a progressive expansion of semi-deciduous forest due to strengthening of dry season replacing the Araucaria forest.

1.5   General objectives and outline of the chapters

This thesis is dedicated to disclose past and present vegetation changes and dynamics and its relations with climate and land use changes in the Atlantic rainforest. As this region is one of the most biodiverse hot-spots in the world (Myers et al. 2000) under strong pressure of human impacts, it is crucial to investigate its palaecology in regional perspective providing information for conservation strategies. Therefore, the main goal is to explore past pattern changes to understand the role of climate change and human land-use in configuring the landscape in biodiverse ecosystems. However, to perform an accurate palaeoecological reconstruction using pollen records as source of information, it is important to handle sophisticated palaecologycal analysis techniques

in order to explore vegetation/climate/human actions relationships adequately. Therefore, the thesis comprises two main parts that seek to link past and present ecological questions related to palynological patterns of Atlantic rainforest vegetation:

1.6   Investigation of fossil pollen spectra from different vegetation types across Atlantic rainforest ecosystems

Palaeoecological interpretations based on palynology are centred on uniformitarism principle which uses the knowledge of current modern pollen/vegetation/climate relationship to interpret the fossil pollen records. Furthermore, the use of modern and robust analysis techniques can be a powerful tool to explore and to track vegetation changes trough time finding their main causes. However, to work with modern pollen spectra is not a trivial task once due to high pollen taxa richness combined with large amount of morphological pollen and bad preservation hamper the assingmnt to a specific group of plant species.

Within this thesis, the following research questions concerning vegetation changes based on pollen spectra are adressed:

- How accurate available surface pollen data can represent the natural vegetation patterns? Can surface pollen data be used as modern analogue?
- What are the magnitude of vegetation changes driven by natural forces and human actions?
- Did the natural vegetation changes during the Holocene occured synchronously?
- Did the vegetation changes during the Holocene follow any floristic pattern?
- What type of vegetation dominated regionally the landscapes of Atlantic rainforest?

In **Chapter 2** it is presented the first palaeoecological investigation that we carried out fo this PhD from the Atlantic rainforest region and its extension to Misiones Province in Argentina and to the Brazilian savanna (Cerrado). The pollen analysis wascarried out by handling robust multivariate exploratory technique of three different periods that allowed us to compare the natural vegetation and thus to esrtimate the intensity of natural and human induced changes.

In **Chapter 3** the periods of vegetation changes were collated to explore regional vegetation changes during the Holocene. This study was developed with application of innovative techniques that highlighted at least 5 periods of broad and synchronous vegetation changes mainly driven by South American monsoon.

Chapter 4 consists on exploration of full pollen records by applying vegetation classification methods. In this study it was possible to explore how bins of 500 years of past landscapes were caraterized according to pollen classification using taxa indicators threshold and unconstrained cluster analysis.

In **Chapter 5** the main findings of the first three chapters are synthezised to give a comprehensive conclusion. Further, possible uncertainties are mentioned and recommendations for improvement of methodological aspects are given. Finally, future research questions are being adressed.

1.7   References

Ab'Saber AN (2003). Os domínios de natureza no Brasil: Potencialidades paisagísticas. São Paulo: Ateliê Editorial.

Absy ML, Cleef ALM, Founier M, Martin L, Servant M, Sifeddine A, Silva MF da, Soubies F, Suguio, K, Turcq B, Hammen TVD (1991). Mises en evidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60000 denières annés. Comptes Rendus de l'Académie des Sciences. Série II: 673-678.

Alvarez CA, Stape JL, Sentelhas PC, Gonçalves JL de M, Sparovek G (2014). Köppen's climate classification map for Brazil. Meteorologische Zeitschrift, 22: 711-728.

Alvarez CA, Stape JL, Sentelhas PC, Gonçalves JL de M (2013) Modeling monthly mean air temperature for Brazil. *Theoretical* and *Applied Climatology, 113: 407-427.*

Antunes FZ (1986) Caracterização climática do estado de Minas Gerais: climatologia agrícola. Informe Agropecuário 12:9-13.

Baptista GMM, Meneses PR (2009) Identificação de sesquióxidos de ferro da fração argila de solos tropicais por meio de decomposição espectral linear dos dados do sensor AVNIR-2 do Sistema ALOS, In: Simpósio Brasileiro de Sensoriamento Remoto, 8 p. Natal. Anais. Brasília: UNB, p. 7655- 7662.

Behling H (1995). Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). Vegetation History and Archaeobotany, 4: 127-152.

Behling H (1995) A high resolution Holocene pollen record from Lago do Pires, SE Brazil: Vegetation, climate and fire history. Journal of Paleolimnology, 14:253-268.

Behling H (1997) Late Quaternary vegetation, climate and fire history in the Araucaria forest and campos region from Serra Campos Gerais (Paraná), S Brazil. Review of Palaeobotany and Palynology, 97:109-121.

Behling H (1997) Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology, 129:407- 422.

Behling H (1998) Late Quaternary vegetational and climatic changes in Brazil. Review of Palaeobotany and Palynology. 99:143-156.

Behling H (2002) South and Southeast Brazilian grasslands during Late Quaternary times: a synthesis. Palaeogeography, Palaeoclimatology, Palaeoecology. 177:19-27.

Behling H (2007) Late Quaternary vegetation, fire and climate dynamics of Serra do Araçatuba in the Atlantic coastal mountains of Paraná State, southern Brazil. Vegetation History and Archaeobotany, 16:77-85.

Behling H, Negrelle RB (1998) Tropical Rain Forest and Climate Dynamics of the Atlantic Lowland, Southern Brazil, during the Late Quaternary. Quaternary Research, 56:383–389.

Behling H, Negrelle R (2001) Late Quaternary tropical rain forest and climate dynamics from the Atlantic lowland in southern Brazil. Quaternary Research, 56: 383-389.

Behling H, Pillar VD, Orlóci L, Bauermann SG (2004) Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology. 203: 277-297.

Boldrini II (2009) A flora dos campos do rio grande do sul. In: Pillar V, Müller SC, Souza Castilhos de ZM, Jacques AVA (eds) Campos sulinos-conservação e uso sustentável da biodiversidade. Ministério do Meio Ambiente, Brasília, pp 63–78.

Coutinho LM (2006) O conceito de bioma. Acta botânica brasílica.

Cordeiro RC, Turcq B, Suguio K, Oliveira A da S, Sifeddine A, Volkmer-Ribeiro C (2008) Holocene fires in East Amazonia (Carajás), new evidences chronology and relation with paleoclimate. Global and Planetary Change, 61:49-62

Cordeiro SH, Lorscheitter ML (1994) Palynology of Lagoa dos Patos sediments, Rio Grande do Sul, Brazil. Journal of Paleoclimatology, 10:35-42.

Dean W (1995) With broadax and firebrand. The destruction of the Brazilian Atlantic forest. University of California Press, Berkeley.

De Câmara IG (2003) Brief history of conservation in the Atlantic forest. In: Galindo-Leal C, Câmara IG (eds) The atlantic forest of south America, biodiversity status, threats, and outlook. IDM Composição e Arte, Washington, pp 31–42.

De Oliveira PE (1992) A palynologycal record from of Late Quaternary vegetational and climatic change in Southeastern Brazil. Ph.D. Thesis, The Ohio State University, Columbus, OH, 238 pp.

Denevan WM (1992) Stone vs metal axes: the ambiguity of shifting cultivation in prehistoric Amazonia. J Steward Anthropol Soc, 20:153–165.

Dias AS, Neubauer F (2010) Um estudo contextual da organização tecnológica do sítio RS-C-61: adelair Pilger (Rio Grande do Sul, Brasil). Cazadores Recolectores del Cono Sur. Revista de Arqueol, 4:187–206.

Dillehay TD, Ramírez C, Pino M, Collins MB, Rossen J, Pino-Navarro JD (2008) Monte verde: seaweed, food, medicine, and the peopling of south America. Science, 320:784–786.

Enters D, Behling H, Mayr C, Dupont L, Zolitschka B (2010) Holocene environmental dynamics of south-eastern Brazil recorded in laminated sediments of Lago Aleixo. Journal of Paleolimnology, 44: 265-277.

FAO. 2006. Global Forest Resources Assessment 2005 - Progress towards sustainable forest management. FAO Forestry Paper, FAO, Rome.

Fonseca GAB, Rylands AB, Mittermeier RA (2004) Atlantic Forest. In: Robles RA, Gil P, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da Fonseca GAB (eds) Hotspots revisted. Mexico City, pp 84–88.

Fundação SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais (INPE) (2013) Atlas dos remanescentes florestais da Mata Atlântica período 2011–2012. http://www.sosma.org.br/link/atlas2011-12/atlas_2011-2012_relatorio_tecnico_2013final.pdf. Accessed 10 Mar 2014

Golfari L, Caser RL, Moura VPG (1978) Zoneamento ecológico esquemático para reflorestamento no Brasil (2ª aproximação). Belo Horizonte: Centro de Pesquisa Florestal da Região do Cerrado. (PRODEPEF. Série Técnica, 11).

Hadler P, Dias AS, Bauermann SG (2013) Multidisciplinary studies of Southern Brazil Holocene: archaeological, palynological and paleontological data. Quat Int, 305:119–126

Higuchi P, Da Silva AC, Ferreira TS, Souza ST, Gomes JP, Da Silva KM, Dos Santos KF (2012) Floristic composition and phytogeography of the tree component of Araucaria Forest fragments in southern Brazil. Braz J Bot, 35:145–157.

Hueck K (1953) Distribuição e habitat natural do Pinheiro do Paraná. (Araucaria angustifolia). Boletim da Faculdade de Filosofia,Ciências e Letras, Universidade de São Paulo. Botânica, 10:1–24.

Hueck K (1966) Die wälder südamerikas. Fischer, Stuttgart.

IBGE-Fundação Instituto Brasileiro de Geografia e Estatística (1995) Zoneamento ambiental e agroecológico do Estado de Goiás: região nordeste. Estudos e pesquisas em geociências 3. IBGE/ Divisão de Geociências do Centro-Oeste, Rio de Janeiro

IBGE-Fundação Instituto Brasileiro de Geografia e Estatı´stica (2010) Censo Demográfico 2010. IBGE, Brasília

Jescke-Pieruschka V, Pillar VD, De Oliveira MAT, Behling H (2012). New insights into vegetation, climate and fire history of southern Brazil revealed by a 40,000 year environmental record from the State Park Serra do Tabuleiro. Vegetation History Archaeobotany, 22: 299-314.

Jeske-Pieruschka V, Behling H (2011). Palaeoenvironmental history of the São Francisco de Paula region in southern Brazil during the late Quaternary inferred from the Rincão das Cabritas core. The Holocene, 22: 1251-1562.

Jomelli V, Argollo J, Brunstein D, Favier V, Hoffman G, Ledru MP, Sicart JE (2008). Multiproxy analysis of climate variability for the last millenium in the tropical Andes. In recent improvements in climate research. Nova Science.

Köppen W (1936) Das geographische System der Klimate. – Köppen WR, Geiger (Eds.): Handbuch der Klimatologie.– Gebrüder Bornträger, Berlin, 1:1–44, part C.

Laird KR, Fritz SC, Cumming BF, Grimm EC (1998) Early-Holocene limnological and climatic variability in the northern Great Plains. The Holocene. 8:275–285.

Ledru M-P (1993) Late Quaternary and climatic changes in central Brazil. Quaternary Research. 39:90-98.

Leonhardt A, Lorscheitter ML (2010). The last 25,000 years in the Eastern Plateaus of Southern Brazil according to Alpes de São Francisco record. Journal of South American Earth Sciences, 29:454-463.

Mahiques MM, Coaracy IK, Burone L, Nagai R, Sousa SH de M, Figueira RCL, Silveira ICA de, Bícego MC, Alves DPV, Hammer O (2009) High-resolution Holocene record on the Southern Brazilian shelf: Paleoenvironmental implications. Quaternary Internacional, 206: 52-61.

Metzger JP, Ribeiro MC, Ciocheti G, Tambosi LR (2008). Uso de índices de paisagem para a definição de ações de conservação e restauração da biodiversidade do Estado de São Paulo. In: Rodrigues RR, Joly CA, Brito MCW, Paese A, Metzger JP, Casatti L, Nalon MA, Menezes N, Ivanauskas NM, Bolzani V, Bononi VLR (Eds.), Diretrizes para Conservação e Restauração da Biodiversidade no Estado de São Paulo. Secretaria do Meio Ambiente and Fapesp, São Paulo, pp. 120–127.

Myers NR, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature, 403:853–858.

Nimer E (1989) Climatologia do Brasil. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro

Overbeck GE, Muller SC, Fidelis A et al (2007) Brazil's neglected biome: the South Brazilian Campos. Perspect Plant Ecol Evol Syst, 9:101–116.

Parizzi MG, Salgado-Labouriau ML, Kohler HC (1998) Gênesis and environmental history of Lago Santa: Southeastern Brazil. The Holocene, 8:311-321.

Pessenda LCR, Gouveia SEM, Aravena R, Boulet R, Valencia EPE (2004) Holocene fire and vegetation changes in southeastern Brazil as deduced from fossil charcoal and soil carbon isotopes. Quaternary International, 114:35-43.

Pessenda LCR, Ledru MP, Gouveia SEM, Aravena R, Ribeiro AS, Bendassolli JA, Boulet R (2005) Holocene paleoenvironmental reconstruction in northeastern Brazil inferred from pollen, charcoal and carbon isotope records. The Holocene, 15:814-822.

Ranta P, Brom T, Joensuu E, Mikko S (1998). The fragmented Atlantic forest of Brazil: size, shape and distribution of forest fragments. Biodivers. Conserv., 7(3):385–403, http://dx.doi.org/10.1023/A:1008885813543

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv., 142:1141–53, http://dx.doi.org/10.1016/j.biocon.2009.02.021

Rodrigues-Filho S, Behling H, Irion G, Müller German (2002) Evidence for lake formation as a response to an inferred holocene climatic transition in Brazil. Quat Res., 57:131–137

Rodrigues JM, Behling H, Giesecke T (2016) Differentiating vegetation types from eastern South American ecosystems based on modern and subfossil pollen samples - evaluating modern analogues. Vegetaîon History Archaeobotany.

Ross JLS (2006) Ecogeografia do Brasil: Subsídios para o planejamento ambiental. São Paulo: Oficina de textos.

Safford HD (1999) Brazilian pa´ramos II. Macro- and mesoclimate of the campos de altitude and affinities with high mountain climates of the tropical Andes and Costa Rica. J Biogeogr., 26:739–760

Sifeddine A, Martin L, Turcq B, Volkmer-Robeiro C, Soubies F, Cordeiro RC, Suguio K (2001) Variations of the Amazonian rainforest environment: a sedimentological record covering 30,000 years. Palaeogeography, Palaeoclimatology, Palaeoecology, 3: 221-235.

Silva IA, Batalha MA (2006). Taxonomic distinctness and diversity of a hyper seasonal savanna in central Brazil. Divers. Distrib., 12(6):725–730, http://dx.doi.org/10.1111/j.1472-4642.2006.00264.x

Tabarelli M, Aguiar AV, Grillo A Da S, Santos AMM (2006) Fragmentação e perda de habitats na Mata Atlântica ao norte do Rio São Francisco. In Fragmentos de Mata Atlântica do Nordeste - Biodiversidade, Conservação e suas Bromélias (Siqueira-Filho, C. & Leme, E.M.C., orgs), Rio de Janeiro: Andrea Jakobsson Estúdio. pp. 80–99.

Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA (2010) Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. Biol Conserv 143:2,328–2,340.

Tollefson J (2015) Battle for the Amazon: Brazil has waged a successful war on tropical deforestation, and other countries are trying to follow its lead. But victory remains fragile. Nature, 520:20-23.

Young CEF (2005) Causas socioeconômicas do desmatamento na Mata Atlântica brasileira. In: Galindo-Leal C, Câmara IG (eds) Mata Atlãntica Biodiversidade, Ameaças e Perspectivas. Center for Applied Biodiversity Science at Conservation International, Washington, pp 103–118.

Veloso HP, Rangel Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira adaptada a um sistema universal. IBGE, Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro.

Ventura A (1978) Problemas técnicos da silvicultura paulista. Silvicultura em São Paulo, São Paulo, 3:61-80.

Veríssimo N, Safford HD, Behling H (2012) Holocene vegetation and fire history of the Serra do Caparaó, SE Brazil. The Holocene, 23:1,243–1,250.

Chapter 2

Differentiating vegetation types from eastern South American ecosystems based on modern and subfossil pollen samples: evaluating modern analogues

Jackson Martins Rodrigues, Hermann Behling, Thomas Giesecke

Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Sciences, University of Göttingen, 37073 Göttingen, Germany

Abstract

In south and southeast Brazil land use caused profound changes in natural vegetation and consequently the value of the pollen composition in surface samples as modern analogues. In order to test the capability of modern pollen to represent the natural vegetation, three different time slices of pollen assemblages from 27 sites spread over southern and south-eastern Brazil and the Misiones Province in Argentina were collated. Pollen samples from the pre-colonization period, selected from the moment just before abrupt changes evidenced on pollen diagrams caused by the colonization process throughout the last 500 years, were assumed to represent the natural vegetation conditions once the climate remained stable within this period. Thus we used pre-colonization assemblages to compare with modern samples to explore to what extent surface pollen may be biased in representing the natural vegetation types. Furthermore, to compare man made vegetation change to climate driven vegetation change we also compared to these 20 out of 27 samples dated to 3,000 years BP. Guided by ordination and cluster analysis, but using abundance thresholds of indicator taxa we classified the pollen spectra of pre-colonization time into seven groups consistent with the main vegetation types in the area. Ordination analyses capture the differentiation between grassland and forested vegetation and between tropical and subtropical vegetation types. Comparing the pre-colonization with other time slices we observed that based on Poaceae abundance, 70 and 85 % respectively of sites from 3,000 BP and modern assemblages maintained their classification. Based on finer classification criteria these values decreased to 40 and 52 % respectively. Square chord dissimilarity indicates that colonization impact altered the pollen composition as strongly as 3,000 years of climate induced vegetation change. The surface samples still represent important environmental gradients; however, their use as modern analogue requires careful treatment and eventual exclusion of highly impacted sites.

2.1 Introduction

Pollen analysis is the most widely used tool to obtain information on past changes in vegetation cover and the associated drivers of change such as climate or human land use (Birks et al. 2000; Seppä and Birks 2002). Since the production and dispersal of pollen differs widely between plants, the relationship between pollen proportions and associated vegetation composition is complex. It is therefore necessary to interpret diagrams of fossil pollen profiles to elucidate the character of past vegetation subjectively, based upon modern ecological knowledge. To make the further link between vegetation and climate, quantitative reconstructions of past vegetation and the corresponding climate characteristics from fossil pollen assemblages require the study of odern pollen samples in order to represent a vegetation composition that is mainly determined by the prevailing and measurable climate conditions (Birks 1995; Brewer et al. 2007; Correa-Metrio et al. 2012). Modern analogues represent the conceptually simplest use of modern pollen samples, where it is assumed that surface pollen represents local vegetation composition and consequentially its relationship with the present environment. Thus, following the principle of uniformitarism, information acquired from modern assemblages can be used to explore fossil pollen samples tracking past environmental conditions (Birks and Birks 1980; Birks and Seppä 2004; Willis et al. 2010).

Many qualitative palaeoecological studies have been carried out in and near the Brazilian Atlantic Rainforest Biome (Mata Atlântica), which have individually contributed to the understanding of local vegetation dynamics through time (De Oliveira et al. 2005). However, these studies have not been used for quantitative assessments of past vegetation change and inferences of past climate change rely on interpretations based on ecological observations. Southern and southeastern Brazil harbour highly diverse biomes including the Atlantic Rainforest (Mata Atlântica) which belongs to the global biodiversity hotspots (Myers et al. 2000). Records from Brazil have also rarely been used in synoptic studies and qualitative reconstructions of biomes or vegetation, with the exception of the biome reconstructions for Latin America by Marchant et al. (2009).

The problem of using the present pollen-climate relationship as an analogue for the past lies in the immense changes of vegetation cover as a result of human land use, including the most significant impacts such as logging, grazing, agriculture or urban

expansion, particularly over the last few 100 years (Marchant et al. 2004). Thus the vegetation composition, and therefore pollen composition, may not be predominantly shaped by the prevailing climate, but by the action of humans.

First humans arrived in South America probably at the end of the Pleistocene and may have altered the vegetation through the use of fire since that time, with the addition of agriculture from about 4,000 years ago (Denevan 1992; Dean 1995; Dillehay et al. 2008). Archaeological sites located in the northeast of the Rio Grande do Sul State document human occupation since 10,000 years BP with evidence of local impact such as accumulation of phosphates and gravels (Dias and Neubauer 2010; Hadler et al. 2013).

The strongest impact and use of natural resources began in the 16th century when European settlers arrived and implemented intensive wood extraction, plantation, gold mining and grazing (Dean 1995; De Câmara 2003; Fonseca et al. 2004). Later during the 20th century, changes to the Brazilian landscapes were intensified as a result of population growth, industrialization and urbanization, which led to an increase of forest replacement by agriculture, currently the predominant land use (Young 2005; De Câmara 2003; Tabarelli et al. 2010). Nowadays 70 % of the Brazilian human population lives in the Atlantic Rainforest area. The present-day Atlantic Rainforest vegetation covers only 7 % of the original area that in the past covered approximately 100,000 km2 (IBGE 2010; Fundação SOS Mata Atlântica and INPE 2013). The Brazilian Savannah, called Cerrado, has also been the target of intense vegetation replacement which accounts for 52 % of its original cover (Machado et al. 2008).

A common practice in the replacement of natural landscape is the introduction of exotic plants such as Pinus and Eucalyptus. Pines in particularl are planted extensively in previously open vegetation types like natural grasslands in southern Brazil. Thus while naturally forested areas are converted into pastures, natural grasslands are converted into tree plantations. In this situation it is questionable whether surface pollen spectra have any value in quantitative reconstructions of past vegetation cover or climate change from fossil pollen assemblages.

Considering present vegetation conditions and the need for understanding environmental changes in Brazilian ecosystems and their main drivers, the objectives of this study are (i) to evaluate to what extent pollen assemblages from surface samples can be used to characterize the different vegetation types, and (ii) to what extent this assignment is altered due to human induced vegetation change. To answer these

questions we selected three distinct time slices from 27 pollen diagrams from different regions of the Atlantic Rainforest Biome (Mata Atlântica) and Savannah (Cerrado). Comparing ordination and classification analyses we evaluated the impact of climate change versus the impact of human land use.

2.2   Materials and methods

2.2.1   *Pollen data and study áreas*

The pollen assemblages used for this study were extracted from 27 pollen diagrams obtained from peat bogs and lake cores. The geographical distribution of the 27 sites is shown in Fig. 1 and Table 1. Araucaria forest includes 9 sites (Ara, Misi, SBV, Ciama, Mate, SJdA, CDS, SFP and RdCa), followed by closed evergreen forest with 7 sites (Capa, SDO, SDB, Ita, VoVe, PG and Tabu), grassland with 6 sites (MDI, Capu, SMar, SFA, Sant and StMon), Savannah (Cerrado) and semi-deciduous forest with 3 (Confu, Botu and SCG) and 2 sites (Pires, Silv), respectively.

The different vegetation formations of the 27 sites, which range from grasslands and extensive shrub-land to different tropical forest types in southern and south-eastern Brazil including the Misiones Province (Argentina), are also shown in Fig. 1.
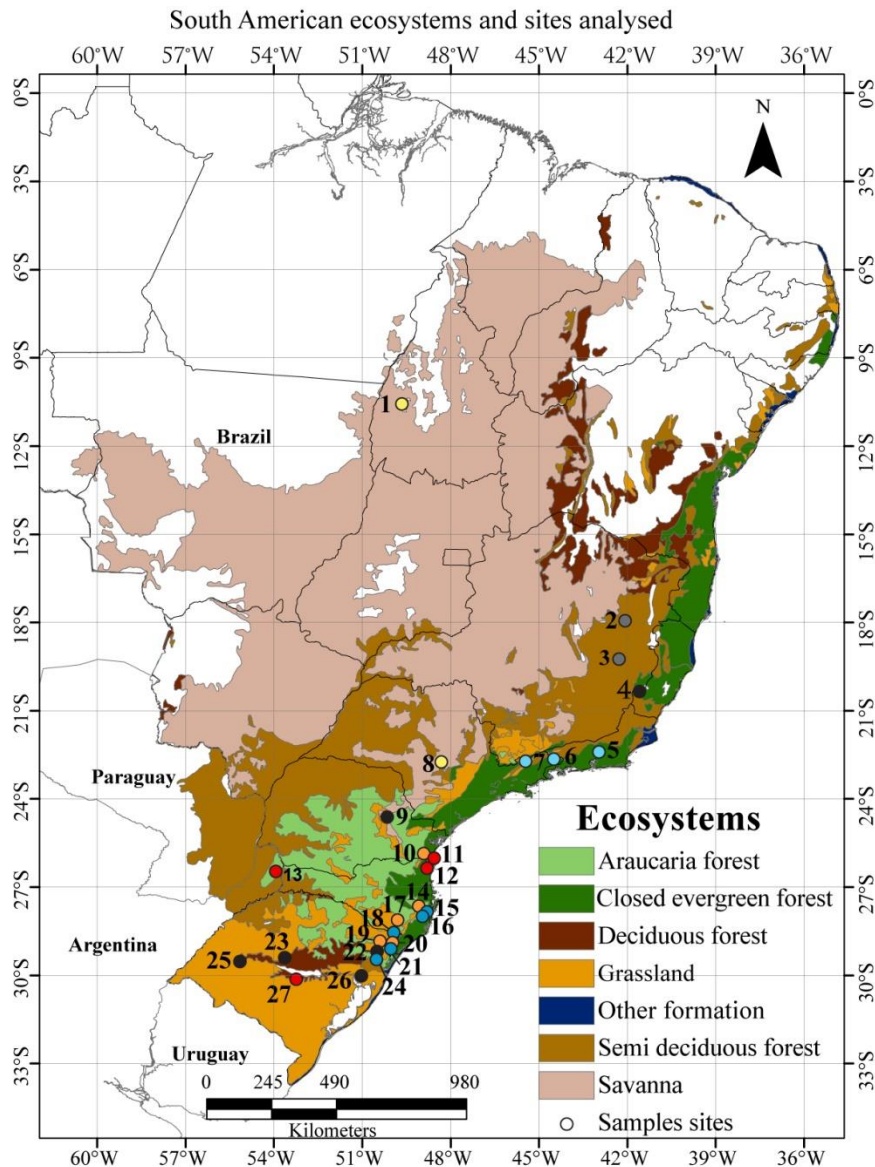
Fig. 1 Study area and ecosystems classification according to RBMA (1999). Circles indicate site location, the colors refer to the classification proposed in this study

These distinct vegetation types cover large areas of the inland and coastal mountains where mainly orographic precipitation and temperatures determine the vegetation composition. Araucaria forests occur in subtropical regions at elevations between 500 and 1,400 m a.s.l. in southern Brazil and in smaller areas at altitudes between 1,400 and 1,800 m in southeastern Brazil. These forests are marked by rainfall rates over 2,000 mm and annual average temperatures around 15 ℃. In the summer maximum temperatures can reach 30 ℃ and the lowest recorded temperature in winter is -10 ℃ (Nimer 1989; Veloso et al. 1991). The most representative taxa of Araucaria forest are Araucaria angustifolia, Podocarpus lambertii, Ilex paraguariensis, Mimosa

scabrella and Drymis brasilensis (Hueck 1953; Rambo 1956a, b; Hueck 1966; Higuchi et al. 2012).

Another important vegetation formation is grassland, Campos, which is characterized by the dominance of Poaceae such as Andropogon lateralis, Axonopus siccus, Paspalum maculosum and Asteraceae such as Acmella bellidioides, Baccharis milleflora and Calea phyllolepis (Boldrini 2009). These formations spread over large areas in the lowlands and highlands of southern Brazil, where temperatures can reach 35 ℃ in summer and the presence of frost is common during the winter. The annual rainfall varies between 1,500 and 2,000 mm without drought periods. In southeastern Brazil such vegetation occurs on escarpments, plateaus and mountain tops above 1,500 m at Serra da Mantiqueira and Serra do Mar with an annual precipitation around 1,800 mm and mean temperatures between 16 and 22 ℃ (Nimer 1989; Safford 1999; Overbeck et al. 2007).

Under tropical conditions, Atlantic coastal forests closed evergreen forest-occur between 0 and 1,000 m elevation with annual average temperatures of 25 ℃ and annual rainfall average of 1,500 mm well distributed over the year. These conditions are often connected to orographic precipitation caused by mountain chains (Serra do Mar and Serra da Mantiqueira) along the coast. The forest composition is rich in lianas, epiphytes and species such as Tabebuia cassinoides, Bignoniaceae, Piperaceae, Alchornea iricurana, Euphorbiaceae, Cecropia sp., Moraceae and Sloanea sp. (Veloso et al. 1991; Sant'Anna Neto and Nery 2005).

Semi-deciduous forests are characterized by two well defined seasons, one rainy season with rainfall ranging between 1,250 and 2,000 mm, followed by a long drought period when plants loose between 20 and 50 % of their leaves. These forests occur discontinuously throughout the Brazilian territory. Common species are Parapiptadenia, Peltophorum, Carininiana, Lecythis, Tabebuia and Astronium (Nimer 1989; Veloso et al. 1991; IBGE 1995).

The Brazilian Savannah-Cerrado is located in central Brazil and is characterized by annual mean temperatures from 20 to 28 ℃, annual rainfall ranging between 800 and 2,000 mm concentrated between months of October and March and a dry season between April and September (Adámoli et al. 1987; Nimer 1989; Ratter et al. 1996). This biome presents a diverse vegetation physiognomy, ranging from dense grassland, usually with a sparse covering of shrubs and small trees, to almost closed woodland with a canopy height of 12–15 m (Werneck et al. 2011). Its main communities include

Caryocar brasiliense, Salvertis convallariodora, Anadanthera peregriana, Curatella americana, Tabebeuia caraiba, Byrsonima sp., Cassia sp. And many others (Veloso et al. 1991; Ratter et al. 2006; Pereira

et al. 2012).

2.2.2   *Data treatment*

All 27 pollen diagrams were harmonized to the same nomenclature and taxonomic level of identification. Pollen counts from plants that were introduced in the last few hundred years like *Eucalyptus* and *Pinus* were removed from the dataset to allow comparisons with older samples. Also Cyperaceae pollen and fern spores were removed since their high abundance is usually due to site specific conditions rather than general vegetation composition.

Numbers	Sites	Codes	Lat	Lon	Elevation	Publications	Classification
1	Lagoa da Confusão	Conf	-10.63	-49.72	180	Behling (2002)	HPPS
2	Lago do Pires	Pires	-17.95	-42.22	390	Behling (1995)	LPSD
3	Lago Silvana	Silv	-19.52	-42.42	230	Rodrigues-Filho et al., (2002)	LPSD
4	Serra do Caparaó	Capa	-20.41	-41.66	2150	Veríssimo et al., (2012)	HPGR
5	Serra dos Órgãos	SDO	-22.46	-43.03	2130	Behling and Safford (2010)	HPST
6	Serra da Bocaina	SDB	-22.71	-44.57	1650	Behling et al., (2007)	HPST
7	Morro do Itapeva	Ita	-22.78	-45.53	2082	Behling (1997)	HPST
8	Botucatú	Botu	-22.8	-48.38	750	Behling et al., (1998)	HPPS
9	Serra dos Campos Gerais	SCG	-24.67	-50.22	1200	Behling (1998)	HPGR
10	Araçatuba	Ara	-25.92	-48.98	1500	Behling (2007)	HPSW
11	Volta Velha	VoVe	-26.07	-48.63	9	Behling et al., (1997)	LPST
12	Poço Grande	PG	-26.42	-48.87	800	Behling (1998)	LPST
13	Misiones	Misi	-26.52	-54	604	Gessert et al., (2011)	LPST
14	Serra da Boa Vista	SBV	-27.7	-49.15	1160	Behling (1998)	HPSW
15	Serra do Tabuleiro	Tabu	-27.78	-48.88	861	Unpublished	LPSF
16	Ciama	Ciama	-27.9	-48.87	860	Jeske-Pieruschka et al., (2012)	LPSF

17	Morro da Igreja	MDI	-28.18	-49.87	1308	Behling (1995)	HPSW
18	Cachoeira do Puma	CaPu	-28.6	-50	1100	Unpublished	LPSF
19	Morro do Matemático	Mate	-28.9	-50.46	837	Unpublished	HPSW
20	São José dos Ausentes	SJdA	-28.94	-50.04	1050	Jeske-Pieruschka et al., (2010)	HPSW
21	Cambará do Sul	CDS	-29.05	-50.1	974	Behling et al., (2004)	LPSF
22	São Francisco de Paula	SFP	-29.4	-50.57	900	Behling et al., (2001)	HPGR
23	São Martinho	SMar	-29.46	-53.7	450	Bauermann et al., (2008)	HPGR
24	Rincão das Cabritas	RdCa	-29.48	-50.57	895	Jeske-Pieruschcka and Behling (2011)	LPSF
25	São Francisco de Assis	SFA	-29.59	-55.22	100	Behling et al., (2005)	HPGR
26	Morro Santana	Sant	-30.08	-51.1	280	Behling et al., (2007)	HPGR
27	Santa Mônica	StMon	-30.34	-53.31	176	Behling et al., (1999)	LPST

Table 1 List of sites analysed and further information. Numbers, sites names, site codes, coordinates, elevation, classified vegetation zone ordered from north to south.

Samples representing the following three time periods were selected from all pollen records:

1. Modern assemblages consisting of the surface samples of each site. They represent the current vegetation conditions ignoring the component of introduced taxa.

2. Pollen assemblages representing the pre-colonization period or the time just before the influence of European settlers can be detected in the pollen diagrams reflecting a strong disturbance of the vegetation. Such disturbances are often characterized by an increase in grasses and decrease in trees and shrubs as a consequence of deforestation in general starting about 300 to 400 years ago. Apart from the appearance of introduced exotic taxa the onset of colonization is usually detectable by abrupt changes of the pollen composition. The pollen diagram of Cambará do Sul (Fig. 2) provides an example showing a marked increase of Poaceae pollen reflecting the opening of the forest by cattle grazing then the colonization and the establishment of the village Cambará do Sul to place near the study site at AD 1780. This is in agreement with the stablished chronology of the record (Behling et al., 2004). Due to the different patterns and

directions of the colonization process there is no specific age assigned for the different sites. The chronologies of upper core parts have large uncertainties and it is therefore difficult to define a specific age for the pre-colonization assemblages. The samples of the pre-colonization period may best represent the natural vegetation with little human disturbance assuming that climate has not changed substantially over the last 300 years.

3. For comparison with the pre-colonization samples, pollen assemblages dating back to 3000 cal yrs BP were also selected. Due to the absence of samples for this time at 7 sites, this group is represented by only 20 samples. This time slice, was used to compare to the pre-colonization assemblages (adjusted to 20 sites for comparability) in order to identify how natural climate fluctuations changed the vegetation in comparison to the changes directed by recent human land use.
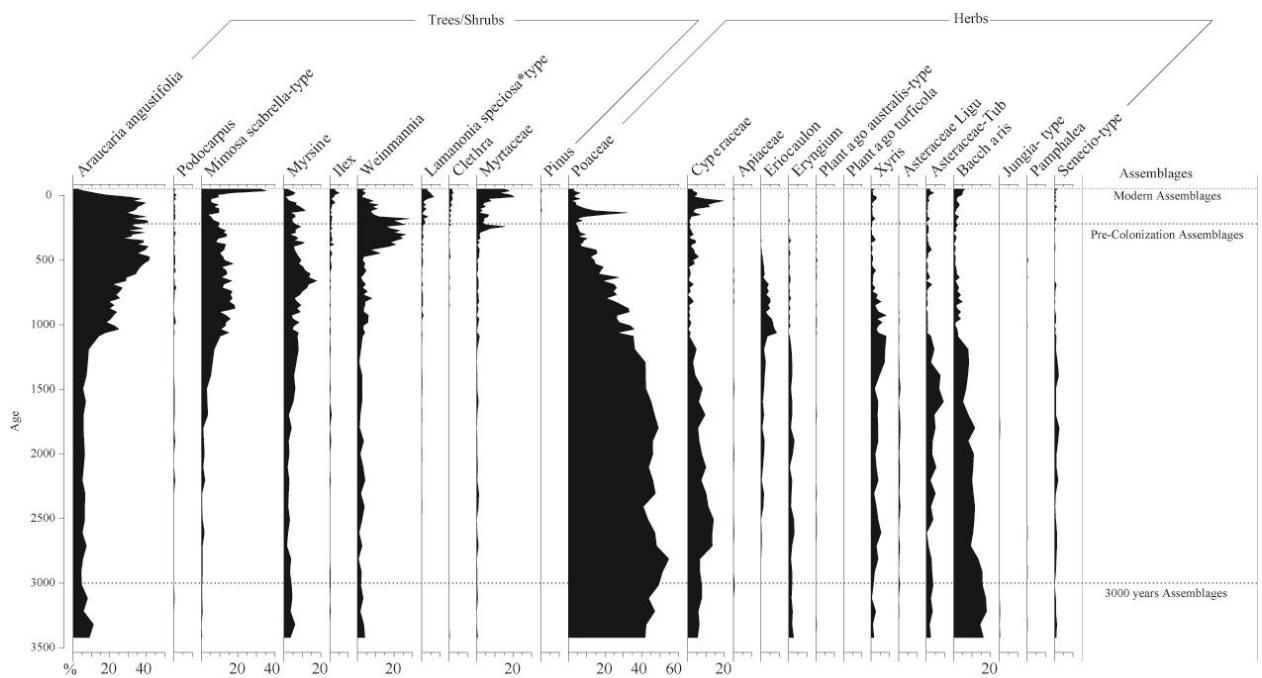
Fig. 2 Pollen diagram from Cambará do Sul with dotted lines showing the three selected time slices: 3,000 BP assemblage, pre-colonization assemblage and modern assemblages

2.2.3 Numerical analysis

Pre-colonization pollen assemblages are assumed as the best representation of potential vegetation cover and were therefore used as reference for further comparisons with other time slices. Thus, pre-colonization samples were treated in two steps in order to select the most significant taxa. The original assemblages contained initially 99 taxa, with many taxa occurring only once. However, the true abundance of single occurrences

per sample cannot be estimated as they may be chance encounters of rare or distant parent species or a chance underrepresentation of a characteristic taxon from the region. Taxa with a single occurrence in all 27 samples were removed and 81 taxa remained. The resulting set was converted into percentages and taxa with less than 0.5 % in samples were removed which resulted in 73 taxa. The same taxa were selected for the other 2 time slices creating comparable datasets. Finally, percentages of the new dataset were recalculated, square root transformed to stabilize the variance and to balance the influences of the most and least abundant taxa (Prentice 1980; Legendre and Birks 2012).

To summarize the latent structure within the entire dataset and explore the palynological composition of the different time slices, we used principal components analysis (PCA) as an ordination technique that captures the environmental gradient of datasets (ter Braak 1995). The change in the composition through time was also investigated by PCA ordinations of the taxon combined dataset linking the samples through time to evaluate the strengths and directions of change. In addition the squared chord distance (SCD) was calculated between adjacent time slices to compare the magnitude of vegetation change. Detrended correspondence analysis (DCA) was performed to identify the environmental gradient for each dataset analysed.

Procrustes analysis was performed in order to compare PCA's of pre-colonization with modern assemblages. Furthermore, its associated sum of squares ($m2$), which varies from 0 (when they are identical) to 1 (indicating completely different ordinations) was assessed to measure their differences (Jackson 1995). Further ordination techniques such as correspondence analysis (CA), nonmetric multidimensional scaling (NMDS) were carried out to explore the data. We applied cluster analysis using Ward's method with squared chord distance and tested for the number of clusters using silhouette width, as well as multivariate classification trees (MCT) and tested biomisation to find an appropriate classification for the sites. Using the insights from unsupervised classifications and ordinations we designed a supervised classification by dividing the dataset in successively smaller groups using indicator taxa. All analysis were performed in R (R Core Team 2012) with the vegan package (Oksannen et al. 2013) and Analogue (Simpson and Oksanen 2007; Simpson 2014).

2.3 Results

2.3.1 Ecosystems classification

The pollen diagrams used in this comparison represent a large region of South America, with the largest distance between sites in the N-S direction of 2200 km, while their proximity to the Atlantic Ocean varies between 3 and 550 km. Despite the resulting huge differences of geographical features, the pollen assemblages compared here are rather similar with few of the more common pollen taxa restricted to particular regions. This is demonstrated by a short gradient of 1,92 sd obtained from the DCA of the pre-colonization assemblages. Also the pollen diagram depicting the 30 most important taxa (Fig. 4) in all samples and time slices is not indicating a strong differentiation between sites or time periods. This is mainly due to the frequent occurrence of pollen types that cannot be identified beyond family level such as Euphorbiaceae, Fabaceae, Moraceae/Urticaceae, Myrtaceae and Poaceae, which often represent different species in different vegetation types and regions.

Automated classification procedures like cluster analysis were not yielding site groupings that made biogeographic sense and we devised therefore a hierarchical supervised classification using the PCA and cluster analysis to split the dataset in two groups and performing the same ordination on the individual groups to obtain further separations. Correspondence analysis (CA) and detrended correspondence analysis (DCA) were also tested but not able to represent the sites in a consistent structure on the biplot, which may be due to the short gradient for which linear approaches are more suitable (ter Braak and Prentice 1988). We then selected abundance thresholds of individual pollen types to separate the groups. This procedure was carried out on pollen spectra of the 27 sites of the pre-colonization assemblages time slice (Fig. 3).
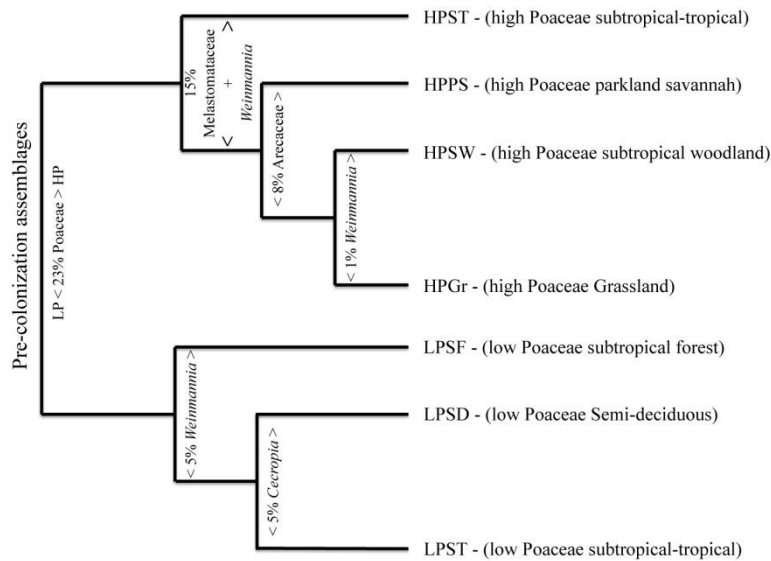
Fig. 3 Dendrogram showing the hierarchical splitting of samples into groups.

Poaceae is one of the most important variable determining the site scores of the PCA in the overall dataset. The cluster analysis using Wards method and squared chord distance separates all sites into two main groups that can be separated based on their Poaceae percentage with a threshold at around 23%. We used this separation to assign samples with Poaceae > 23% to group HP (high Poaceae) with 16 sites and Poaceae < 23% to group LP (low Poaceae) with 11 sites. The first subdivision of group HP was determined by combining Melastomataceae/Combretaceae with *Weinamnnia*, separating 3 sites with values higher than 15%. This subgroup HPST (high Poaceae subtropical-tropical) contains sites in the mountains of southeast Brazil where open areas and tropical rainforest occur together influenced by aspect and elevation. Another subgroup containing 2 sites was separated from the remaining sites in HP based on values of Arecaceae exceeding 8%. These sites (HPPS-high Poaceae parkland savannah) represent a mixture of dry grassland with some tropical trees adapted to a long dry season. The 11 remaining sites were subdivided based on the occurrence of *Weinamnnia* with more or less than 1%. The group of sites with more than 1% *Weinamnnia* pollen (HPSW – high Poaceae subtropical woodland) encompasses 5 sites characteristic of open landscape with some incursions of subtropical trees and shrubs such as taxa of the genus *Ilex* and *Podocarpus*, colonizers such as *Myrsine* or tropical components such as Myrtaceae and Moraceae/Urticaceae. The last 6 sites with *Weinmannia* percentages lower than 1% form the group HPGr (high Poaceae grassland) which is characterized as the most open landscape, where trees and shrubs are rare or absent.

The group LP is characterized by the low presence of herbs and a high diversity of trees and shrubs, varying from typical tropical formations where among others *Cecropia*, Melastomataceae/Combretaceae and Arecaceae are abundant to subtropical forest features rich of *Araucaria angustifolia* and *Weinmannia*. Also within this group *Weinmannia* is a good indicator, in this case for the differentiation between tropical and subtropical vegetation. Using 5% as a threshold, 5 sites with higher *Weinmannia* percentages were split of into a subgroup LPSF (low Poaceae subtropical forest) with a strong subtropical character and *Araucaria angustifolia* as another characteristic pollen type. The remaining 6 sites were further divided into two subcategories of tropical vegetation based on the occurrence of *Cecropia* with a threshold of 5%. The resultant final leaf LPSD (low Poaeceae Semi-deciduous), is represented by 2 sites with high *Cecropia* percentages geographically near each other and characterized by Semi-deciduous vegetation with high values of Euphorbiaceae and Moraceae/Urticaceae. The last cluster (LPST – low Poaceae subtropical-tropical) collects 4 sites representing a transition area between subtropical vegetation with some *Araucaria angustifolia* and tropical elements evidenced by Myrtaceae, Arecaceae and *Myrsine*.
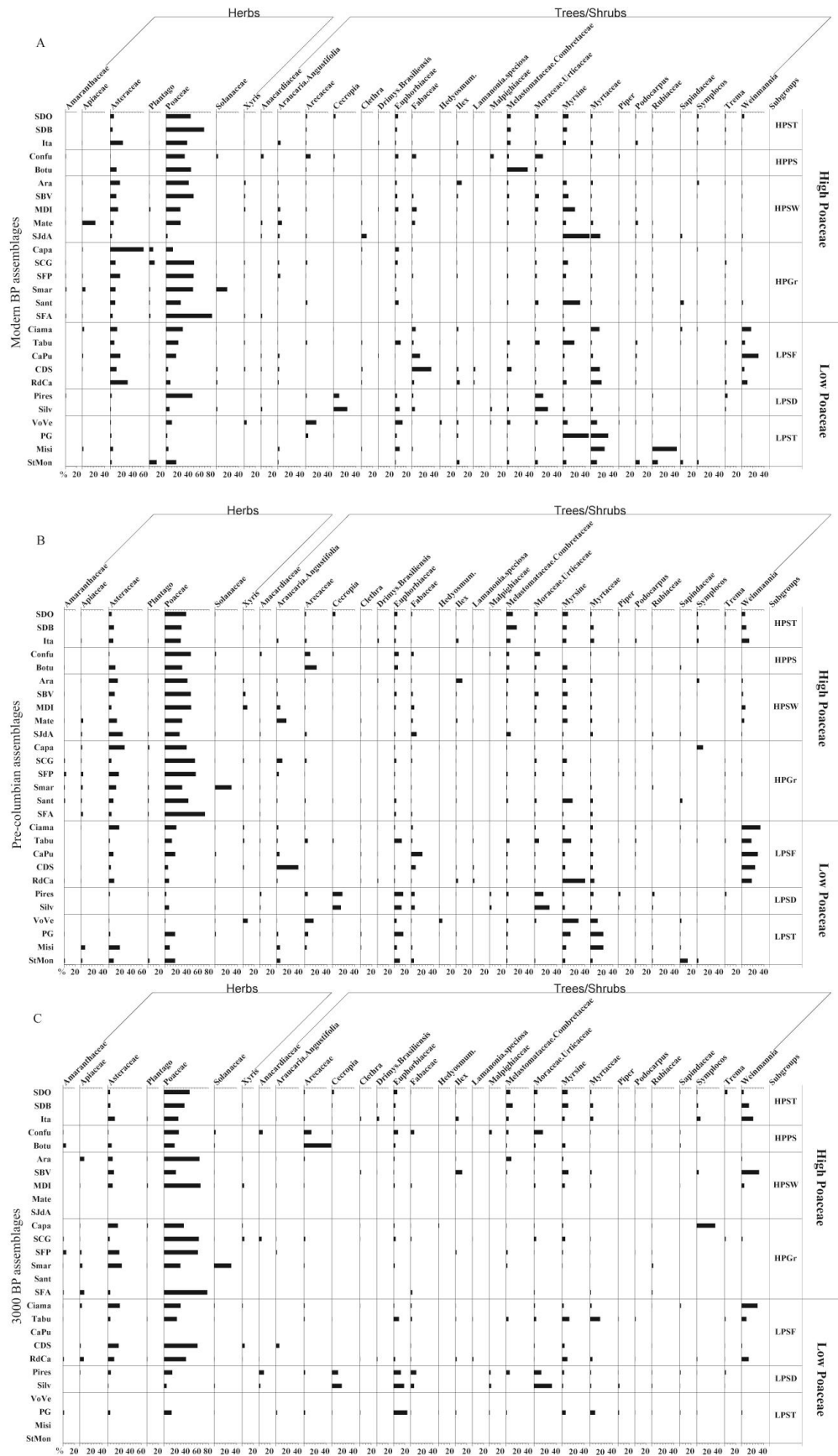
Fig. 4 Pollen diagram of 27 pollen assemblages and respective time slices. A – Modern assemblages; B – Pre-colonization assemblages; C – 3000 BP assemblages.

2.3.2 Ordination of the three different time slices

Of the different ordination methods that were applied to the three datasets PCA was best able to separate the sites into meaningful groups. The PCA biplot of the pre-colonization assemblages showing the first two axes (Fig. 5b) separates the above defined groups. However, the first two axes only explain 20.8% and 18.5% of the variance, respectively, and a total of 5 axes are significant based on the comparison with the broken stick model whereas the gradient lengths based on DCA measures 1.92 sd. The comparably low amount of variance captured by the first PCA axis and the large number of significant axes represents the complexity to the dataset. Even though the PCA biplot of the first two axes separates the species vectors and site scores into three domains: tropical forest rich in Euphorbiaceae, Moraceae/Urticaceae, Arecaceae, *Cecropia*, subtropical woodlands characterized by *Weinmannia*, *Araucaria angustifolia*, *Lamanonia speciosa*, *Podocarpus* and a grasslands dominated by herbs such as Poaceae, Asteraceae and *Plantago* among others. The differentiation between tropical and subtropical vegetation is captured by the first axis, while the second axis separates open vegetation types, which are more common among subtropical sites resulting in a gradient of Poaceae pollen in a diagonal to the two axes, running from the first to the third quadrant. This ordination together with the above described classification adequately describes the differences and similarities between sites including their transitional character where different vegetation types interact.
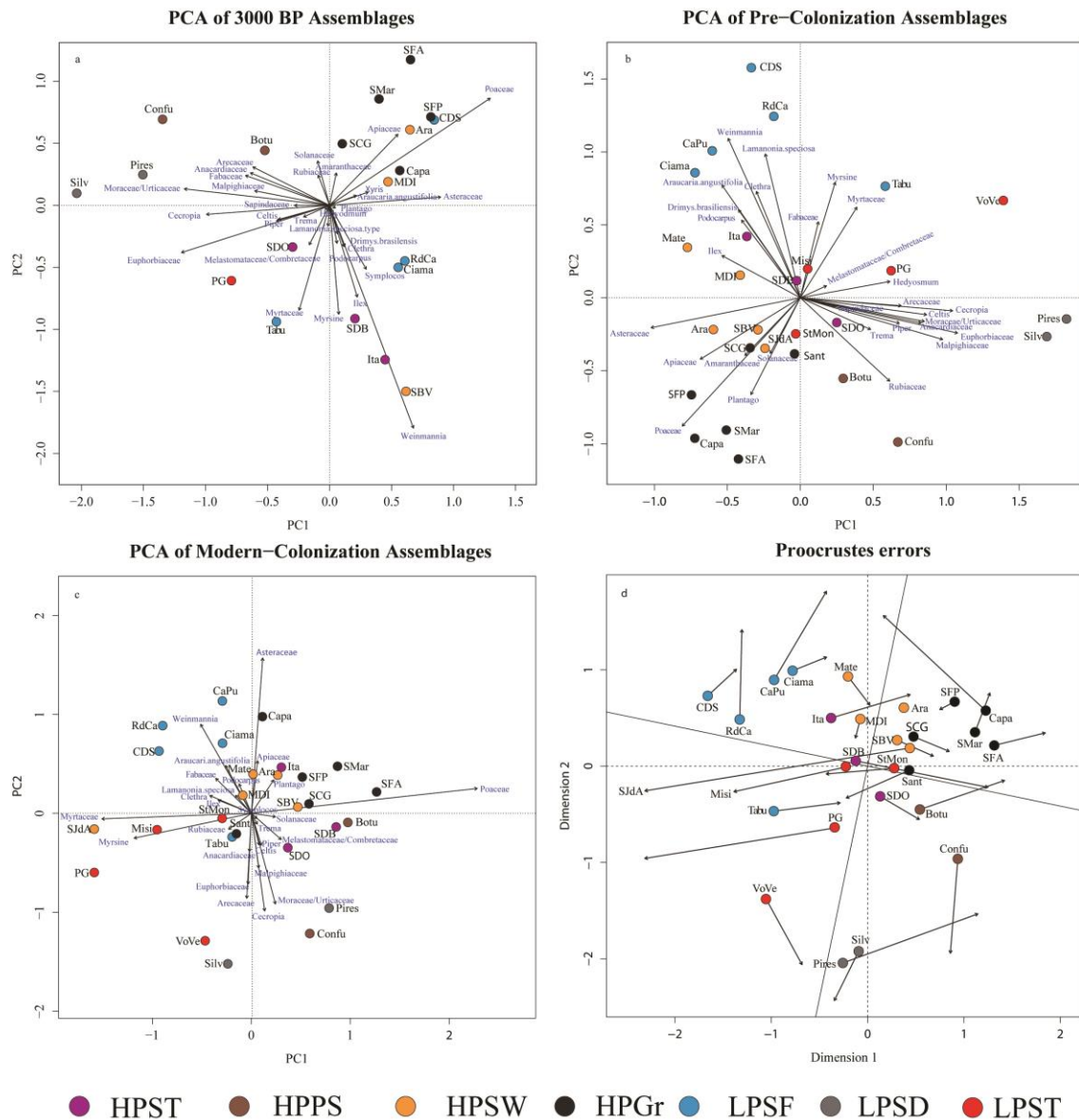
Fig. 5 Principal Components Analysis biplot for the individual time slices 3000 BP (a), pre-colonization assemblages (b), modern assemblages (c) as well as the comparison between the PCAs for pre-colonization and modern assemblages though Procrustes rotation (d). Each site is characterized by a dot colored according to its respective classification - purple for HPST (high Poaceae subtropical-tropical), brown for HPPS (high Poaceae parkland savannah), orange for HPSW (high Poaceae subtropical woodland), black for HPGr (high Poaceae grassland), blue for LPSF (low Poaceae subtropical forest), grey for LPSD (low Poaceae semi-deciduous) and red for LPST (low Poaceae subtropical-tropical). Arrows in the Procrustes plot indicate the direction of change from pre-colonization to modern.

The pattern identified by the classification and PCA of pre-colonization assemblages were used to explore the differences in relation to modern pollen assemblages. However, to put these differences into perspective we choose to compare the pre-colonization samples also to samples dating to approximately 3000 cal years

ago, representing a drier vegetation prior to the main expansion of Araucaria forest. Samples dating to this age are not available from all sites and the overall variance in this reduced set of 20 sites is consequently lower. Only the first two PCA-axes are statistically significant explaining 28.4% and 18.5% of the variance, respectively, having a DCA gradient length of 2.33 sd. The PCA biplot (Fig. 5a) shows the tri-partition of species vectors even more pronounced than for the pre-colonization assemblages. Noteworthy is the changed strength and direction of the vector for *Araucaria angustifolia* that is associated to species characterizing the subtropical moist forests in the pre-colonization PCA, while for the 3000 BP data it plots between Poaceae and Asteraceae, although with little strength. While the orientation is mirrored and rotated compared to the pre-colonization PCA, sample scores show similar orientation to each other and to the species vectors so that the site classification based on the pre-colonization assemblages is a good predictor for their grouping in the biplot. Like in the pre-colonization PCA, the first principal component separates between tropical and subtropical sites and the second axis shows the gradient between open subtropical vegetation and forest dominated sites. Particularly sites classified into HPST, HPPS, HPGr and LPSD have a similar orientation in the PCA-biplot for the samples dating to 3000 years ago and the pre-colonization assemblages. The vegetation around most sites in group LPSF shifted over the last 3000 years from grassland to *Weinmannia* dominated woodland, which is most strongly expressed at Cambará do Sul (CDS). This site was dominated by Poaceae during the late Holocene as evidenced at time slice 3000 years ago highlighted by dashed line (Fig. 2) and thus plots with the group of grassland sites in this PCA-biplot and apart from *Weinmannia* also shows a major increase in *Araucaria angustifolia* towards the present (Fig. 2) (for details see Behling et al. 2004). Sites classified into group HPSW have an intermediate position between grassland and subtropical forest in the pre-colonization PCA, and two of these sites, Morro da Igreja (MDI) and Araçatuba (Ara), plot with the grassland sites and one site, Serra da Boa Vista (SBV), documents a reverse trend in vegetation history with high proportion of *Weinmannia* pollen 3000 years ago and a dominance of Poaceae in pre-colonization assemblages.

The PCA of the core-top samples has 4 significant axes, with the first two accounting for 22.1% and 15.2% of the variance, respectively. The biplot of the first two axes show an orientation different from the species vectors with four main directions compared to the previous tri-partition. Here, the vector for Asteraceae plots

almost perpendicular to Poaceae, indicating that these two pollen types associated to open vegetation are uncorrelated, which changes the overall configuration. Also the angle between Apiaceae and Poaceae has increased compared to the other two PCA-biplots and correlates strongly with Asteraceae, perhaps characterizing natural grasslands, while high Poaceae pollen percentages are now also indicating man made pastures in naturally wooded areas. Consequently most of the sites classified as grasslands based on the pre-colonization pollen composition fall in between the species vectors for Poaceae and Asteraceae. The opposing directions of Asteraceae and tropical pollen types like Euphorbiaceae and Moraceae/Urticaceae is maintained in this ordination, although this gradient is now captured by the second PCA-axis, while it is described by the first axis in the other ordinations. *Cecropia* is a common plant of tropical deforested areas, but it maintains its position between Euphorbiaceae and Moraceae/Urticaceae, perpendicular to Poaceae.

The differences in the sample scores between both PCA configurations, pre-colonization and modern assemblages are visualized by the Procrustes rotation (Fig. 5d). The arrows show the direction of change from the pre-colonization to the modern assemblages. While the shift of individual sites between the two PCA's seems chaotic, sites classified to different groups often move together in the same direction so that the classification of sites that is based on the pre-colonization pollen composition describes the similarities between modern assemblages reasonably well. Clear examples of conjunct changes are noticed for sites of group LPSF that shifted over a similar distance to lower values on the second PCA axis. Another parallel shift is visible for 3 sites of group LPST named Misiones, Santa Mônica and Poço Grande (Misi, StMon and PG, respectively) shifting towards a higher abundance of *Myrsine* and Myrtaceae. Also the sites São José dos Ausentes (SJdA) and Morro Santana (Sant) from groups HPSW and HPGr respectively, shift in the same direction due to increased *Myrsine* pollen percentages, while the forth site Volta Velha (VoVe) in group LPST moves in the opposite direction as the proportion of *Myrsine* pollen is lower in the modern sample. The overall gradient lengths of the modern samples as assessed by DCA is 1.8 sd and thus somewhat shorter than the gradient for the other two sample sets.

The combined PCA analysis of all three time slices provides another perspective of the changes in pollen composition between the tree time slices. In Fig. 6 sites are connected with the arrow pointing to the modern sample. However, the first two axes of this biplot only describe 19.9% and 16.3% of the variance and a total of 9 axes are

significant as suggested by comparison to the broken stick model. As a result the distance between samples in the PCA biplot are not always indicative of the overall difference between samples and we therefore present the squared chord distance (SCD) between samples from the same site in Table 2. The paired SCD of each site, showed that there is no clear pattern in the magnitude of changes. The average of scores shows a similar amount of change for the two comparisons interpreted as mainly climate and human induced changes. The overall gradient length of the combined dataset accessed by DCA is with 2.06 sd, which is shorter than that for the set of samples dating to 3000 years ago. The arrangement of species scores is a combination of the individual PCA plots with a bundle of vectors of mainly tropical pollen types versus Asteraceae pointing in the opposite directions and with Poaceae almost perpendicular and therefore unrelated to it. The forth direction is characterized by *Weinmannia* and Myrtaceae characterizing subtropical woodlands.
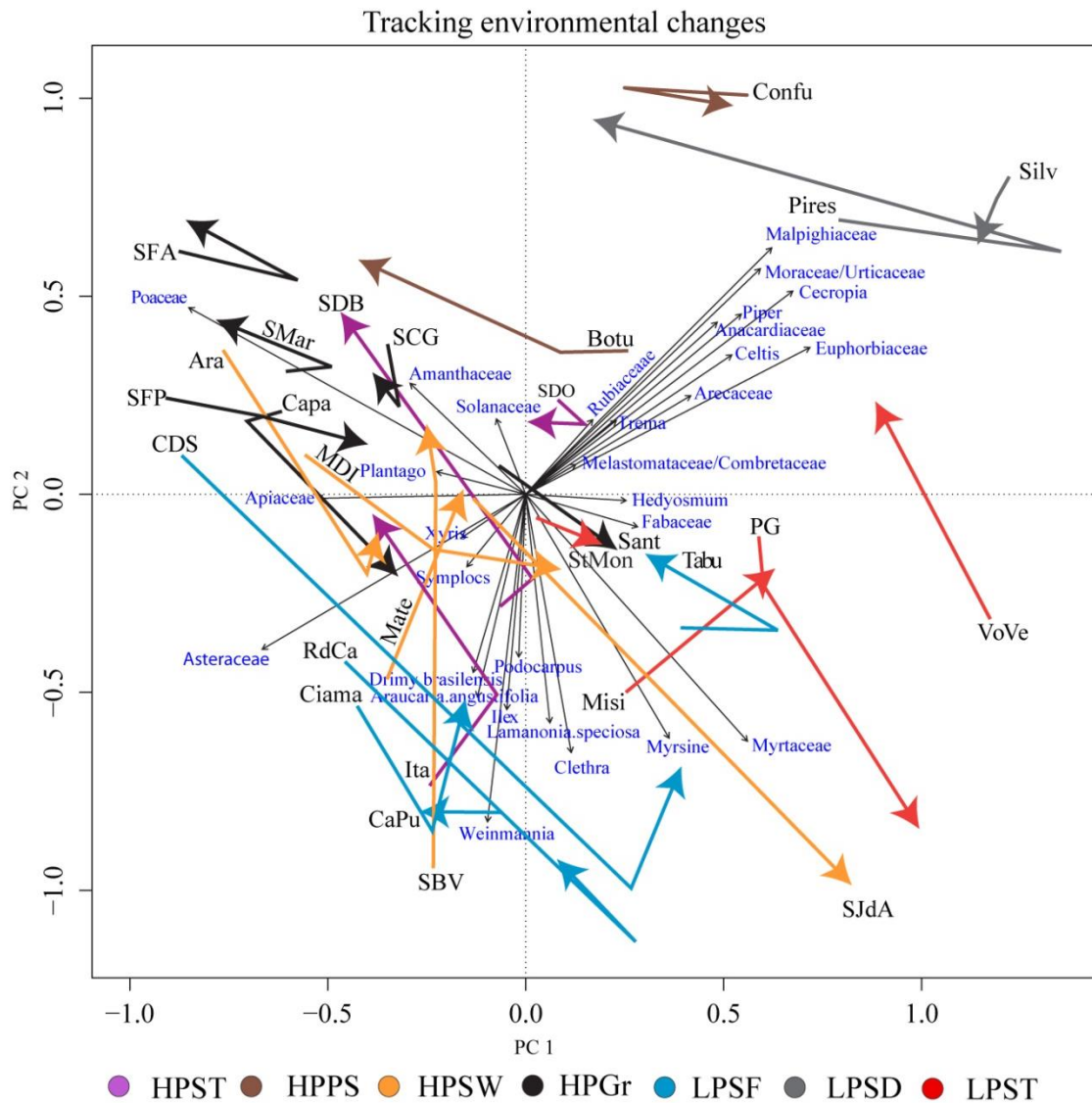
Fig. 6 Principal Components Analysis biplot combining three time slices (3,000 BP assemblages, pre-colonization assemblages and modern assemblages). Each site is represented by a vector linking the time slices and pointing to the modern sample, colours are according to its respective classification

The biplot of the combined PCA shows that the pollen composition of individual sites has shifted markedly between all three time periods and the dissimilarities in Table 2 support the visual impression that the vegetation change over the last few hundred years was often as strong or stronger as within the previous 3000 years. As mentioned before, sites within group LPSF shifted from grassland to *Weinmannia* dominated woodland, and for two of the sites (Cambará do Sul - CDS and Rincão das Cabritas - RdCa) this shift is much larger than the following change to modern conditions. Several other sites however show larger changes between the younger two assemblages. The direction and intensity of change between the pre-colonization and modern assemblages

is not as group specific compared to the changes between the earlier time slices. For many sites the changes in pollen composition over the last few hundred years show a reversed trend to earlier developments indicated by arrows doubling back onto themselves (e.g. São Francisco de Assis - SFA, Serra do Tabuleiro - Tabu, Lago do Pires - Pires, Lagoa da Confusão - Confu, Rincão das Cabritas - RdCa). The largest shift is observed between pre-colonization and modern assemblages for São José dos Ausentes (SJdA) classified to group HPSW, while all other sites in this group show particularly small difference between pre-colonization and modern assemblages and large differences to the samples dating to 3000 years ago.

	Confu	Pires	Silv	Capa	SDO	SDB	Ita	Botu	SCG	Ara
Pre-Colonization – Modern	4.54	10.42	10.06	11.60	8.11	16.46	9.91	19.71	11.37	13.64
3000 BP – Pre-Colonization	4.75	9.66	9.99	7.34	5.61	9.93	7.37	5.98	8.70	16.34
	VoVe	PG	Misi	SBV	Ciama	Tabu	MDI	CaPu	Mate	SJdA
Pre-Colonization – Modern	11.48	9.79	13.86	2.76	12.53	7.17	4.04	7.52	10.01	28.93
3000 BP – Pre-Colonization	-	7.43	-	14.53	11.20	12.35	4.89	-	-	-
	CDS	SFP	Smar	RdCa	Sant	SFA	StMon	Average	SD	
Pre-Colonization – Modern	12.47	8.44	7.30	11.75	9.90	13.14	16.00	10.26	4.08	
3000 BP – Pre-Colonization	18.50	8.30	16.24	13.76	-	9.99	-	10.14	4.01	

Table 2: Squared chord distance scores quantifying the difference between paired time slices of each site and the average of changes between time slices considering all 20 sites that have samples for both time slices together

2.4 Discussion

2.4.1 Ecosystems classification

Our results show that 27 pollen samples of pre-colonization assemblages can be differentiated into 7 ecoregions. The final groupings presented here are based on extensive trials of ordination techniques aiming to identify the inherent structure within the pollen data (Legendre and Legendre 1998). We evaluated the results based on taxonomical and geographical coherence ignoring information of vegetation classifications. Initial unsupervised cluster analysis yielded groups that were not meaningful. A splitting test based on silhouette width, which is used to select an 'appropriate' number of clusters (Rousseeuw 1987; Borcard et al. 2011) showed 2 groups as the best partitioning, separating 3 sites with the strongest tropical signal from the rest. Omitting these 3 tropical samples, the same test suggests a division of data into

3 groups, with one characterized by high proportion of *Weinmannia* pollen, and with the remaining two separated by their proportion of herbaceous pollen. Variations inside each cluster were however not further resolved following this procedure and it was therefore rejected.

Multivariate classification trees (MCTs), a supervised method, was performed to explore how the groups may be defined by threshold abundances of indicative pollen types (Borcard et al. 2011; Simpson and Birks 2012; Felde et al. 2014). Using the lowest cross-validation error to choose the number of splits results in 2 groups based on the abundance of Asteraceae pollen roughly dividing sites with tropical versus subtropical affinities. Decreasing the prediction accuracy, more groups were intentionally selected revealing the indicator value of taxa such *Weinmannia* and Melastomataceae/Combretaceae, which were used in our group divisions. Nevertheless, MCTs resulted in inconsistent grouping of sites and the results were therefore not presented here.

Biomisation is a form of supervised classification (Prentice et al. 1992, 1996), which first amalgamates pollen types into plant functional types (PFT) which are then used to compute affinity scores for different biomes. Marchant et al. (2009) defined PFTs for all of Latin America and showed that using this biomisation procedure, pollen proportions represented the broad biomes from which they were collected. Using this definition of PFTs and biomes we applied the technique to the pre-colonization dataset which resulted in most sites being classified as tropical seasonal forest, two as cool grass shrublands and one as warm temperate rainforest. This classification was unsatisfactory, as it did not distinguish well between tropical and subtropical features. Also, this biomisation protocol treats the biomes Cerrado and Campos as the same environment in consequence of high proportions of Poaceae pollen in samples from both environments. This problem may stem from the simplification of pollen data to functional groups that cause a suppression of the indicator value of particular pollen types. Marchant et al. (2002) applied biomisation to Colombian pollen samples covering an area significantly smaller than ours in both zonal and meridional orientations and achieved a good separation of vegetation types. This may be due to the fact that the Colombian landscape contains much stronger environmental gradients with the Andean mountain chain rising to more than 4000 m a.s.l. and vegetation types ranging from grasslands to rainforests.

The weak results achieved with the above discussed techniques highlight the complexity of our data hampering clear differentiation between sites. One likely cause is the low taxonomic resolution achievable in these highly diverse vegetation and the necessary taxa harmonization contributed to it, reducing several pollen taxa to family level. However, Jantz et al. (2014) analysed pollen samples from a large altitudinal gradient in the Ecuadorian Andes and noticed that the family level is sufficient for linking pollen to vegetation along the strong elevation gradient and on a similarly strong gradient also the biomisation technique showed strong linkage (Marchant et al. 2002). The here presented data contain two major gradients namely the one from open grassland to forest as well as subtropical to tropical vegetation types and most classifications resolve only one of this gradients. Inspired by the MCTs, we used PCA and cluster analysis to find pollen thresholds that would split groups of sites and searched for consecutive splits within the groups. Each step of this procedure explored the variability of individual taxa that would describe the separation of sites based on multivariate techniques. In the resulting classification we used the variability of Poaceae pollen to define the two major groups (HP and LP), which has advantages and problems. Wild grass pollen can generally not be recognized beyond family level. Worldwide the Poaceae family comprises about 12000 species in about 700 genera (Schüler and Behling 2011). In Brazil Longhi-Wagner and Renvoize (2006) list 99 genera and 421 species for the northeast, 91 genera for the Cerrado (Rezende et al. 2008), in south Brazil including neighbor countries Morrone et al. (2008) recognized 203 genera and 1528 species. While Poaceae generally thrive in open habitats and make therefore a good indicator for open vegetation types, Brazil also harbors many species in the tribe Olyreae subfamily Bambusoideae that grow in the understory of tropical and subtropical forests (Longhi-Wagner 2012). In addition some woody vegetation types like the Cerrado contain high proportions of grasses making a clear separation between forest and open vegetation difficult. The difficulty of separating vegetation types based on pollen an in particular including Poaceae was also noticed by other studies (Gosling et al. 2009; Jones et al. 2011). Schüler and Behling (2011) show that different natural grasslands may be separated based on the frequency distribution of measurements of Poaceae pollen grain size and this may also work for separation of savannahs from grasslands. However, such measurements are time consuming and not available for the here investigated samples.

Despite the above discussed problems regarding Poaceae, their abundance differentiated regionally or locally open vegetation types reliably. Nevertheless, this separation was based on pre-colonization samples and here surface samples are not able to distinguish naturally open vegetation types. The best agreement between pollen classification and vegetation classification can be seen for the following three groups: The naturally open vegetation types of Campos and Campos de Altitude are vast open landscapes with few gallery forests and often a mosaic of Araucaria forest (e.g. Boldrini 2009; Coelho et al. 2013) and the pollen samples collected in group HPGr (4 from Campos and 2 from Campos de altitude) reflect this with high proportions of pollen types from herbaceous vegetation and Poaceae (31-72%). Also the samples from the 2 sites classified to group HPPS are characterized by high proportions of Poaceae, although with higher tree pollen proportions compared to the grassland samples and agree thus with the vegetation formation of Cerrado. Oliveira-Filho and Ratter (2002) compare 5 physiognomies of Cerrado vegetation, and according to this classification HPPS falls within the physiognomy classification known as Campo Cerrado, which according to the authors is characterized by a vast extensions of grasses scattered among many different tropical trees and shrubs. Samples from the group LPSD indicate a dense tropical forest with few herbaceous plants (2.4 and 7.4% of Poaceae proportions). This agrees with Semi-deciduous forest, which according to Oliveira-Filho and Ratter (1995) falls between central Brazilian gallery forests and Atlantic and Amazonian forests. This transitional position is documented by the observation of Oliveira-Filho and Fontes (2000), who report that more than 50% of trees are shared between rain and Semi-deciduous forest. The authors analysed the floristic composition of 125 locations spread over southeastern Brazil including localities close to the sits in group LPSD, which they classified as lower and upper montane Semi-deciduous forest.

The other 4 groups separated based on pollen cannot be linked to classical vegetation classification: 5 samples from LPSF are characterized by high proportions of herbaceous pollen with few pollen grains of *Araucaria angustifolia*, rare occurrences of *Podocarpus* and large amount of *Weinmannia*. Such a pollen composition and the geographical position of sites suggest an association with the ecosystem known as Araucaria forest. However such of connection cannot be made because according to Higuchi et al. (2012) the main feature of Araucaria forest is a landscape characterized by *Araucaria angustifolia*, and this distinction is not apparent in the pollen samples, where the presence of *Araucaria angustifolia* pollen is not restricted to samples from

this group. The pollen composition of the last 3 groups indicates transitional positions between the above described ecosystems. The pollen composition of group HPST indicates a mosaic of herbs with rain forest and some elements of subtropical forest. However, the region where the samples were collected are situated in open highlands of the Serra do Mar mountain chain in southeastern Brazil up to 1650 m a.s.l., above the forest canopy, in this way the presence of forest pollen belong to wind pollinated taxa (Behling and Safford 2010). Sites from group HPSW are geographically near each other, at elevations between 800 and 1500 m a.s.l. in southern Brazil within a mosaic of subtropical forest and grassland. The high proportions of Poaceae and herbaceous pollen types in the samples of this group indicate a transition between a grass dominated landscape (HPGr) and subtropical forest (LPSF). The group LPST is characterized by low Poaceae values (0.6-18.5%), and the respective 4 sites come from a range of vegetation types with tropical taxa, from the coast to the hinterland with a strong gradient in altitude. Thus the here adopted classification of sites based on pollen proportions have good agreement with vegetation types and the geography of the sites for the time prior to extensive land-use.

The groups here recognized and their geometry on PCA biplot, document a cross of environmental gradients associated to precipitation differentiating the groups LPSF and HPPS, while temperature differentiates mainly the groups HPGr and HPSW and eventually LPSD. Such patterns were also identified by Oliveira-Filho et al. (2013), in analysis of tree species distribution of southeast and south Brazil. The authors detected a differentiation between tropical and subtropical forest is mainly associated to temperature variation, whereas the contrast between subtropical forest and southern grassland occurs in consequence of different moisture availability. Furthermore, their comparison between environmental parameters and tree distribution could only explain about 30% of the variance, which is similar to the low amount of variance explained by the PCA in the here presented analysis.

2.4.2 *Exploring surface samples reliability*

The two changes different types of in vegetation composition that were selected for comparison have different causes. The oxygen isotope record from speleothems in Botuverá Cave situated within the study region in southern Brazil shows a steady

decline over the course of the Holocene, which is interpreted as increased intensity of the South American monsoon. This increased moisture availability has led to the shift from open vegetation to woodland in the Araucaria region in southern Brazil (Behling et al. 2004). The shift in vegetation composition over the last few hundred years on the other hand is mainly due to human land use. Our comparison shows that based on square chord dissimilarity (Table 2) the compositional changes due to land use are in average as large as the climatically driven change over the last 3000 years.

The impacts caused by European colonizers during the last centuries have been documented by several studies worldwide. In eastern North America the native weed *Ambrosia* spread with the clearance of the forest by settlers. Its high pollen production makes the pollen type an ideal indicator and since the time of clearance is regionally known it can be used as a dating tool (Donders et al. 2008). In naturally open areas of western North America and southern South America introduced herbs such as *Rumex acetosella* document the change in land-use initiated by the arrival of European Settlers (Huber and Markgraf 2003; Anderson and Stillick Jr. 2013). In Brazil, there is no clear indicator of human disturbance available in our pollen samples. Where the first activities practiced by settlers required logging we observe an expansion of native herbs chiefly Poaceae and Asteraceae. The exotic plants on the other hand, although introduced few years after the colonization establishment in Brazil, did not spread or become abundant and thus did not leave a strong signal on pre-colonization assemblages. The strongest impact caused by exotic plants, markedly *Pinus* and *Eucalyptus,* is noticed only on current landscape and its respective modern assemblages. Both were introduced during the 19th century for ornamental purposes and became popular decades later as a source of timber to meet the industries demand. We used the classification of sites designed for the pre-colonization time slice and applied it to the older as well as to the modern assemblages to explore the classification and evaluate the shift in sample composition due to land use. The first differentiation between high and low Poaceae pollen percentages maintained the initial division for the 3000 year old samples in 14 out of 20 cases (70%). For the modern assemblages this division was maintained in 23 out 27 sites (85%). However, with regards to the classification, the direction of change goes in opposit directions with 2 sites São José dos Ausentes (SJdA) and Serra do Caparaó (Capa) changing from high to low Poaceae due to reduction in fire frequency, and at other 2 sites from low to high Poaceae (Ciama and Lago do Pires - Pires) due to intense human deforestation. Despite all changes to the vegetation cover

caused by the colonization during the last centuries, modern pollen samples are still able to differentiate the environmental gradient associated to precipitation, which splits between open or forested landscapes (groups HP and LP, respectively). However, the gradient associated to temperature casing the classification in tropical and subtropical vegetation types is not as well detected in the modern assemblages due to strong decrease in *Weinmannia,* which is the main indicator of subtropical forest.

Nevertheless, the final classification was maintained in 8 out 20 sites for the 3000 BP assemblages and in 14 out 27 sites (52%) for the modern assemblages. The changes noticed in surface samples occurred mainly in sites of the high Poaceae branch such as those the form HPST and HPSW. Moreover, the number of sites classified as HPGr, which represents the most open feature, increased from 6 to 10 due to the increase of Poaceae and decrease of *Weinmannia* abundances. This change can be attributed to landscape clearance by fire and selective logging or grazing. Sites classified on the branch of low Poaceae presented only few changes in their classification.

The ordination documented that the modern assemblages maintained the overall environmental gradient while the classifications shows that modern assemblages may not be able to differentiate well between the different naturally open vegetation types. In this way, the surface samples are useful for studies requiring modern analogues. However, it is important to be careful once some sites suffered strong changes that can mislead interpretations due to altered vegetation and subsequently pollen composition.

2.5   Conclusion

Based on the comparison of modern samples with pre-colonization assemblages and samples dating to 3000 BP, from 27 sites in south and southeast Brazil and Argentinian Misiones province, we made the following observations and conclusions:

- A fully supervised classification of the pollen samples based on the pre-colonization assemblages, resulted in 7 groups that compare well to the established vegetation classification such as Campos, Campos de Altitude, Semi-deciduous forest, Subtropical forest, Parkland Savannah (one physiognomy of Cerrado) and ecotones in between two or more vegetation types. The often used classification of Araucaria forest cannot be unambiguously recognized in pollen assemblages.

- The ordinations of the samples captured two important environmental gradients: One associated to precipitation, which is responsible for splitting between open vegetation with low rainfall and woodland with high precipitation and short drought periods. The second gradient is related to temperature distinguishing between tropical and subtropical vegetation types.

- A quantitative assessment of the differences in pollen composition shows that 3 millennia of climate driven vegetation change are as strong as the compositional change of the last 300 years due to colonization and associated human impacts.

- The modern pollen assemblages reflect the environmental gradient responsible for the distinction between open and forested landscapes. However, the intensive logging and consequent increased abundance of herbs caused strong changes in some sites, making the distinction between tropical and subtropical vegetation types difficult.

- Regardless of land use induced vegetation change modern pollen assemblages capture some aspects of the gradient in natural vegetation and may thus be useful as modern analogues. However, at some location the vegetation is strongly altered with a loss of characteristic species affecting the pollen composition. Therefore, a careful selection of sites for modern analogue analyses is recommended. A dataset of pre-colonization pollen samples is preferable in terms of modern analogues.

Acknowledgements

2.6 References

Adámoli J, Macêdo J, Azevedo LG, Netto JM (1987) Caracterização da região dos Cerrados. In: Goedert WJ (ed) Solos dos Cerrados: tecnologias e estratégias de manejo. Nobel, São Paulo, pp 33-98

Anderson RS, Stillick RD (2010) 800 years of vegetation change, fire and human settlement in the Sierra Nevada of California, USA. The Holocene 23:823–832

Behling H (2002)Late Quaternary vegetation and climate dynamics in southeastern Amazonia inferred from Lagoa da Confusão in Tocantins State, northern Brazil. Amazoniana17:27-39

Behling H (1995) A high resolution Holocene pollen record from Lago do Pires, SE Brazil: Vegetation, climate and fire history. Journal of Paleolimnology 14:253-268

Behling H (1995) Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). Vegetation History and Archaeobotany 4:127-152

Behling H (1997) Late quaternary vegetation, climate and fire history from the tropical mountains region of Morro de Itapeva, SE Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 129:407-422

Behling H (1997) Late Quaternary vegetation, climate and fire history in the Araucaria forest and campos region from Serra Campos Gerais (Paraná), S Brazil. Review of Palaeobotany and Palynology 97: 109-121

Behling H (1998) Late quaternary vegetation and climatic changes in Brazil. Review of Palaeobotany 99:143-156

Behling H (2007) Late Quaternary vegetation, fire and climate dynamics of Serra do Araçatuba in the Atlantic coastal mountains of Paraná State, southern Brazil.*Vegetation History and Archaeobotany* 16:77-85

Behling H, Dupont L, Safford HD, Wefer G (2007) Late quaternary vegetation and climate dynamics in the Serra da Bocaina, southeastern Brazil. Quaternary International 161:22-31

Behling H, Irion G, Müller G (2002) Evidence of lake formation as a response to a inferred Holocene Climatic transition in Brazil. Quaternary Research 57:131-137

Behling H, Lichte M, Miklos AW (1998) Evidence of a forest free landscape under dry and cold climatic conditions during the last glacial maximum in the Botucatú region (São Paulo), Southeastern Brazil. Quaternary of South America and Antarctic Peninsula 11:99-110

Behling H, Negrelle RRB, Colinvaux PA (1997) Modern pollen rain data from the tropical Atlantic rain forest, Reserva Volta Velha, South Brazil. Review of Palaeobotany and Palynology 97:287-299

Behling H, Pillar V, Bauermann SG (2005) Late Quaternary grassland (Campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in western Rio Grande do Sul (southern Brazil). Review of Palaeobotany and Palynology, 133:235-248

Behling H, Pillar VD, Orlóci L, Bauermann SG (2004) Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution

pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 203:277-297

Behling H, Pillar VD, Müller S, Overbeck GE (2007) Late-Holocene fire history in a forest-grassland mosaic in southern Brasil: Implications for conservation. Journal of Vegetation Science 10:81-90

Behling H, Safford HD (2010) Late-glacial and Holocene vegetation, climate and fire dynamics in the Serra dos Órgãos Mountains of Rio de Janeiro State, southeastern Brazil.-Global Change Biology 16:1661-1671

Boldrini II (2009) A flora dos Campos do Rio Grande do Sul. In: Pillar V, Müller SC, Souza Castilhos de ZM, Jacques AVÁ (ed) Campos Sulinos – conservação e uso sustentável da biodiversidade. Ministério do Meio Ambiente, Brasília, pp 63-78

Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer, New York.

Brewer S, Guiot J, Barboni D (2007) Use of pollen as climate proxies. In: Elias SA (ed) Encyclopedia of Quaternary Science. Oxford, pp.2497-2508

Birks HJB (1995) Quantitative palaeoenvironmental reconstructions. In: Maddy D, Brew J S (ed) Statistical Modelling of Quaternary Science Data. Cambrige, pp. 161–254

Birks HH, Battarbee RW, Birks HJB (2000) The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the late glacial and early Holocene – a synthesis. Journal of Paleolimnology 23:91-114

Birks HJB, Birks HH (1980). Quaternary palaeoecology. Edward Arnold, London.

Birks HJB, Seppä H (2004) Pollen-based reconstructions of late-Quaternary climate in Europe – progress, problems, and pitfalls. Acta Palaeobotanica 44:317–334

Boldrini II (2009) Biodiversidade dos Campos do Planalto das Araucárias. Ministério do Meio Ambiente, Brasília

Câmara IG de (2003) Brief history of conservation in the Atlantic forest. In: Galindo-Leal C, Câmara IG (ed) The Atlantic Forest of South America, biodiversity status, threats, and outlook. IDM Composição e Arte, Washington, pp 31–42

Coelho MS, Carneiro MAA, Branco C, Borges RAX, Fernandes GW (2013) Gall-inducing insects from Campos de Altitude, Brazil. Biota Neotropica 13:139-151

Correa-Metrio A, Bush MB, Cabrera KR, Sully S, Brenner M, Hodell DA, Escobar J, Guilderson T (2012) Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. Quaternary Science Reviews 38:63-75

Dean W (1995) With broadax and firebrand. The destruction of the Brazilian Atlantic forest. University of California Press, Berkeley and Los Angeles

Denevan WM (1992) Stone vs metal axes: The ambiguity of shifting cultivation in prehistoric Amazonia. Journal of the Steward Anthropological Society 20:153-165

De Oliveira PE, Behling H, Ledru M-P, Barberi M, Bush M, Salgado-Laboriau ML, Garcia M J, Medeanic S, Barth OM, Barros MA de, Ybert-Scheel R (2005) Paleovegetação e paleoclimas do quaternário do Brasil. In: Souza CRG, Suguio K, Oliveira AMSP, Oliveira PE (ed) Quaternário do Brasil. Holos Editora, Ribeirão Preto, pp 52-74

Dias AS, Neubauer F (2010) Um estudo contextual da organização tecnológica do sítio RS-C-61: Adelair Pilger (Rio Grande do Sul, Brasil). Cazadores Recolectores del Cono Sur. Revista de Arqueología 4:187- 206

Dillehay TD, Ramírez C, Pino M, Collins MB, Rossen J, Pino-Navarro JD (2008) Monte Verde: Seaweed, Food, Medicine, and the Peopling of South America. Science 320:784–786

Donders TH, Gorissen PM, Sangiorgi F, Cremer H, Wagner-Cremer F, McGee V (2008) Three-hundred-year hydrological changes in a subtropical estuary, Rookery Bay (Florida): Human impact versus natural variability. Geochemistry Geophysics Geosystems 9:1-15

Felde VA, Peglar SM, Bjune AE, Grytnes J-A, Birks HJB (2014) The relationship between vegetation composition, vegetation zones and modern pollen assemblages in Setesdal, southern Norway. The Holocene 4:1-17

Fonseca GAB, Rylands AB, Mittermeier RA (2004) Atlantic Forest. In: Robles RA, Gil P, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Fonseca GAB da (ed) Hotspots Revisted. Mexico City, pp 84-88

Fundação SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais (INPE) (2013) Atlas dos remanescentes florestais da Mata Atlântica período 2011-2012. http://www.sosma.org.br/link/atlas2011-12/atlas_2011-2012_relatorio_tecnico_2013final.pdf. Accessed 10 March 2014

Gessert S, Iriarte J, Ríos RC, Behling H (2011) Late Holocene vegetation and environmental dynamics of the Araucaria forest region in Misiones Province, NE Argentina. Review of Palaeobotany and Palynology 166:29-37

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. Review of Palaeobotany and Palynology 153:70-85

Hadler P, Dias AS, Bauermann SG (2013) Multidisciplinary studies of Southern Brazil Holocene: Archaeological, palynological and paleontological data. Quaternary International 305:119-126

Higuchi P, da Silva AC, Ferreira TS, Souza ST, Gomes JP, da Silva KM, dos Santos KF (2012) Floristic composition and phytogeography of the tree component of Araucaria Forest fragments in southern Brazil. Brazilian Journal of Botany 35:145-157

Huber UM, Markgraf V (2003) European impact on fire regimes and vegetation dynamics at the steppe-forest ecotone of southern Patagonia. The Holocene 13:567–579

Hueck K (1953) Distribuição e habitat natural do Pinheiro do Paraná. (*Araucaria angustifolia*). Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Botânica, Botânica 10:1-24

Hueck K (1966) Die Wälder Südamerikas. Fischer, Stuttgart

IBGE - Fundação Instituto Brasileiro de Geografia e Estatística (1995) Zoneamento ambiental e agroecológico do Estado de Goiás: região nordeste. Rio de Janeiro: IBGE/Divisão de Geociências do Centro-Oeste. (Estudos e pesquisas em geociências, n. 3).

IBGE - Fundação Instituto Brasileiro de Geografia e Estatística (2010) Censo Demográfico 2010. IBGE, Brasília

Jackson DA (1995) PROTEST: A PROcrustean Randomization Test of community environment concordance. Ecoscience 2:297-303

Jantz N, Homeier J, Behling H (2014) Representativeness of tree diversity in the modern pollen rain of Andean montane forests. Journal of Vegetation Science 25:481–490

Jeske-Pieruschka V, Behling H (2011) Palaeoenvironmental history of the São Francisco de Paula region in southern Brazil during the late Quaternary inferred from the Rincão das Cabritas core. The Holocene 22:1251-1262

Jeske-Pieruschka V, Pillar VD, De Oliveira MAT, Behling H (2012) New insights into vegetation, climate and fire history of southern Brazil revealed by a 40,000 year environmental record from the State Park Serra do Tabuleiro.Vegetation History and Archaeobotany 22: 299-314

Jones HT, Mayle FE, Pennington RT, Killeen TJ (2011) Characterization of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. Review of Palaeobotany and Palynology 164:223-237

Legendre P, Birks HJB (2012) Clustering and partitioning. In: Birks HJB, Lotter AF, Juggins S, Smol JP (ed) Tracking environmental change using lake sediments: Data Handling and Numerical Techniques. Springer, Dordrecht pp 167-200

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

Longhi-Wagner HM (2012) Poaceae: an overview with reference to Brazil. Rodriguésia 63:89-100

Longhi-Wagner HM, Renvoize SA (2006) Poaceae. In: Barbosa MRV, Sothers C, Mayo S, Gamarra Rojas CFL, Mesquita AC (ed) Checklist das plantas do nordeste brasileiro. Brasília, pp 91-97

Machado ABM, Drummond GM, Paglia AP (2008) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Ministério do Meio Ambiente – MMA, Brasília.

Marchant R, Behling H, Berrio JC, Cleef A, Duivenvoorden J, Hooghiemstra H, Kuhry P, Melief B, Schreve-Brinkman E, Van Geel B, Van der Hammen T, Van Reenen G, Wille M, (2002) Pollen-based biome reconstructions for Colombia at 3000, 6000, 9000, 12 000, 15 000 and 18 000 ^{14}C yr ago: Late Quaternary tropical vegetation dynamics. Journal of Quaternary Science 17:113–129

Marchant R, Boom A, Behling H, Hooghiemstra H, Melief B, Geel BV, Hammen TVd, Wille M (2004) Colombian vegetation at the Last Glacial Maximum: a comparison of model- and pollen-based biome reconstructions. Journal of Quaternary Science 19:721–732

Marchant R, Harrison SP, Hooghiemstra H, Markgraf V, Van Boxel JH, Ager T, Almeida L, Anderson R, Baied C, Behling H, Berrio JC, Burbridge R, Bjorck S, Byrne R, Bush MB, Cleef AM, Duivenvoorden JF, Flenley JR, De Oliveira P, Van Geel B, Graf KJ, Gosling WD, Harbele S, Van Der Hammen T, Hansen BCS, Horn SP, Islebe GA, Kuhry P, Ledru M-P, Mayle FE, Leyden BW, Lozano-Garcia S, Melief ABM, Moreno P, Moar NT, Prieto A, Van Reenen GB, Salgado-Labouriau ML, Schasignbitz F, Schreve-Brinkman EJ, Wille M (2009) Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years. Climate of the Past 5:725–467

Morrone O, Zuloaga FO, Longhi-Wagner HM, Izaguirre P, Beyhaut R, Cialdella AM, Giussiani L, Denham SS, Guglieri A, Boldrini II, Zanin A, Salariato D, De Gennaro D (2008) Poaceae. In: Zuloaga FO, Morrone O, Belgrano MJ (ed) Catálogo de las plantas vasculares del Cono Sur (Argentina, sur de Brasil, Chile, Paraguay y Uruguay). Saint Louis, pp 705-1063

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858

Nimer E (1989) Climatologia do Brasil. Fundacão Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro

Oliveira-Filho A T, Budke JC, Jarenkow JA, Eisenlohr PV, Neves RM (2013) Delving into variation in tree species composition and richness across South American subtropical Atlantic and Pampean forests. Journal of Plant Ecology 2:1–23

Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in south-eastern Brazil, and the influence of climate. Biotropica 32:793–810

Oliveira-Filho AT, Ratter JA (1995) A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. Edinburg Journal Botany 52:141–94

Oliveira-Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the Cerrado Biome. In: Oliveira PS, Marquis RJ(ed) The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna, Columbia University Press, New York pp 91-120

Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Wagner H (2013) Vegan: Community Ecology Package. Verson 2.0-8. http://cran.r-project.org/web/packages/vegan/index.html

Overbeck GE, Muller SC, Fidelis A, Pfadenhauer J, Pillar VD, Blanco CC, Boldrini I, Both R, Forneck ED (2007) Brazil's neglected biome: the South Brazilian Campos. Perspectives in Plant Ecology, Evolution and Systematics 9:101-116

Pereira LR, Cabette HSR, Juen L (2012) Trichoptera as bioindicators of habitat integrity in the Pindaíba river basin, Mato Grosso (Central Brazil). Annales de Limnologie 48:295–302

Prentice IC (1980) Multidimensional scaling as a research tool in Quaternary palynology: A review of theory and methods. Review of Palaeobotany and Palynology 31:71-104

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon, AM (1992) A global biomemodel based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19:117–134

Prentice IC, Guiot J, Huntley B, Jolly D, Cheddadi R (1996) Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. Climate Dynamics 12:185–194.

Rambo B (1956a) A flora fanerogâmica dos Aparados riograndenses. Sellowia 7:235-298

Rambo B (1956b) A Fisionomia do Rio Grande do Sul. Livraria Selbach, Porto Alegre

Ratter JA, Bridgewater S, Atkinson R, Ribeiro JF(1996) Analysis of the floristic composition of the Brazilian cerrado vegetation II: Comparison of the wood vegetation of 98 areas. Edinburgh Journal of Botany 53:153-180

Ratter JA, Bridgewater S, Ribeiro F (2006) Biodiversity patterns of the woody vegetation of the Brazilian Cerrado. In Pennington RT, Lewis GP, Ratter JA (ed) Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation. Taylor & Francis, London, pp 31-65

RBMA – Reserva da Biosfera da Mata Atlântica (1999) Caderno n° 15 Mata Atlântica: Ciência, conservação e políticas. Workshop científico, São Paulo

R Core Team (2012) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org/.

Rezende AV, Walter BMT, Fagg CW, Felfili JM, Silva Júnior MC, Nogueira PE, Mendonça RC, Filgueiras TS (2008) Flora vascular do bioma cerrado. In: Sano SM, Almeida SP, Ribeiro JF (ed) Cerrado: ecologia e flora. Embrapa, Brasília, pp 1028-1059

Rousseew PJ (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. Journal of Computational and Applied Mathematics 20:53-65

Safford HD (1999) Brazilian páramos II. Macro- and mesoclimate of the campos de altitude and affinities with high mountain climates of the tropical Andes and Costa Rica. The Journal of Biogeography 26:739-760

Sant'Anna Neto JL, Nery JT (2005) Variabilidade e mudanças climáticas no Brasil e seus impactos. In: Souza GRG, Suguio K, Oliveira MAS, Oliveira PL (ed) Quaternário do Brasil. Holos Editora, Ribeirão Preto, pp 28–50

Schüler L, Behling H (2011) Poaceae pollen grain size as a tool to distinguish past grasslands in South America: a new methodological approach. Vegetation History and Archeobotany 20:83-96

Sëppa H, Birks HJB (2002) Holocene climate reconstructions from the Fennoscandian tree-line area based on pollen data from Toskaljavri. Quaternary Research 57:191-199

Simpson GL (2007) Analogue Methods in Palaeoecology: Using the analogue Package. Journal of Statistical Software 22:1-29

Simpson GL, Birks HJB (2012) Statistical Learning in Palaeolimnology. In: Birks HJB, Lotter AF, Juggins S, Smol JP (ed) *Tracking Environmental Change Using Lake Sediments: Data Handling and Numerical Techniques.* Springer, Dordrecht, pp 249-327

Simpson GL, Oksanen J (2014) Analogue: Analogue matching and Modern Analogue Technique transfer function models. (R package version 0.16-0). (http://cran.r-project.org/package=analogue).

Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA (2010). Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. Biological Conservation 143:2328–2340

ter Braak CJF (1995) Ordination. In: Jogman RHG, ter Braak CJF, van Tongeren OFR (ed) Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, pp 91-173

ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Advances in ecological research 18:271-317

Veloso HP, Rangel Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira adaptada a um sistema universal. IBGE, Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro

Veríssimo N, Safford HD, Behling H (2012) Holocene vegetation and fire history of the Serra do Caparaó, SE Brazil. The Holocene 23:1243-1250

Young CEF (2005) Causas socioeconômicas do desmatamento na Mata Atlântica brasileira. In: Galindo-Leal C, Câmara IG (ed) Mata Atlântica Biodiversidade, Ameaças e Perspectivas. Center for Applied Biodiversity Science at Conservation International, Washington, pp. 103-118

Werneck FP, Costa GC, Colli GR, Prado DE, Sites JW Jr (2011) Revisiting the Seasonally Dry Tropical Forests historical distribution: new insights based on palaeodistribution modelling and palynological evidence. Global Ecology and Biogeography 20:272–288

Willis KJ, Bailey RM, Bhagwat SA, Birks HJB (2010) Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. Trends in Ecology and Evolution 2:583-591

Chapter 3

Holocene patterns and dynamics of vegetation change in Southern and Southeastern Brazil

Jackson Martins Rodrigues[1,1], Hermann Behling[1,2], Thomas Giesecke[1,3*],

1 – Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for

Plant Sciences, Georg-August-University of Göttingen, Untere Karspüle 2, 37073

Göttingen/Germany

Abstract

At mid to high northern latitudes postglacial vegetation change was determined by the immigration of taxa, soil development and climate change, resulting in regionally consistent patterns of change, some of which were synchronous between regions and caused by abrupt climate change. Based on 19 pollen diagrams from southern and southeastern Brazil we explore if similar synchronicities in vegetation change were also characteristic for the vegetation dynamics in low latitudes, where postglacial immigration of taxa and soil development are less important. We used sequence splitting to detect past vegetation change in the pollen diagrams and computed principal curves and rates of change to visually evaluate the changes in composition and dynamics. Detected vegetation change occurred mostly during the second half of the Holocene with distinct episodes of change. The character of vegetation change is generally consistent with shifts to wetter conditions and agrees with inferred shifts of the South American Monsoon. Speleothems as well as the titanium record from the Cariaco Basin indicate several episodes of rapid shifts in the precipitation regime, which are within the dating uncertainty of the here detected periods of vegetation change (8900, 5900, 2800, 1200 and 550 cal yrs BP). Our results indicate that low latitude vegetation composition follows precession forcing of the hydrology, while change is often triggered and synchronized by rapid climate change much like in high and mid latitudes.

3.1 Introduction

Already 100 years ago Lennart van Post documented that Holocene vegetation change across Southern Scandinavia occurred at more or less the same time at different sites within a region (Von Post, 1918). He assumed that large scale climate change controlled the shifts in vegetation composition so that they were synchronous also between regions where different taxa were involved in the change (Von Post, 1946).

Not all Holocene regional vegetation changes turned out to be synchronous (Smith and Pilcher, 1973) while particularly in northwestern and central Europe some parallel and synchronous changes can be observed (Giesecke et al., 2011). Especially the climate forcing of the 8.2 event finds its representation in many pollen diagrams on both sides of the Atlantic (e.g., Shuman et al., 2002; Seppä et al., 2007; Tinner and Lotter, 2001).

At mid to high latitudes glacial-interglacial cycles caused continental scale shifts in biomes and the resetting of soil developments though glacial drift, cryoturbation and loess deposition. Postglacial colonization of trees, soil development and climate change caused major shifts in vegetation composition with glacial interglacial cycles (e.g. Birks and Birks, 2004; Cheddadi et al., 2005), often leading to parallel developments in vegetation change over large regions. The vegetation at low latitudes was less severely affected by glacial-interglacial cycles with comparably small change in biome distributions, apart from vertical movements of vegetation belts in the mountains (Marchant et al., 2009). Although enhanced dust deposition during the last glacial maximum (LGM) may have had a fertilizing effect it did not reset soil formation in the low latitudes in the same way as in high latitudes. In addition to temperature changes associated to glacial interglacial cycles, low latitudes were influenced by changes in precipitation following the changes in solar insulation, mainly determined by the precession component of Earth's orbital variability. The importance of precession forcing for hydrology in low latitudes has been demonstrated using climate models (Clement et al., 2004) and documented in lakes sediments (Verschuren et al., 2009) and speleothems (Wang et al., 2007).

Changes in climate driven by Earth's orbital variation are gradual and would not necessarily lead to synchronous shifts in vegetation composition in ecosystems consisting of long-lived woody species. Climatic excursions, or rapid shifts in ocean or atmosphere circulation are necessary to break the inertia of woody plant communities and cause synchronous changes over large regions. These causalities have been interpreted for Europe and North America where synchronous and parallel changes in vegetation composition have been documented (Giesecke et al., 2011; Grimm and Jacobson, 1992; Shuman et al., 2002), but little is known whether regionally synchronous shifts in vegetation composition have characterized vegetation dynamics in species diverse low latitude ecosystems.

South America stretches over both hemispheres from the low to the high latitudes so that the different beats of orbital cyclicity and their combinations may have

influenced vegetation dynamics in different regions (Fontana et al., 2012). A marked and rapid shift in vegetation composition in the low latitudes of South America is the expansion of the Araucaria forest in southern Brazil. This southern region of the Atlantic Rainforest (Mata Atlântica) in eastern Brazil was characterized by species rich campos (grasslands) during the last glacial which changed little in composition until the mid-Holocene (Behling et al., 2004; Pieruschka et al., 2012). The expansion of the forest is interpreted to result from increased moisture availability (Behling, 2002) and this interpretation is generally consistent with the oxygen isotope record from Botuverá Cave (Wang et al., 2006). However, while the isotope data indicate a general increase through the Holocene pollen data document a rapid change (Behling et al., 2007b). The rapid vegetation change may be a threshold response of the vegetation or the result of a fast shift in precipitation regime, which may have been short lived or sustained. In the cased of a fast shift in climate, synchronous changes in vegetation composition may be expected over a larger region, while a threshold response should find expressions in diachronous changes.

The aim of this manuscript is to explore the regional dynamics of vegetation change in southern and southeastern Brazil and to evaluate whether rapid shifts in climate may have caused synchronous patterns in low latitude vegetation dynamics.

3.2   Study area

The study area comprises tropical and subtropical ecosystems of southeastern and southern Brazil between approximately 18° and 30° southern latitude (Fig. 1). A total of 19 pollen records covering different periods of the Holocene (16 extending over 10000 years and more, 2 covering at least 3000 and 1 covering at least 6000 years) are used from this region mainly derived from small wetlands and lakes representing vegetation types such as grassland, shrublands, tropical and subtropical forest types (Fig. 1, Table 1).
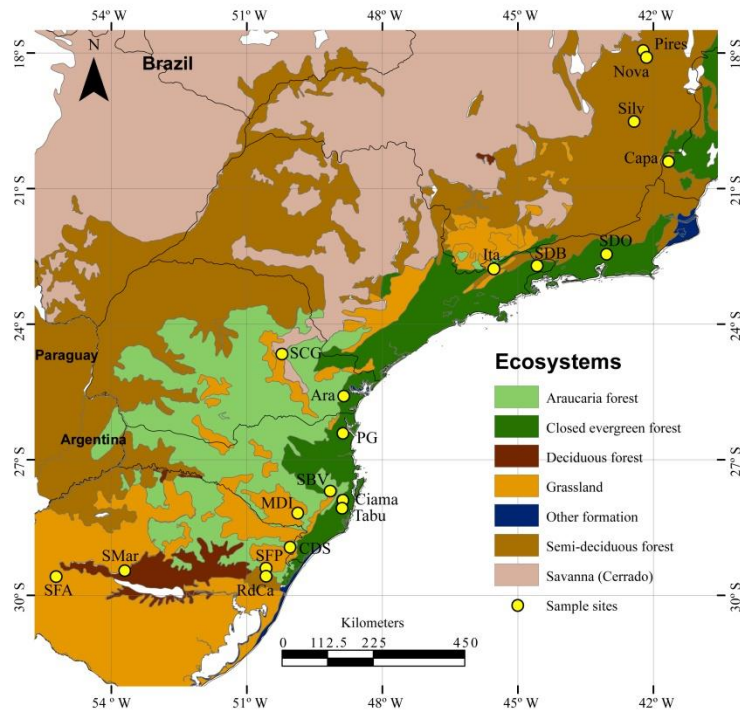
Figure 1 – Map with the ecosystems according to RBMA (1999) in eastern South America. Yellow circles indicate the location of the sites of the pollen diagrams.

The vegetation formations include the subtropical forest known as *Araucaria* forest, which is located in the southern highlands where rainfall rates are over 1400 mm per year and annual average temperature is around 15 °C. In the summer, the maximum temperatures can reach 30 °C and the lowest recorded temperature in winter is -10 °C (Nimer, 1989; Veloso et al., 1991). Herb dominated campos vegetation forms a mosaic with *Araucaria* forest, which spreads over large areas on the highlands of southern Brazil, where temperatures can reach 35 °C in summer and the presence of frost is common during the winter (Boldrini, 2009); Nimer, 1989) Small areas of grassland vegetation (campos de altitude) are also found in southeastern Brazil, where it occurs at escarpments, plateaus and mountain tops above 1800 m a.s.l. at Serra da Mantiqueira and Serra do Mar with an annual precipitation rate around 1800 mm and mean temperatures between 16 and 22 ºC (Nimer, 1989; Overbeck et al., 2007; Safford, 1999). The mountain chains Serra da Mantiqueira and Serra do Mar divide the coastal and hinterland vegetation associations. The coastal vegetation is formed by closed evergreen forest in general located between 0 and 1000 m elevation with high precipitation rates from Atlantic in consequence of orographic features (Sant'Anna Neto and Nery, 2005; Veloso et al., 1991). In leeward locations of southeastern Brazil, there is the occurrence of semi-deciduous forests, that are characterized by two well defined

69

seasons, one rainy season followed by a long drought period from 3 to 4/5 months when plants loose between 20-50% of their leaves (IBGE, 1995; Nimer, 1989, Veloso et al., 1991).

3.3   Methods

3.3.1   Age depth model

In order to compare the timing of events between pollen records, we constructed Bayesian age models using Oxcal version 4.2 (Bronk Ramsey, 2009) and SHCal13 calibration curve (Hogg et al., 2013). Considering that deposition though time may have changed randomly, including periods of steady and irregular deposition, we used the Poisson process to describe the sedimentation across profiles as implemented in the deposition model *P_Sequence (name, k_0, p, D)*. The parameter k_0 describing the sedimentation rate as the number of accumulation events per unit depth was set to 1. The parameter p (interpolation rate) was set as of 0.2, which means 1 output every 5 cm. *D* describes the possible variation of *k* and setting it to range between -2 and 2 allows *k* to vary between 0.01 and 100 cm^{-1} (Bronk Ramsey and Lee, 2013).

Probability distribution functions (PDF) of entire profiles were built by placing the prior age information for individual depth within paired *Boundary()* functions defining a uniformly distributed group. The upper boundary was constrained by an age for the top sample, which was assumed to represent the year of core collection, described by a normal distribution with a standard deviation of 25 years. The resulting posterior age distributions for individual stratigraphic levels vary greatly, with stratigraphic levels at or near a radiocarbon date being relatively narrow and steep, while probable ages for poorly dated sections are smeared over several thousand years. The final PDF of each depth calculated by Oxcal is based on the Gregorian calendar, however, we transformed all ages to the cal. BP scale by subtracting 1950 years.

3.3.2   Numerical Analysis

The pollen samples of all 19 records were treated in two steps in order to reduce the noise of the dataset. Initially, pollen counts from Cyperaceae and local fern spores (e.g. *Blechnum* type, *Salvinia* type, *Isoetes* and others) were removed as their counts are highly influenced by local conditions rather than general vegetation composition.

Further, within all samples single occurrences were removed, since their true abundance per sample cannot be estimated because they may be chance encounters of rare or distant parent species or a chance underrepresentation of a characteristic taxon from the region. The second step to select the most representative taxa was carried out by removing those taxa with abundance less than 0.5%. Finally, the percentages of the new dataset of each site were recalculated, square root transformed to stabilize the variance and to balance the influences of the most and least abundant taxa (Legendre and Birks, 2012; Prentice, 1980).

The focus of this study is to investigate the vegetation changes during the Holocene as a response to climate variations. Therefore, we removed samples dated younger than 500 years BP depicting disturbances caused by first European settlers. This recent human induced vegetation change was as strong as the accumulated climate driven change over the last 3000 years (Rodrigues et al., 2016) and its omission reduces the overall variance and therefore increasing the sensitivity of subsequent analyses.

3.3.3 Zonation

Pollen zones are used to divide pollen diagrams into sections so that the boundary between zones mark the point of major shift in pollen composition between adjacent samples. Several statistical techniques have been developed to obtain pollen zones (Gordon and Birks, 1972), which work either from the sample up (constraint cluster analysis) or from the full diagram down (sequence splitting). Splitting a sequence into smaller and smaller sections is conceptually similar to the broken-stick model (MacArthur, 1957), which is thus providing an assessment of the number of statistically significant zones by comparison (Bennett, 1996). Sequences can be split in a binary way, evaluating the variance in successively smaller sections, or in an optimal way searching for a given number of best splits over the entire length of the sequence. These two ways of splitting may produce slightly different results depending on the strength and overall pattern of change. Also variance can be assessed in different ways and here we used the information content criterion and the sum of squared deviations. The resulting four combinations of sequence splitting and their evaluation with the broken stick model are implemented in PSIMPOLL version 4.27 (Bennett, 2007), which was used for this analysis.

The resulting ages of pollen zone boundaries are associated with uncertainties derived from the age model as described above. In order to explore whether there are periods of pronounced vegetation change, the probabilities of all individual events were added into a summary curve of accumulated probabilities of the time of vegetation change. To improve the visibility of the signal in this summary curve it was smoothed by applying a moving average over 375 years before and after each point of the curve. Where the stratigraphic position of a detected vegetation shift coincides with a radiocarbon date this resulted in sharp peaks of probabilities, which were reduced somewhat by averaging the probability distributions of 1 cm above and below individual radiocarbon dates.

To obtain a geographical perspective on past vegetation changes, we selected periods with district peaks in the accumulated probability curve and mapped the sites where vegetation change was detected at that time. We used a window of 800 years for the early and mid-Holocene and 400 years for the late Holocene and mapped sites where at least 20% of the probability of the age of vegetation change falls within in the interval. Sites with more than 50% of the age probability falling into these intervals were mapped with a different symbol in Fig. 3.

The magnitude of vegetation change that occurred through time at each site was evaluated by rate of change analysis (Jacobson et al., 1987). Rate of change analysis is effected by uneven sampling distribution in time and the 19 pollen diagrams were therefore resampled to equal time intervals varying between 100 and 400 years depending on the sample resolution of the pollen diagram. Rate of change was evaluated as squared cord distance (SCD) between adjacent samples and divided by time to make the results comparable between sites with different sample resolution.

The latent structures within all datasets were explored with principal curves (PC) that are smooth one-dimensional curves fitted in a multidimensional data space (Hastie and Stuetzle, 1989). PC minimizes the sum of squared deviations between the observations and the fitted curve in an iterative process from an initial configuration (De'ath, 1999) for which we used the order of samples based on the result from the correspondence analysis (CA).

3.4   Results

3.4.1   Ages of detected vegetation change

The four combinations of splitting techniques and associated variation criteria yielded zones at similar positions in the pollen diagrams, indicating that the detected shifts in pollen composition are robust indicators of times of past vegetation change.

Splits of pollen spectra become more frequent during the mid-Holocene and substantially increased after 4000 cal yr BP (Fig. 2). For the different splitting techniques, the curve of accumulated probabilities over individual events consistently indicate 5 periods composed by at least 2 splits that may be simultaneous within dating uncertainty. These periods are centered on 8900, 5900, 2800, 1200 and 550 cal yrs BP, with the older three being apparent in the results all four splitting approaches, while the younger two peaks differ between the variance measures. We selected the peaks found with sum of squares variance measure, while information content yields a broad peak with two maxima at 730 and 450 cal yrs BP. In the following we describe the results obtained mainly with the sum of squares variance.
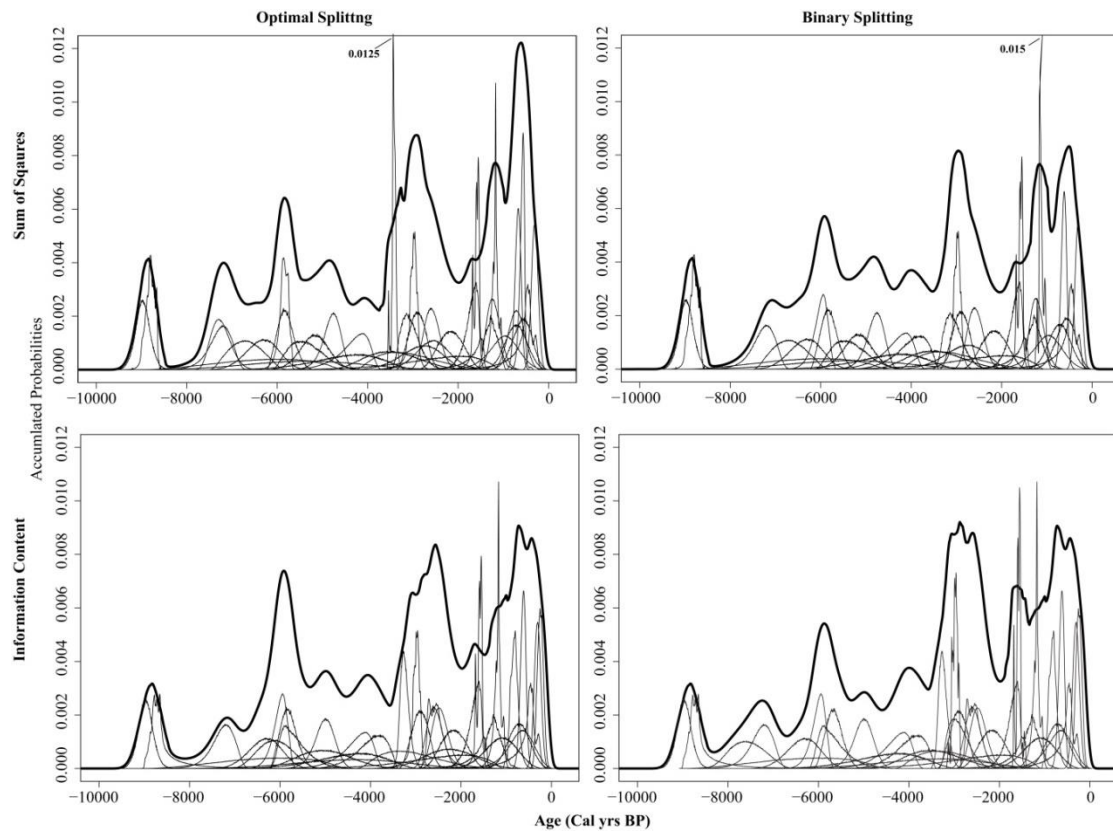
Figure 2 – Curves of individual probabilities for ages of vegetation change as detected by optimal and binary splitting in combination with two variance measures sum of squares and information content. The thick line represents a running mean of the accumulated probabilities over individual events.

The oldest peak centered at around 8900 cal yrs BP consists of splits from two pollen diagrams (Silv and Capa) situated 116 km apart (Fig. 3a). The two probability distributions overlap by 50% suggesting that the underlying vegetation change may have occurred at the same time at both sites. In combination, probability distributions of the inferred vegetation change stretch over the period from 9500 to 8600 cal yrs BP. At Lago Silvana this period marks the main vegetation change at the site with a shift from a mainly open landscape dominated by Poaceae to a dominance of pollen from tropical shrub and trees (e.g *Alchorna*, Moraceae/Urticaceae, *Cecropia*). Sediment geochemistry from the same core indicates rising lake levels (Rodrigues-Filho et al., 2002). At Serra do Caparaó the vegetation change at this time follows the same direction with a marked increase of pollen from *Symplocos*. The genus occurs in the area with two species *S. densiflora* and *S. itatiaiae*, both members of the upper mountain forest growing on rocky soils in areas of high humidity (Veríssimo et al., 2012). It is important to notice that although only 16 out 19 sites cover the early Holocene, no other site indicates vegetation changes during this period.
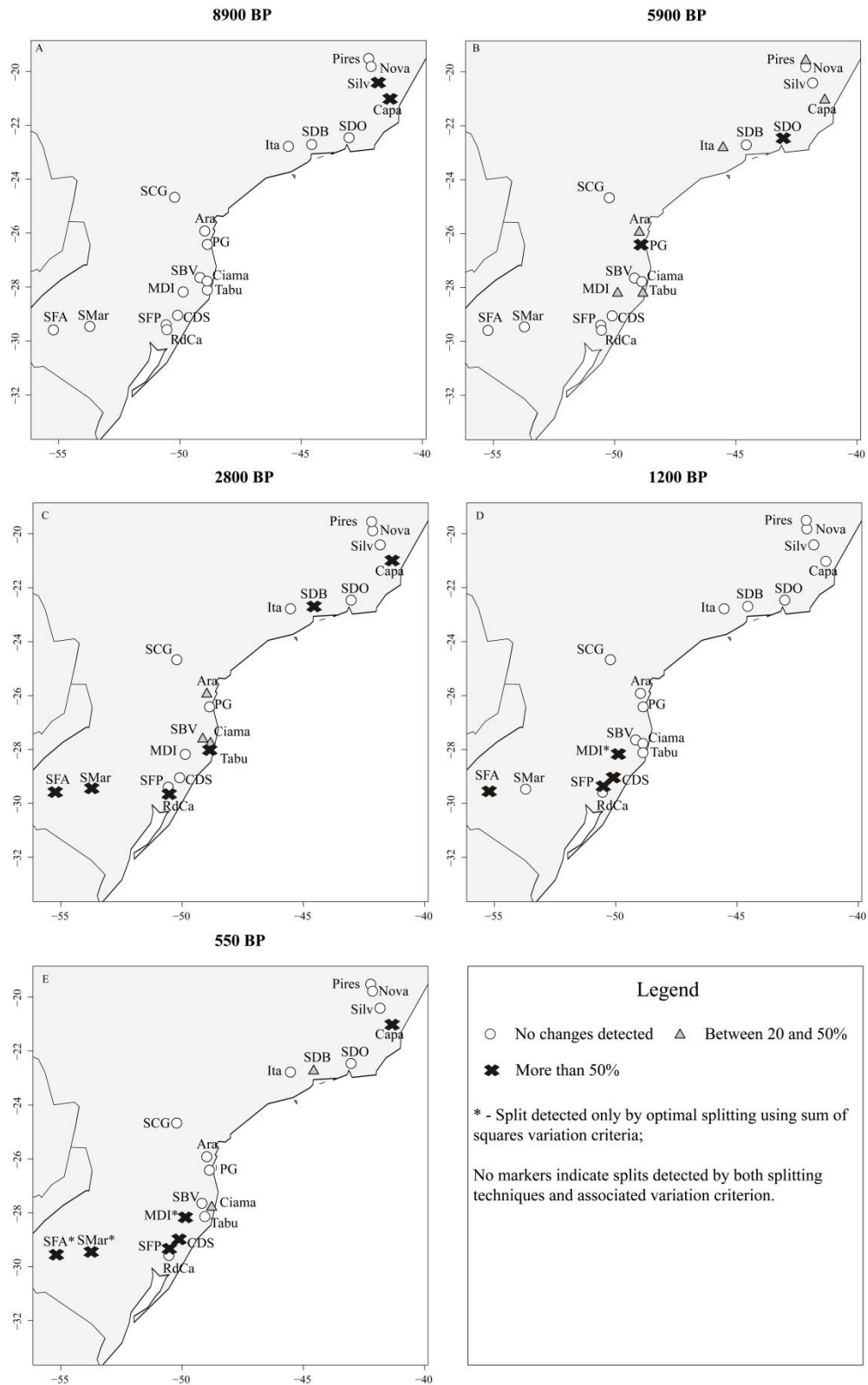
Figure 3 – Geographical representation of the occurrence of vegetation changes with relevance to the five time periods: 8900, 5900, 2800, 1200 and 550 cal yrs BP.

The changes for the peak centered at 5900 cal yrs BP, has probabilities of detected vegetation change in 11 pollen diagrams. However, only 2 of them (SDO and PG) have more than 50% of their individual probability distribution within the interval of 800 years around that date. The events at both sites overlap with 57% of their age probabilities indicating high chance of synchronous changes. These sites are situated about 730 km apart (Fig. 3b). The vegetation changes detected for this period at both places are characterized by different trends such as decrease of Poaceae and increase of trees and shrubs taxa like Moraceae/Urticaceae, Melastomataceae and Myrsine at SDO whereas at PG, Myrtaceae decreased sharply while Arecaceae and *Weinmannia* increased. Six more sites (Pires, Capa, Ita, Ara, Tabu and MDI) have indications for vegetation change dated to this period within 20 to 50% of age probabilities within the interval. These pollen records are characterized by relatively stable conditions without marked change at the time, although at Ara the principal curve indicates a major compositional shift starting around that time (Fig. 5).

The third period of combined events is centered at around 2800 cal yrs BP and highlights intense vegetation changes. The total number of splits falling in this period increased to 18 and 16 for optimal and binary splitting, respectively. Despite high number of pollen zone boundaries detected, only 6 of these splits (Capa, SDB, Tabu, SMar, RdCa and SFA) have 50% or more of their probability distribution within the time window of 2400-3200 years and in combination only share 13% of their respective age probabilities. Their maximal probabilities (3220, 3280, 2890, 3360, 3110 and 3760 cal yrs BP, respectively) suggest the occurrence of events in a narrow time window. In 4 out 6 sites (Capa, Tabu, SMar and SFA) the vegetation change is characterized by an increase in Poaceae abundance whereas trees and shrubs decreased. At SDB and RdCa the opposite trend is visible with decrease in Poaceae and an increase of trees such as Melastomataceae at SDB and *Weinmannia* at RdCa. There are 3 others sites (Ara, SBV and Ciama) with 20 to 50% (Fig. 3c) probability of a detected vegetation change falling into the time period, although the character of the change is not obvious. For SBV and to some extend Ciama the principal curve indicates a shift in vegetation composition just prior to 2800 cal yrs BP (Fig. 5).

The period considered for the two youngest peaks was set to only 400 years. The period centered at around 1200 cal yrs BP overlaps with age probabilities of splits at 8 and 10 sites for optimal and binary splitting techniques, respectively. Only 4 sites (MDI, CDS, SFP and SFA) have more than 50% of their probability distribution for the event

within the constrained time window (Fig. 3d). Particularly the splits for SFP and SFA indicate a high chance of simultaneous vegetation change with 86% overlapping probability ranges. The 4 main sites are located in the southern region, characterized by a mosaic of grasslands and forests with a dominance of herbaceous, mainly Poaceae pollen around 1200 cal yrs BP. At CDS a continuous replacement of grasslands by *Araucaria* forest characterized by taxa of *Araucaria angustifolia, Myrsine* and *Weinmannia,* is visible since 4300 cal yrs BP, however, 1200 cal yrs BP marks a rapid shift in this development as indicated by the principal curve (Fig 4). The main vegetation change at MDI, SFP and SFA are characterized by a partial replacement of Poaceae by *Araucaria angustifolia* with *Xyris, Baccharis and Eryngium*, respectively.

The youngest period centered at 550 cal yrs BP captures changes detected at 6 locations (Capa, MDI, CDS, SMar, SFP and SFA) with at least 50% of the age probability falling between 350 and 750 cal yrs BP. At Capa, CDS and MDI the vegetation change consists of a further decrease in Poaceae abundance while *Baccharis* increses at the northernmost site and forest taxa such as *Weinmannia* and *Araucaria angustifolia* increased at southern locations. At SFP, SMar and SFA the pollen diagrams show a slight increase in Poaceae and *Baccharis*.

In addition to the above described periods of vegetation change optimal splitting using sum of squares identifies vegetation changes at SDO and SDB at around 7750 cal yrs BP with 86% overlap in their probability distributions. This change is characterized by an increase in Poaceae at SDO and Melastomataceae at SDB. At around 4000 cal yrs BP the splits at Tabu and CDS overlap with 59% of their age uncertainties and the change is characterized by the increase of forest taxa, with *Myrsine*, Melatomataceae and Myrtaceae at Tabu, and *Araucaria angustifolia* at CDS. Another simultaneous change, not represented by high peaks on the curve of accumulatedprobabilitiesw, is noticed at 1900 cal yrs BP for SMar and SFA with a 56% overlap in age probabilities, although there are no strong changes visible in the pollen diagram of either site.

3.4.2   *Principal Curves*

Principal curves (PC) are one-dimensional curves that pass through the middle of a multidimensional data-set and can thus explain a larger proportion of variance than the first axis in a principle component or correspondence analysis (Simpson and Birks, 2012). Nevertheless, PC explain between 55 and 85% of variance only for 10 out of 19

pollen diagrams, while for remaining 9 diagrams only between 14 and 47% of the variance is captured. These low amounts of explained variance indicate that there are no strong gradients in vegetation change depicted by these pollen diagrams and this is indeed visible. The 10 PCs that explain more than 50 % variance are based on pollen diagrams (Capa, Ara, PG, SBV, MDI, Ciama, Tabu, CDS, RdCa and SFP) with a strong change in vegetation composition often during the second half of the Holocene, generally characterized by a replacement of grassland by forest taxa. The PC's of Silv, SCG, Ita and Nova explain 38, 41, 44 and 47% of total variance, respectively. These diagrams show a change in vegetation around 9000 cal yrs BP and relative stable composition thereafter. No strong change in vegetation composition is visible in the pollen diagrams SMar, SFA, SDO, SDB and Pires for which the variance explained by the PC's range from 14 to 28%, nevertheless the PC's still describe some general trends in vegetation change also for these sites.

The five periods of potentially synchronous vegetation change identified based on sequence splitting find representation in many of the PC curves of the individual sites (Fig. 4). The oldest detected change (8900 cal yrs BP) is not only well represented in the PC curves of Capa and Silv, but shifts in vegetation composition near this age can also be deduced from the PC's of Nova, Ita and SCG. The change detected around 5900 cal yrs BP was determined mainly by PG and SDO, but is also marked in Tabu, with trends in SBV, MDI and RdCa. The PC's indicate vegetation composition change around 2800 cal yrs BP particularly for Capa, SCG, SBV and RdCa, with minor shifts at several other sites. While many sites have also contributed to the detected shift around 1200 cal yrs BP, it is most pronounced in the PC's of SDB, Ara, CDS and SFP. Of the pollen diagrams with good sample resolution for the youngest sediments the vegetation shifts around 550 cal yrs BP are best visible in the PC's of Ciama, CDS and SMar.
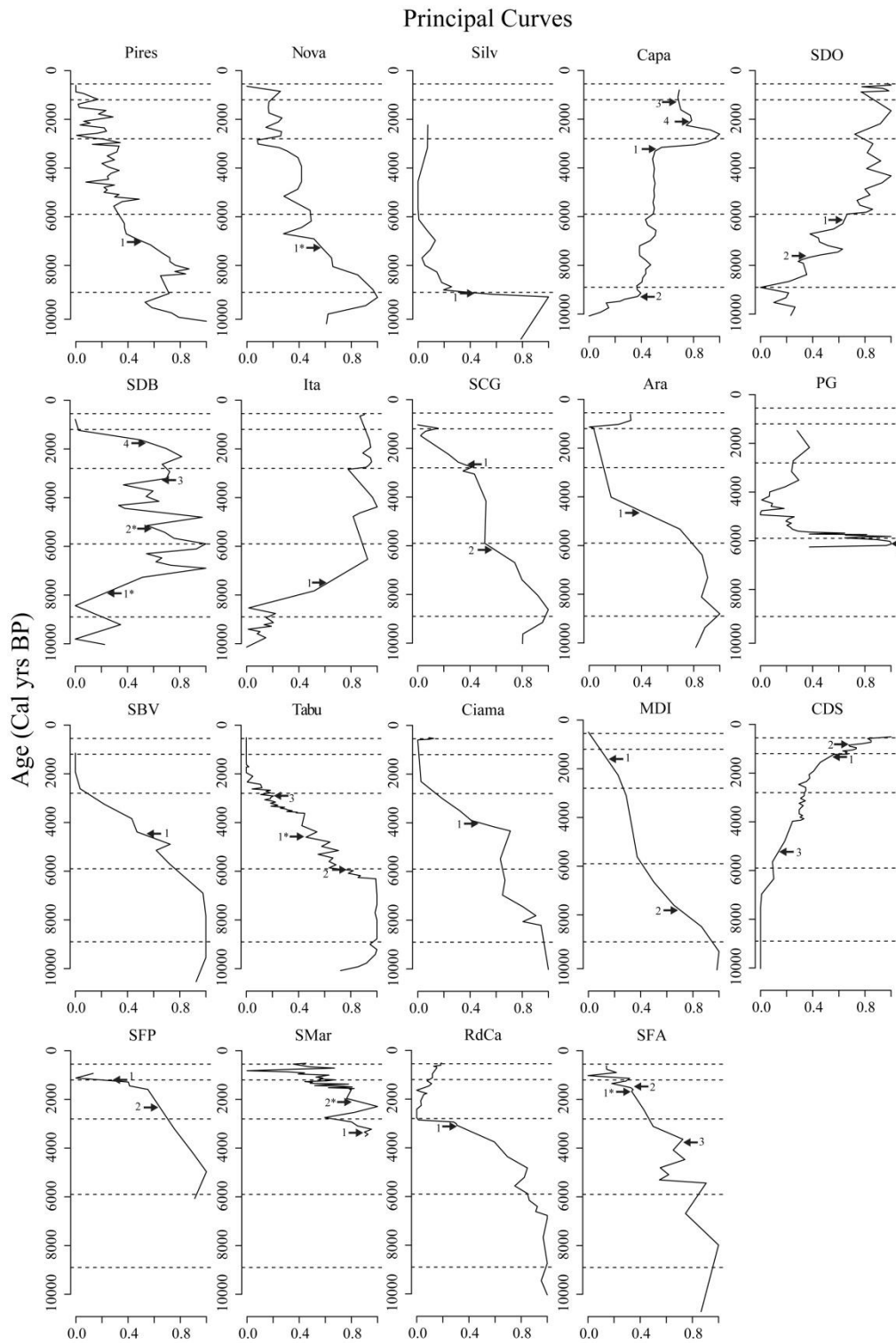
Figure 4 – Principal curves (PC's) for all individual diagrams ordered from north to south (Table 1). Arrows indicate the position of a vegetation change as detected by binary splitting with sum of squares and the numbers mark the hierarchical importance of the split with "1" being the most important. Asterisks beside the numbers indicate changes that did not contribute with at least 20% of their age probability to one of the fife periods of change marked by the broken lines.

3.4.3 Rates of Change

Due to changes in the rate of sediment accumulation though time at most of the sites the sample resolution in time varies strongly for most of the used pollen diagrams and this would affect assessments of rates of change. Therefore, diagrams had to be resampled to even time steps and dissimilarities were divided by these time steps to make the rates between different diagrams comparable to each other. The results show that changes were gradual at most sites, with most rapid shifts in sample composition at Ciama and Ita (Fig. 5). Peaks in rate of change often correspond to pronounced shifts in the PC's indicating that some shifts in sample composition occurred rapidly, nevertheless, there are fewer peaks in the rate of change curves than detected vegetation changes using sequence splitting. The rate of change curves of several sites show peaks for the two younger periods (1200 and 550 cal yrs BP), while peaks coinciding with older periods of common vegetation change are less frequent. Differences in rates of change between sites seem to be independent of sample resolution and the amount of variance explained by PCs.

Rate of Change Analysis
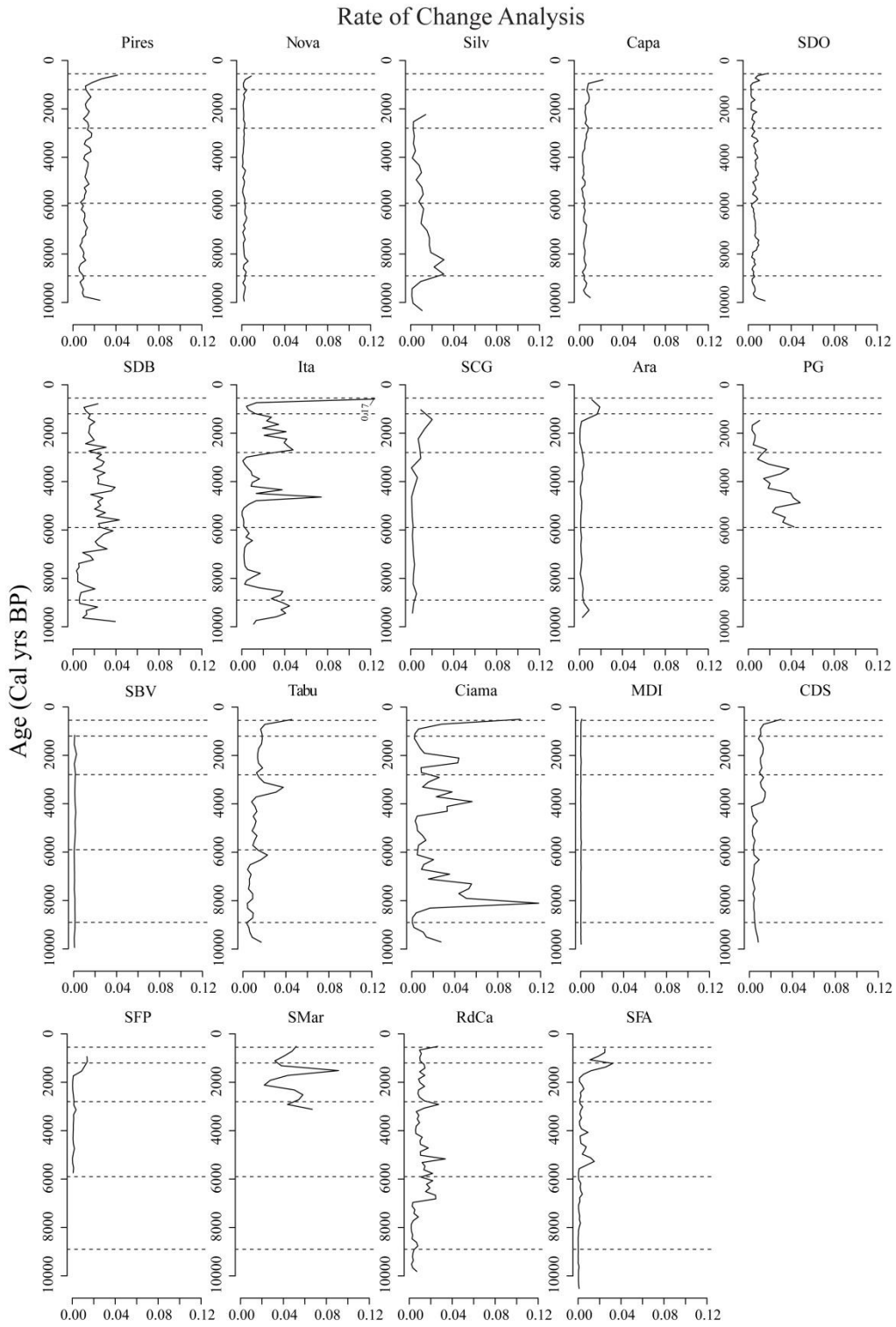
Figure 5 – Rate of Change Analysis performed for each pollen record evidencing the velocity of vegetation change through the Holocene ordered from north to south.

3.5   Discussion

A visual inspection of Fig. 2 clearly shows that events of major vegetation change did not occur randomly through time within the study region, but happened predominantly during the last 4000 years. Although the sites are not evenly distributed on a latitudinal gradient. Older changes occurred predominantly at sites further north with younger changes being more frequent at southern sites. Most of the detected shifts in vegetation composition are consistent with shifts from dryer to wetter climatic conditions.

The oxygen isotope records of stalagmites from Botuverá cave (27°13'S, 49°09'W) show a trend of decreasing values of the heaver isotope though the Holocene, which is interpreted as an increased supply of water from the Amazon basin linked to an enhanced South American Monsoon (SAM) (Fig. 6; Wang et al., 2006). The strength of the SAM bringing increased summer precipitation follows changes in solar radiation as determined by Earth's precession cycle (Cruz et al., 2005; Wang et al., 2007). The stalagmite record from Cristal cave (24°35' S, 48°35' W) also shows the trend of increasing summer precipitation during the late Holocene (Taylor, 2010; Vuille et al., 2012). However, oxygen isotope measurements from speleothems in northeastern Brazil indicate the opposite direction of change. Stalagmites from Rainha, Furna Nova and Abissal caves (05°36'S, 37°44'W) indicate an increase in precipitation during the early Holocene until about 8000 years ago and a decline thereafter (Cruz et al., 2009). This northeastern pattern parallels the titanium concentration data from the anoxic Cariaco Basin which is an indicator for erosion and runoff from the area draining into the basin and thus provides a record of precipitation of around 10°N, 65°W (Haug et al., 2001). The trend of generally decreasing precipitation was also inferred for the last 3000 years from speleothems in northeastern Brazil near the city of Iraquara around 12°S, 41°W (Novello et al., 2012).
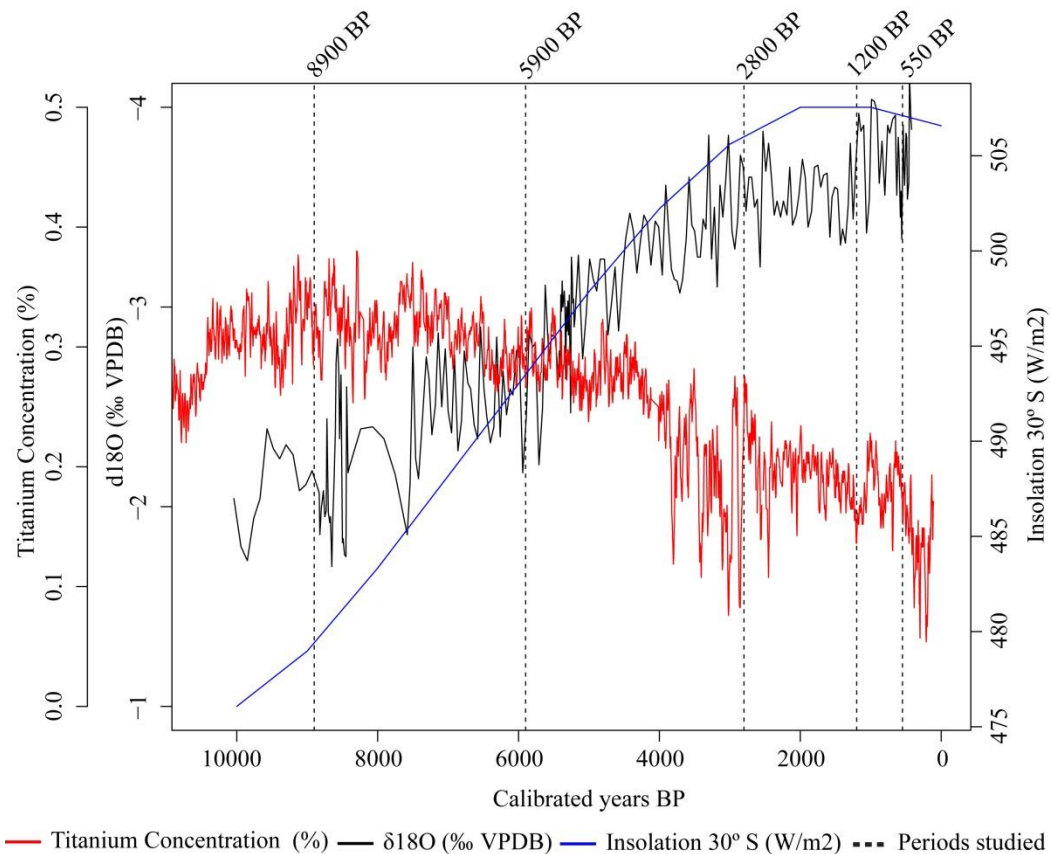
Figure 6 – Comparison of proxy records for precipitation change in northern South America with the periods of vegetation change detected in the here presented analysis. Black line: oxygen isotope record from Botuverá Cave (Wang et al., 2006), note that more negative values are interpreted to reflect a stronger South American monsoon with more summer precipitation at 27°13'S. Blue line: December insulation values at 30°S (Berger, 1978). Red line: Cariaco Basin titanium concentrations (Haug et al., 2001) indicating the strength of riverine discharge from the neighboring land at around 10° N.

The sites in these investigation spread from around 18°S to 30°S and thus the two opposing trends in moisture availability and their combination may be expected to have influenced the vegetation change portrayed in the pollen diagrams. At the two northernmost sites Lago do Pires (17° 57' S, 42° 13' W) and Lagoa Nova (17°58'S, 42°12'W) an expansion of gallery forests occurred between around 9500 and 8300 cal yrs BP with afterwards a return to drier conditions until around 6000 cal yrs BP (Behling 1995, 2003). This return to dryer conditions did not lead to a strong decline of any individual tree taxa and thus this reversal was not captured by the splitting techniques or the PC (Fig 4). Somewhat further south (around 20°S) the pronounced expansion of woody taxa in the diagrams of Siv and Capa occurred somewhat later around 8900 cal yrs BP and gave rise to a zone boundary and are marked signal in the

PC. These diagrams do not indicate a return to dryer conditions during the first half of the Holocene, although, at Capa the upper mountain forests gives way to campos de altitude during the last 3000 years (Veríssimo et al., 2012). At around 22°S the diagrams from SDO and Ita, both at high elevations, indicate a gradual increase in Atlantic rain forest taxa including a stepwise increase that is dated in SDO to around 5900 cal yrs BP (Behling, 1997; Behling and Safford, 2010). At Ita this shift is preceded by a shift in sediment accumulation and not precisely dated, but may have occurred at the same time. Sites further south document shifts in vegetation composition consistent with the oxygen isotope records from Botuverá cave.

The high frequency of zone boundaries during the late Holocene at southern sites represents to a large degree the successive vegetation changes associated with the expansion of *Araucaria* on the highland and tropical rainforest along the coastal slopes of mountain chains (Behling, 1995, 1997; Behling et al., 2001). The pollen diagram from CDS (Behling et al., 2004), for example, shows that at around 4300 cal yrs BP *Araucaria* starts to expand followed by a rapid increase around 1100 cal yrs BP.

The above reviewed proxy records of past precipitation change do not only indicate general trends, but also periods of deviations from these trends as well as times of increased variability. Most of the high resolution records indicate a deviation from the general trend for the time of the Little Ice Age (LIA) with the isotope values from Cristal cave in the south suggesting increased precipitation, while the Iraquara record (Novello et al., 2012) and the Cariaco Basin (Haug et al., 2001) indicate reduced precipitation towards the north. However, also in the Cristal cave record (Taylor, 2010) the onset of the LIA deviation is marked by a strong positive excursion (drought) at around 500 cal yrs BP followed by more negative values (increased summer precipitation) and this high variability could have triggered the rapid vegetation change dated to around 550 cal yrs BP in this study. The expansion of *Weinmannia* trees within *Araucaria* forest during this period at CDS (Behling et al., 2004), indicates moist and warm conditions, and its reduced abundance since then, indicates cooler modern climate.

Similarly, the increased change in vegetation around 1200 cal yrs BP may be linked to the onset of the Medieval Climate Anomaly (MCA), during which the mean state of the SAM may have been weakened (Vuille et al., 2012). In particular, the period around 2800 cal yrs BP is marked in several records as a major deviation of the general trend in the form of a wet phase at Iraquara (Novello et al., 2012) or the end of a period

with increased amplitude of the fluctuations in the titanium values in the Cariaco Basin (Haug et al., 2001). The high resolution speleothem record from Lapa Grande cave (14°25′S; 44°22′W) consist of two stalagmites and together cover the full Holocene (Stríkis et al., 2011). While their oxygen isotope records do not follow any trend in solar radiation, they document abrupt shifts in monsoon precipitation matching the Bond events of ice rafted debris in the north Atlantic (Bond et al., 1997). The previously mentioned intervals as well as the vegetation shifts around 5900 cal yrs BP coincide with Bond events. The age uncertainty of the oldest shift around 8900 cal yrs BP is wide and while it does not include high probability around the year 8200 cal. BP it may correspond to the onset of the border anomaly around the 8.2 event (Rohling and Pälike 2005).

Browsing through palaeo-environmental archives and picking out events that match in time is potentially problematic as a large number of events and wiggly lines can be found in the literature. Reported periods of change like the Bond events have the danger of sucking unrelated events in. Given the dating uncertainty the here reported time of change at 8900 cal yrs BP could be assigned to any of the two neighboring Bond events, while it may be completely unrelated to any major shift in atmospheric or ocean circulation pattern. The generally dry conditions prevailing during the early Holocene at the here investigated sites often resulted in low sediment accumulation and/or possibly loss of sediment during dry years. As a result, few centimeters of sediment represent long periods of time, making it difficult to infer precise ages for particular events and smearing their occurrence in time. Thus linking the here detected times of vegetation change to Holocene climate excursions suffer the problem of suck and smear described by Baillie (1991). Within our study of comparing the timing of rapid vegetation change we dealt with the problem of suck and smear by creating Bayesian age depth models and comparing the age probabilities of these events (Blaauw et al., 2007). As a result, detected changes in vegetation composition that were not well constrained by an age depth model did not contribute much to the detection of overall changes (Fig. 2).

Although we detected some general pulses in vegetation change sites near each other did not always experience synchronous changes, which is illustrated by the example of CDS and RdCa which are situated about 70 km apart. Both sites document a rapid shift from a domination of campos to Atlantic rainforest in a similar manner, however, the strongest shift occurred at RdCa around 2800 cal yrs BP and at CDS only at around 1200 cal yrs BP (Fig. 4). Many of the pollen diagrams in this study come from

small wetlands so that the pollen diagrams are often dominated by local vegetation dynamics, which may deviate from regional patterns, due to different edaphic conditions. Local dynamics could be dominated by reoccurring successional dynamics or be initiated by disturbances that are not related to climate such as human set fires, slash and burn agriculture or the plantation of trees that provide sought after foods like *Araucaria angustifolia*.

While many of the sites in this analysis change from a predominantly open situation to increased forest cover or even forest domination there is not a large turnover of pollen types through time. This is in part due to the problem that most pollen types can only not be identified to family level with species in the same family having potentially different responses to environmental change. On the other hand, this region did not experience a large shift in biome similar to the postglacial immigration of trees in previously glaciated areas of the northern high latitudes, but rather an expansion and decline in the abundance of individual species and vegetation formations. The low turnover of pollen taxa over the Holocene also explains the low amount of variance captured by the PCs (Fig. 4) and the often flat curves of rates of change (Fig. 5). Rates of change were assessed by square cord distance, which gives weight to compositional changes. Since compositional changes are small in most diagrams as discussed above the results are therefore dominated by abundance changes which may have been dominated at some sites by the local dynamics so that there is little value in comparing the absolute amounts or stacking them to obtain an overall impression of change (Grimm and Jacobson, 1992). The number of significant pollen zone boundaries is lower compared to a similar study in Europe (Giesecke et al., 2011) and may be influenced by the number of samples per sequence which are also lower in this study. Bennett (1996) showed that for a Holocene and postglacial sequence in the UK the number of zones increased until about 40 and 80 samples respectively. Even for high resolution diagrams in this study the different splitting techniques did generally not select more than 3 zones and a maximum of 4 zones were only found for Capa and SDB. Thus also the zonation indicates that, compared to mid and high latitude sites, fewer significant vegetation changes occurred during the Holocene at these tropical and subtropical locations in southeastern and southern Brazil.

3.6   Conclusions

Based on 19 pollen diagrams from south-eastern and southern Brazil we find that Holocene vegetation change occurred frequently during common intervals indicating that rapid shifts in climate conditions acted as large scale disturbance events, reducing the inertia to change in the vegetation and facilitating change. Vegetation change in the region is mainly determined by changes in available moisture controlled by the South American Monsoon (SAM). This monsoon system has gradually changed over the Holocene changing the amount of precipitation and the length of the dry season over large regions, while it has also changed rapidly in its mean state causing uncommon drought or flooding over consecutive years. Thus the climate system provides general trends and sudden shifts and our results show that shifts in vegetation composition culminated at common periods that are consistent with changes in SAM. The overall amount of Holocene vegetation change in these tropical and subtropical regions was not as strong as in mid- to high latitudes of the northern Hemisphere where species had to immigrate after being expelled by the ice, which together with soil and climate changes determined the vegetation composition. In contrast the processional forcing of hydrology is directly visible in these low latitude vegetation changes as shifts in species abundances.

3.7   References

Baillie, M.G.L., 1991. Suck in and smear: two related chronological problems for the 90s. Journal of Theoretical Archaeology. 2, 12-16.

Bauermann, S.G., Macedo, R.B., Behling, H., Pillar, V., das Neves, P.C.P., 2008. Dinâmicas vegetacionais, climáticas e do fogo com base em palinologia e análise multivariada no quaternário tardio do sul do Brasil. Rev Bra Paleontol. 11, 87–96.

Behling, H., 1995. Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). Vegetation History and Archaeobotany. 4, 127-152.

Behling, H., 1997. Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology. 129, 407-422.

Behling, H., 1998. Late Quaternary vegetational and climatic changes in Brazil. Review of Palaeobotany and Palynology. 99, 143-156.

Behling, H., 2002. South and Southeast Brazilian grasslands during Late Quaternary times: a synthesis. Palaeogeography, Palaeoclimatology, Palaeoecology. 177, 19-27.

Behling, H., 2003. Late Quaternary vegetation, climate and fire history inferred from Lagoa Nova in the southeastern Brazilian lowland. Vegetation History and Archaeobotany, 12, 263-270.

Behling, H., 2007. Late quaternary vegetation, fire and climate dynamics of Serra do Araçaatuba in the Atlantic coastal mountains of Paraná State, southern Brazil. Veget Hist Archaeobot. 16, 77–85.

Behling, H., Bauermann, S.G., Neves, P.C., 2001. Holocene environmental changes from the São Francisco de Paula region, southern Brazil. Journal of South American Earth Sciences. 14, 631-639.

Behling, H., Dupont, L., Safford, H.D., Wefer, G., 2007a. Late Quaternary vegetation and climate dynamics in the Serra da Bocaina, southeastern Brazil. Quaternary International. 161, 22-31.

Behling, H., Pillar, V., Bauermann, S.G., 2005. Late Quaternary grassland (Campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in western Rio Grande do Sul (southern Brazil). Rev Palaeobot Palynol. 133, 235–248.

Behling, H., Pillar, V., Müller, S., Overbeck, G., 2007b. Late-Holocene fire history in a forest-grassland mosaic in southern Brazil: Implications for conservation. Journal of Applied Vegetation Science. 10, 81-90.

Behling, H., Pillar, V.D., Orlóci, L., Bauermann, S.G., 2004. Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology. 203, 277-297.

Behling, H., Safford, H.D., 2010. Late-glacial and Holocene vegetation, climate and fire dynamics in the Serra dos Órgãos Mountains of Rio de Janeiro State, southeastern Brazil. Glob Chang Biol. 16, 1,661–1,671.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytologist. 132(1), 155–170.

Bennett, K.D., 2007. Psimpoll and Pscomb Programs for Plotting and Analysis. http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html.

Berger, A., 1978. Long-term variations of caloric insolation resulting from the earth's orbital elements. Quaternary Research. 9, 139–167.

Birks, H.J.B., Birks, H.H., 2004. The rise and fall of forests. Science. 305, 484-485.

Blaauw, M., Christen, J.A., Mauquoy, D., van der Plicht, J., Bennett, K.D., 2007. Testing the timing of radiocarbon-dated events between proxy archives. The Holocene. 17: 283-288.

Boldrini, I.I., 2009. Biodiversidade dos Campos do Planalto das Araucárias. Ministério do Meio Ambiente, Brasília.

Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal, P., Priore, P., Cullen, H., Hajdas, I., Bonani, G., 1997. "A Pervasive Millennial-Scale Cycle in North Atlantic Holocene and Glacial Climates". Science. 278 (5341), 1257–1266.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon. 51(1), 337–60.

Bronk Ramsey, C., Lee, S., 2013. Recent and Planned Developments of the Program Oxcal. Radiocarbon. 55(2-3), 720-730.

Cheddadi, R., de Beaulieu, J.L., Jouzel, J., Andrieu-Ponel, V., Laurent, J.M., Reille, M., Raynaud, D., Bar-Hen, A., 2005. Similarity of vegetation dynamics during interglacial periods. Proceedings of the National Academy Sciences USA. 102,13939-13943.

Clement, A.C., Hall, A., Broccoli, A.J., 2004. The importance of precessional signals in the tropical climate. Climate Dynamics. 22, 327-341.

Cruz, F.W., Karmann, I., Viana, O., Bruns, S.J., Ferrari, J.A., Vuille, M., Sial, A.N., Moreira, M.Z., 2005. Stable isotope study of cave percolation waters in suntropical Brazil: Implications for paleoclimate inferences from speleothems. Chemical Geology. 220(3-4), 245-262.

Cruz, F.W., Vuille, M., Burns, S.J., Wang, X., Cheng, H., Werner, M., Edwards, R.L., Karmann, I, Auler, A.S., Nguyen, H., 2009. Orbitally driven east–west antiphasing of South American precipitation. Nature Geoscience. 2, 210 - 214.

De'ath, G., 1999. A New Technique for Indirect and Direct Gradient Analysis. Ecological Society of America. 80(7), 2237-2253.

Fontana, S.L., Bianchi, M.M., Bennett, K.D., 2012. Palaeoenvironmental changes since the Last Glacial Maximum: Patterns, timing and dynamics throughout South America. The Holocene. 22-1203-1206.

Giesecke, T., Bennett, K.D., Birks, H.J.B., Bjune, A.E., Bozilova, E., Feurdean, A., Finsinger, W., Froyd, C., Pokorný, P., Rösch, M., Seppä, H., Tonkov, S., Valsecchi, V., Wolters, S., 2011. The pace of Holocene vegetation change e testing for synchronous developments. Quaternary Science Reviews. 30(19–20), 2805–2814.

Gordon, A.D., Birks, H.J.B., 1972. Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. New Phytologist. 71, 961-979.

Grimm, E.C., Jacobson, G.L. Jr., 1992. Fossil-pollen evidence for abrupt climatic Change during the past 14,000 years in eastern North America. Climate dynamics. 6, 179-184.

Hastie, T., Stuetzle, W., 1989. Principal Curves. Journal of American Statistical Association. 84, 502-516.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.S., Röhl, U., 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. Science, 293(5533), 1304-1308.

Hogg, A.G., 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.H., 2013. SHCal13 Southern Hemisphere Calibration, 0-50,000 Years cal BP. Radiocarbon. 55(4), 1-15.

IBGE - Fundação Instituto Brasileiro de Geografia e Estatística, 1995. Zoneamento ambiental e agroecológico do Estado de Goiás: região nordeste. Rio de Janeiro: IBGE/Divisão de Geociências do Centro-Oeste. (Estudos e pesquisas em geociências, n. 3).

Jacobson, G.L., Webb, T., Grimm, E.C., 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. in: Ruddiman, W.F., Wright, H.E. (Eds.), North America and adjacent oceans during the last deglaciation. Volume K-3: The geology of North America. Geological Society of America, Boulder, pp. 277–288.

Legendre, P., Birks, H.J.B., 2012. Clustering and partitioning. in: Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (Eds.), Tracking environmental change using lake sediments: Data Handling and Numerical Techniques. Dordrecht: Springer, pp. 167-200.

MacArthur, R.H., 1957. On the relative abundance of bird species. Proceedings of the National Academy of Sciences of the United States of America. 43, 293–295.

Marchant, R., Harrison, S.P., Hooghiemstra, H., Markgraf, V., Van Boxel, J.H., Ager, T., Almeida, L., Anderson, R., Baied, C., Behling, H., Berrio, J.C., Burbridge, R., Bjorck, S., Byrne, R., Bush, M.B., Cleef, A.M., Duivenvoorden, J.F., Flenley, J.R., De Oliveira, P., Van Geel, B., Graf, K.J., Gosling, W.D., Harbele, S., Van Der Hammen, T., Hansen, B.C.S., Horn, S.P., Islebe, G.A., Kuhry, P., Ledru, M-P., Mayle, F.E., Leyden, B.W., Lozano-Garcia, S., Melief, A.B.M., Moreno, P., Moar, N.T., Prieto, A., Van Reenen, G.B., Salgado-Labouriau, M.L., Schasignbitz, F., Schreve-Brinkman, E.J., Wille, M., 2009. Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years. Climate of the Past. 5, 725–467.

Nimer, E., 1989. Climatologia do Brasil. Fundacão Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Novello, V.F., Cruz, F.W., Karmann, I., Burns, S.J., Stríkis, N.M., Vuille, M., Cheng, H., Edwards, R.L., Santos, R.V., Frigo, E., Barreto, E.A.S., 2012. Multidecadal climate variability in Brazil's Nordeste during the last 3000 years based on speleothem isotope records, Geophysical Research Letters. 39.

Overbeck, G.E., Muller, S.C., Fidelis, A., Pfadenhauer, J., Pillar, V.D., Blanco, C.C., Boldrini, I., Both, R., Forneck, E.D., 2007. Brazil's neglected biome: the South Brazilian Campos. Perspectives in Plant Ecology, Evolution and Systematics. 9, 101-116.

Pieruschka, V.J, Behling, H., 2011. Palaeoenvironmental history of the São Francisco de Paula region in southern Brazil during the late Quaternary inferred from the Rincão das Cabritas core. The Holocene. 22, 1251-1562.

Pieruschka, V.J., Pillar, V.D., De Oliveira, M.A.T., Behling, H., 2012. New insights into vegetation, climate and fire history of southern Brazil revealed by a 40,000 year environmental record from the State Park Serra do Tabuleiro. Vegetation History Archaeobotany. 22, 299-314.

Prentice, I.C., 1980. Multidimensional scaling as a research tool in Quaternary palynology: A review of theory and methods. Review of Palaeobotany and Palynology. 31, 71-104.

RBMA – Reserva da Biosfera da Mata Atlântica, 1999. Caderno n° 15 Mata Atlântica: Ciência, conservação e políticas. Workshop científico, São Paulo.

Rodrigues-Filho, S., Behling, H., Irion, G., Müller, G., 2002.Evidence for lake formation as a response to an inferred holocene climate transition in Brazil. Quaternary Research. 57, 131-137.

Rodrigues, J.M., Behling, H., Giesecke, T., (2016) Differentiating vegetation types from eastern South American ecosystems based on modern and subfossil pollen samples - evaluating modern analogues. Vegetation History Archaeobotany.

Rohling, E.J., Pälike, H., 2005. Centennial-scale climate cooling with a sudden cold event around 8,200 years ago. Nature. 434, 975–979.

Safford, H.D., 1999. Brazilian páramos II. Macro- and mesoclimate of the campos de altitude and affinities with high mountain climates of the tropical Andes and Costa Rica. The Journal of Biogeography. 26, 739-760.

Sant'Anna Neto, J.L., Nery, J.T., 2005. Variabilidade e mudanças climáticas no Brasil e seus impactos, in: Souza, G.R.G., Suguio, K., Oliveira, M.A.S., Oliveira, P.L. (Eds.), Quaternário do Brasil. Ribeirão Preto: Holos Editora, pp 28–50.

Seppä H., Birks H.J.B., Giesecke T., Hammarlund, D., Alenius, T., Antonsson, K., Bjune, A.E., Heikkilä, M, MacDonald, G.M., Ojala, A.E.K., Telford, R.J., Veski, S., 2007. Spatial structure of the 8200 cal yr BP event in northern Europe. Climate of the Past. 3, 225–236.

Shuman, B., Bartlein, P., Logar, N., Newby, P., Webb III, T., 2002. Parallel climate and vegetation responses to the early Holocene collapse of the Laurentide Ice Sheet. Quaternary Science Reviews. 21, 1793-1805.

Simpson, G.L., Birks, H.J.B., 2012. Statistical Learning in Palaeolimnology. in: Birks, H.J.B, Lotter, A.F., Juggins, S., Smol, J.P. (Eds) Tracking Environmental Change Using Lake Sediments. Springer, Dordrecht, pp. 249-327.

Smith, A.G., Pilcher, J.R., 1973. Radiocarbon dates and vegetational history of the British Isles. New Phytol 72(4),903–914.

Stríkis, N.M., Cruz, F.W. Jr., Cheng, H., Karmann, I., Edwards, R.L., Vuille M., Wang, X., de Paula, M.S., Novello, V.F., Auler, A.S., 2011. Abrupt variations in South American monsoon rainfall during the Holocene based on a speleothem record from central-eastern Brazil. Geology. 39 (11),1075-1078.

Taylor, B. L., 2010. A speleothems-based high resolution reconstruc-tion of climate in southeastern Brazil over the past 4,100 years,M.S. thesis, University of Massachusetts.

Tinner, W., Lotter, A.F., 2001. Central European vegetation response to abrupt climate change at 8.2 ka. Geology 29, 551–554.

Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991. Classificação da vegetação brasileira adaptada a um sistema universal. IBGE, Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro.

Veríssimo, N., Safford, H.D., Behling, H., 2012. Holocene vegetation and fire history of the Serra do Caparaó, SE Brazil. The Holocene. 23, 1,243–1,250

Verschuren, D., Sinninghe Damsté J.S., Moernaut, J., Kristen, I., Blaauw, M., Fagot, M., Haug, G.H., CHALLACEA Project Members, 2009. Half-precessional dynamics of monsoon rainfall near the East African equator. Nature. 462, 637–641.

Von Post, L., 1918. Skogsträdpollen i sydsvenska torvmosselagerföljder. Forhandlinger ved de 16. Skand Naturforskeresmøte 1916:433–465.

Von Post, L., 1946. The Prospect for Pollen Analysis in the Study of the Earth's Climatic History. In: New Phytologist, Bd. 45, S. 198-203.

Vuille, M., Burns, S.J., Taylor, B.L., Cruz, F.W., Bird, B.W., Abbott, M.B., Kanner, L.C., Cheng, H., Novello, V.F., 2012. A review of the South American monsoon history as recorded in stable isotopic proxies over the past two millennia. Clim. Past. 8, 1309-1321.

Wang, X.F., Auler, A.S., Edwards, R.L., Cheng, H., Ito, E., Solheid, M., 2006. Interhemispheric anti-phasing of rainfall during the last glacial period. Quaternary Science Reviews. 25(23-24), 3391-3403.

Wang, X.F., Auler, A.S., Edwards, R.L., Cheng, H., Ito, E., Wang,Y.J., Kong, X.G., Solheid, M., 2007. Millennial-scale precipitation changes in southern Brazil over the past 90,000 years. Geophysical Research Letters. 34.

Chapter 4

Vegetation patterns in south and southeast Brazil during the Late Quaternary

Jackson Martins Rodrigues[1,1], Hermann Behling[1,2], Thomas Giesecke[1,3*],

1 – Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for Plant Sciences, Georg-August-University of Göttingen, UntereKarspüle 2, 37073 Göttingen/Germany

Abstract

Pollen spectra are a strong tool for identification of the vegetation features. Regarding past periods, fossil pollen samples are used to reconstruct the past vegetation patterns and its related changes through time. In this study aiming to identify the vegetation patterns during the late Quaternary, we used 2 different types of exploratory techniques -1 uncontrained cluster analysis and 1 classification based on indicator taxa threshold – to explore pollen averages in bins of 500 cal yrs from 16 pollen records. Moreover, the pollen variability was explored by principal curves (PC), For that, the chronology of all samples used was reconstructedusing Oxcal. Both, classification and cluster analysis, firstly divided the pollen samples into two major groups (high Poaceae – HP, low Poaceae – LP, A and B, respectively) represented by open and forested features. Moreover, both showed that the environment of south and southeast Brazil was largely dominated by taxa from open landscapes during long periods. PC also captured the oscillation between open and forested landscapes. The more detailed cluster analysis could not interpret the differences, as good as threshold classification, but a

combination of both give a reliable perspective of how vegetation in the past was at different locations.

Keywords: Pollen classification, cluster analysis, Brazilian vegetation, vegetation types, late Quaternary

4.1   Introduction

Analytical pollen records are important proxy for reconstructions of Quaternary vegetation history. Long-term records provide detailed time-series assessment of ecosystem variability and consequential vegetation changes as responses to past disturbances (Willis and Birks 2006). Therefore, they have been widely used to identify vegetation composition patterns and to provide insights about vegetation dynamics through time.

However, the relationship between pollen composition and surrounding vegetation may not be linear (Prentice and Webb, 1986). The complex pollen/vegetation representation comes from variations in pollen production, preservation, dispersion, sorting in sedimentation and disturbance on sediments (Nakagawa et al. 2002; Brewer et al. 2007). In order to deal with such of limitations, researchers have been developing and improving techniques that aim to infer the local and regional structure of the past vegetation that originated the fossil pollen (see Birks and Birks, 1980; Birks et al. 2010). Despite the methodology used for either palaeovegetation interpretations or reconstructions, the changes on terrestrial vegetation distributions during the Quaternary are interpreted as response to climatic fluctuations. The underlying background for understanding past vegetation is the principle of ''uniformitarianism'', which assumes that environmental preferences and tolerances of modern taxa are the same in fossil samples (Birks and Seppä 2004; Birks et al. 2010). Thus assuming that this relationship has not changed through time, the modern pollen assemblages can be used as analogue for past conditions (Birks and Birks, 1980).

Most of Quaternary vegetation reconstructions, due to data density available, report the northern hemisphere environmental history (e.g. Huntley 1990; Giesecke et al. 2011).The South America, on the other hand, despite the increasing interests during the last decades, is still poorly explored and the individual studies are barely connected. Although lacking a better integration, the local researches carried out in Brazil have

identified timing similarities on landscapes. These studies suggest that during the late Pleistocene the dry forest and tropical seasonal forest, common on southeastern Brazil, were restricted to isolated refugees while most of landscape was characterized by open semi-arid formations (Behling and Lichte 1997; Ledru et al. 1998; Behling 2002). For Araucaria forest, typical subtropical forest at southern Brazil, similar conditions is reported once its taxa indicators were rare and restricted to few forest galleries on mountains and slopes where certain limits of moisture and temperature propitiated its preservation (Behling 1997).

Fossil pollen samples revealed that the transition to the Holocene, was marked by slightly increase on moisture mainly in central and southeastern Brazil, where replacement of glacial grasslands occurred by expansion of cerrado or semi deciduous forests (Behling 1998). Later, from the mid to late Holocene, the climate became warmer and moister in due to intensification of South American Monsoon (Behling and Hooghiemstra 2001) allowing the expansion of Araucaria forest through water sources, mainly after 4000 years BP and rapidly after 1000 BP (Oliveira and Pillar 2004).

Some combinations of pollen records have been used aiming to draw a broad perspective of vegetation dynamics through time, rather than local. Marchant et al. (2009), for example, using Biomisation technique assigned several modern pollen assemblages from Latin America into plant functional types and well represented the biomes where they were collected from. The analysis was extended to a set of fossil pollen records and produced a clear portray of biomes occurrence on study region for 18000 and 6000 years BP.

Despite all efforts applied, pollen records are difficult to use for reconstruction of past vegetation (Anderson et al. 2006) mainly in non-analogue situations. Such of conditions can result from unique biotic interactions, vegetation dynamics, novel climates, anthropogenic influence and lack of modern samples (Jackson and Williams 2004). Moreover, a poorly constrained pollen vegetation relationship, such as inter-taxonomic differences in pollen productivity and dispersal, and the spatial structure of the surrounding vegetation may hamper or lead to errors on fossil interpretations (Mazier et al. 2015). In recent study, Rodrigues et al. (2016) by exploring similarities combined with abundance threshold of taxa from the Atlantic rainforest classified the pre-colonization pollen assemblages, the best representation of natural vegetation, into 7 groups. The authors applied the same methods to 2 other time slices and noticed that 3000 cal years of natural changes were equivalent in intensity to 500 cal years of

anthropic impacts. Furthermore, they concluded that the human induced landscape may have compromised the capability of surface pollen to act as modern analogues.

Vegetation distribution across landscapes is mainly controlled by climate (Woodward and Williams, 1987). Due to plants high sensibility, the vegetation types can quickly reflect any variation of environmental patterns (Gosz 1992) and the palaeochanges identified in pollen diagrams are often gradual in space and time and may be a result of steady climate change (Giesecke et al. 2011). In this context, the Atlantic rainforest, the second largest tropical moist forest in the world, gains considerably importance once it is highly threatened and fragmented biome (Ribeiro et al. 2011) and poorly studied in palaeoecological perspective. Thus, the main aim of this study is to addresses the detection of natural vegetation patterns in time using pollen records from southern and southeastern Brazilian biome Mata Atlântica during the Late Quaternary.

4.2   Study area

The study area comprises tropical and subtropical ecosystems of southeastern and southern Brazil between approximately 22° and 30° southern latitude (Fig. 1). A total of 16 pollen records covering different periods of the Late Quaternary extending up to 49000 years are used from this region mainly derived from small wetlands and lakes representing vegetation types such as grassland, shrublands, tropical and subtropical forest types (Fig. 1, Table 1).
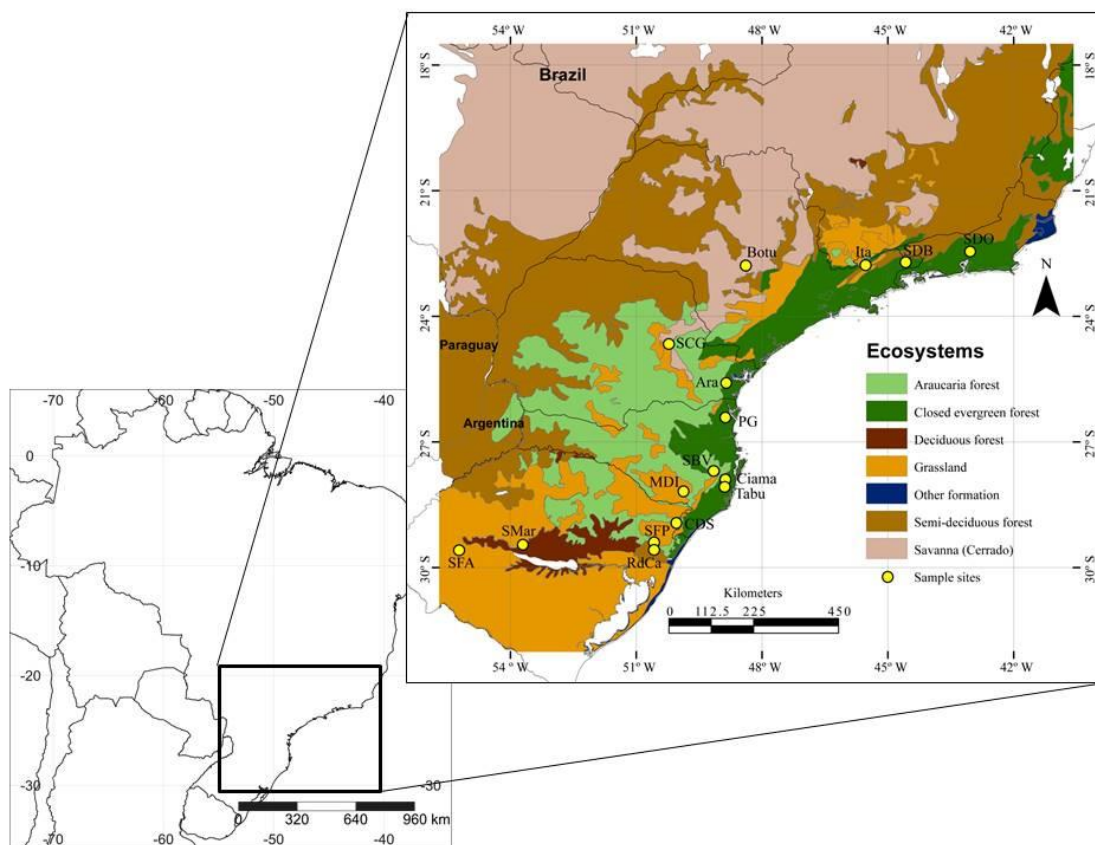
Figure 1 – Map with the ecosystems according to RBMA (1999) in eastern South America. Yellow circles indicate the location of the sites of the pollen diagrams.

Numbers	Sites	Codes	Lat.	Lon.	Elevation m.a.s.l	Publications
1	Serra dos Órgãos	SDO	-22.46	-43.03	2130	Behling and Safford (2010)
2	Serra da Bocaina	SDB	-22.71	-44.57	1650	Behling et al. (2007)
3	Morro do Itapeva	Ita	-22.78	-45.53	2082	Behling (1997)
4	Botucatu	Botu	-22.8	-48.38	750	Behling et al.(1998)
5	Serra dos Campos Gerais	SCG	-24.67	-50.22	1200	Behling (1998)
6	Araçatuba	Ara	-25.92	-48.98	1500	Behling (2007)
7	Poço Grande	PG	-26.42	-48.87	800	Behling (1998)
8	Serra da Boa Vista	SBV	-27.7	-49.15	1160	Behling (1998)
9	Serra do Tabuleiro	Tabu	-27.78	-48.88	861	Unpublished
10	Ciama	Ciama	-27.9	-48.87	860	Jescke-Pieruschka et al. (2012)
11	Morro da Igreja	MDI	-28.18	-49.87	1308	Behling (1995)
12	Cambará do Sul	CDS	-29.05	-50.1	974	Behling et al. (2004)

13	São Francisco de Paula	SFP	-29.4	-50.57	900	Behling et al., (2001)
14	São Martinho	SMar	-29.46	-53.7	450	Bauermann et al. (2008)
15	Rincão das Cabritas	RdCa	-29.48	-50.57	895	Jescke-Pieruschcka and Behling (2011)
16	São Francisco de Assis	SFA	-29.59	-55.22	100	Behling et al. (2005)

Table 1: List of sites analysed

The vegetation formations include the subtropical forest known as Araucaria forest which is characterized by dominance of *Araucaria angustifolia*, *Podocarpus lambertii*, *Ilex* and others. This vegetation type is located predominantly at southern plateau but it can occurs in small patches at southeast highlands, where rainfall rates are over 1400 mm per year and annual average temperature is around 15 °C. In the summer, the maximum temperatures can reach 30 °C and the lowest recorded temperature in winter is -10 °C (Nimer 1989; Veloso et al. 1991). Herbs dominate campos vegetation and form a mosaic with *Araucaria* forest, spreading over large areas of southern Brazil, where temperatures can reach 35 °C in summer and the presence of frost is common during the winter (Boldrini 2009; Nimer, 1989). Small areas of grasslands vegetation (campos de altitude) are also found in southeastern Brazil, where it occurs at escarpments, plateaus and top of mountains above 1800 m a.s.l. of Serra da Mantiqueira and Serra do Mar where the annual precipitation rate is around 1800 mm and temperatures vary between 16 and 22 ºC (Nimer 1989; Overbeck et al. 2007; Safford 1999). The mountain chains of Serra da Mantiqueira and Serra do Mar divide the coastal and hinterland vegetation. The coastal vegetation is formed by closed evergreen forest in general located between 0 and 1000 m elevation with high precipitation rates that come from Atlantic ocean in consequence of orography (Sant'Anna Neto and Nery 2005; Veloso et al. 1991). At leeward locations of southeastern Brazil, there is the occurrence of semi-deciduous forests that are characterized by two well defined seasons, one rainy season followed by a long drought period up to 5 months when plants loose between 20-50% of their leaves (IBGE 1995; Nimer 1989;Veloso et al. 1991).

4.3 Methods

4.3.1 Age-depths model

The pollen dataset covers 16 sites which results were published between 1997 and 2012 (Table 1) includes different numbers of radiocarbon dates ranging from 2 up to 7 depending on the core length and resolution. As number of C^{14} dated pollen samples varies significantly from site to site, age-depth model for each site was recalculated in order to acquire a consistent and comparable chronology. Thus, we constructed for all pollen records a Bayesian age models using Oxcal version 4.2 (Ramsey 2009) and SHCal13 calibration curve (Hogg et al. 2013). The Poisson process was used to describe the sedimentation across profiles as performed in the deposition model *P_Sequence (name, k_0, p, D)* in which, k_0 describes the sedimentation rate in events per unit depth, *p* (interpolation rate) was set as of 0.2 resulting in 1 output every 5 cm and *D* was set to range between -2 and 2 allows *k* to vary between 0.01 and 100 cm^{-1} (Ramsey and Lee 2013).

Probability distribution functions (PDF) of entire profiles were built by placing the prior age information for individual depth within paired *Boundary()* functions defining a uniformly distributed group. The upper boundary was constrained by an age for the top sample, which was assumed to represent the year of core collection, described by a normal distribution with a standard deviation of 25 years. The resulting age distributions spread over different periods depending on number and proximity to radiocarbon dates. Thus, the unique age for a single level on stratigraphy was achieved by weight averaging each probability distribution, and the maximum value noticed was assumed as the most likely age for a specific depth. Once the probability distribution calculated by Oxcal is based on the Gregorian calendar, we transformed all ages to the cal. BP scale by subtracting 1950 years.

4.3.2 Data treatment

All 16 pollen diagrams were harmonized to the same nomenclature and taxonomic level of identification allowing comparisons, furthermore, they were treated in two steps in order to reduce the noise. Initially, pollen counts from Cyperaceae, local fern spores (e.g. *Blechnum* type, *Salvinia* type, *Isoetes* and others) and exotic plants (*Eucalyptus* and

Pinus) were removed. The first two pollen sets removed are highly influenced by local conditions rather than general vegetation composition and the last one do not represent the natural vegetation once they were introduced by human during the last few hundred years.

Then, to obtain a time perspective on past vegetation classifications, bins of every 500 years were produced by averaging pollen counts within this interval. The further treatment was applied to resulting data matrices which consisted on removing all single occurrences, since their true abundance per sample cannot be estimated because they may be chance encounters of rare or distant parent species or a chance underrepresentation of a characteristic taxon from the region. The pollen counts were transformed into percentages and finally, the most representative taxa were selected by removing those with abundance less than 0.5%. Thus, the percentages of the new dataset of each site were recalculated, square root transformed to stabilize the variance and to balance the influences of the most and least abundant taxa (Legendre and Birks 2012; Prentice 1980).

4.3.3   Numerical Analysis

4.3.3.1   Cluster Analysis

Once individual taxa patterns are easily detectable within a pollen dataset (Huntley and Webb 1989), local and time variability conditions among sites are achieved by exploring the "noise" in entire the data. This noise can be explored with distance measurements that provide dissimilarity coefficients site-to-site. Here we used squared chord distance (SCD), which has been used in many palaeoecological studies e.g. Overpeck et al. 1985; Anderson et al. 1989; Davis et al. 2000), because it balances the importance of less abundant taxa and dampens the dominant ones. Moreover, SCD optimizes characteristics in relationship to other dissimilarity measures when used with pollen assemblages from a wide variety of vegetation types (Gavin et al. 2003; Whal 2004).

Aiming to recognize discontinuous subsets in combined pollen records, which is sometimes discrete (as in taxonomy), and most often perceived as continuous in ecology (Borcard et al. 2011) we used the dissimilarity matrix created by SCD and performed an unconstrained hierarchical agglomerative cluster analysis to 16 combined pollen records

ordered from north to south. Thus, the dendrogram was built based ward's minimum variance clustering which aims to define groups in such a way that the within-group sum of squares is minimized (Borcard et al. 2011) This method involves an agglomerative clustering algorithm that look for groups of leaves forming branches, amalgamates branches into limbs and so on, until all the observations are included into one cluster.

The IndVal (Indicator Species Analysis) index was used to evaluate the indicator species within clusters of sites (Dufrêne and Legendre 1997). This method combines a species mean abundances and its frequencies of occurrence in the groups. A high indicator value is obtained by a combination of large mean abundance within a group compared to the other groups (specificity) and presence in most sites of that group (fidelity) (Borcard et al. 2011).

The final number of clusters was subjectively selected based in part upon examination of the indicator species (IndVal) criteria that has *p value* $<= 0.05$ (Borcard et al. 2011) and assessment of their palynological reliability.

4.3.3.2 Principal Curve

The latent structures within all 16 combined datasets were explored with principal curves (PC) that are smooth one-dimensional curves fitted in a multidimensional data space (Hastie and Stuetzle 1989). PC minimizes the sum of squared deviations between the observations and the fitted curve in an iterative process from an initial configuration (De'ath 1999) for which we used the order of samples based on the result from the correspondence analysis (CA).

4.3.3.3 Pollen classification

Rodrigues et al. (2016) based on abundance indicators taxa (Poaceae, *Weinmannia*, Melastomataceae/Combretaceae, *Cecropia* and Arecaceae) carried out an ecosystem classification, of the 27 pollen assemblages that best represents the natural vegetation, and noticed a good agreement between pollen assemblages and the surrounding vegetation. The threshold of 23% of Poaceae splits the sites with either low or high Poaceae.

On high Poaceae branch further divisions were performed based on combination of Melastomataceae and *Weinmannia*, the values higher than 15% were classified as HPST (High Poaceae Subtropical-tropical) and the lower ones were split into two other subgroups. Based on 8% Arecaceae abundance, values higher than this threshold was classified as HPPS (high Poaceae Parkland savannah) and lower were further split into two final groups. The last two groups of high Poaceae branch were yielded based on *Weinmannia* abundance, in which abundances high than 1% were classified as HPSW (high Poaceae Subtropical woodland) and lower values were classified as HPGr (high Poaceae Grassland)

The sites classified as low Poaceae were initially split based on *Weinmannia* abundance. The pollen assemblages with values higher than 5% was identified LPSF (low Poaceae Subtropical forest). Those samples with values lower than 5% were further split into two final branches that explored *Cecropia* abundance. Those pollen assemblages with values higher than 5% of *Cecropia* were grouped into LPSD (low Poaceae Semi-deciduous) while the rest of samples with values lower than this threshold were classified as LPST (low Poaceae subtropical-tropical).

All analysis were performed in R (R Core Team 2012) with the vegan package (Oksannen et al. 2013), Analogue (Simpson and Oksanen 2007; Simpson 2014), labdsv (Roberts 2010), cluster (Maechler et al. 2005).

4.4 Results

4.4.1 Vegetation patterns evidenced by unconstrained cluster

The unconstrained cluster analysis (Fig. 2) firstly divided the 435 pollen samples into two major groups A and B formed 190 and 245 samples, respectively. This division is driven by combination dominance of taxa indicators of open landscapes and forested ones. For group A, IndVal index with *p value* lower than 0.05 pointed out 13 taxa of herbs and 6 of tree/shrubs as the most representative for group determination. In this group, taxa of Apiaceae, *Plantago*, Asteraceae and Poaceae presented IndVal higher than 0.5 and frequency superior to 323 occurrences (table 2). Moreover, their average abundance is 7.9, 3.5, 14.9 and 60.7 %, respectively while others herbs and tre/shrubs occurs in lower values. The dominant pollen composition of group B is the combination of open landscapes and woodland indicators once IndVal index with *p value* lower than

0.05 highlighted 102 taxa of tree/shurbs and 23 of herbs as the most important for its characterization. Furthermore, for major cluster B, the taxa of *Weinmannia*, *Myrsine*, Myrtaceae, Euphorbiaceae, *Ilex*, Moraceae/Urticaceae, *Symplocos*, Arecaceae, Sapindaceae and Fabaceae are those that have IndVal of 0.5 or higher and frequency ranging from 183 up to 378 occurrences while their average abundances are respectively, 10.5, 6.11, 4.4, 2.71, 1.54, 1.8, 0.8, 1.2, 0.42, 1.19 %.
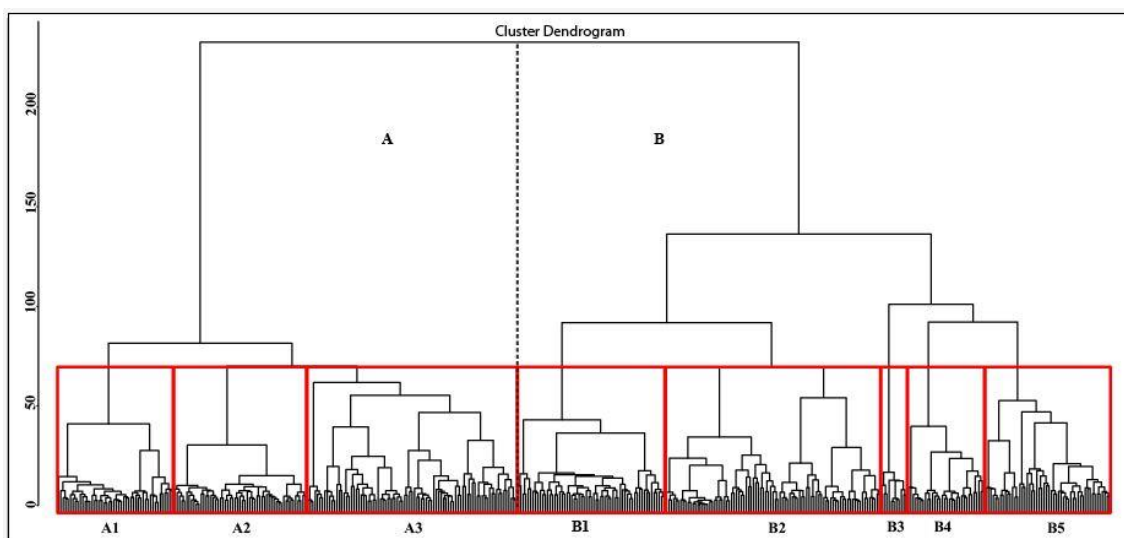
Figure 2 - Unconstrained cluster analysis of 16 combined pollen records

Taxa	Type	cluster	IndVal	p-value	Freq.		Taxa	Type	cluster	IndVal	p-value	freq
Apiaceae	Hb	A	0.73	0.001	393		Trema.type	Tr/Sh	B	0.36	0.001	147
Plantago	Hb	A	0.67	0.001	323		Lamanonia speciosa	Tr/Sh	B	0.35	0.001	119
Asteraceae	Hb	A	0.57	0.001	433		Solanaceae	Hb	B	0.30	0.001	159
Poaceae	Hb	A	0.54	0.001	435		Gordonia	Tr/Sh	B	0.27	0.001	71
Amaranthaceae	Hb	A	0.42	0.001	253		Piper	Tr/Sh	B	0.27	0.001	79
Euriocaulaceae	Hb	A	0.38	0.001	193		Griselinia ruscifolia	Tr/Sh	B	0.26	0.001	65
Rubiaceae	Tr/Sh	A	0.37	0.001	198		Araliaceae	Tr/Sh	B	0.25	0.001	71
Convulvaceae	Tr/Sh	A	0.18	0.001	37		Sabiaceae	Tr/Sh	B	0.24	0.001	81
Ranunculus	Hb	A	0.18	0.001	57		Banara xylosma	Tr/Sh	B	0.22	0.001	57
Caryophyllaceae	Hb	A	0.17	0.001	48		Hyeronima	Tr/Sh	B	0.22	0.001	58
Oxalis	Hb	A	0.14	0.049	81		Hedyosmum.	Tr/Sh	B	0.21	0.001	54
Ephedra	Tr/Sh	A	0.13	0.007	64		Stryax	Tr/Sh	B	0.20	0.001	79
Lytraceae	Hb	A	0.09	0.013	38		Loranthaceae	Tr/Sh	B	0.18	0.001	81
Schrophulariaceae	Tr/Sh	A	0.08	0.001	18		Anacardiaceae	Tr/Sh	B	0.18	0.001	83
Thymelaeceae	Tr/Sh	A	0.05	0.006	16		Rutaceae	Tr/Sh	B	0.17	0.001	71
Hypericum	Hb	A	0.05	0.001	11		Tetrorchidium rubriveium	Tr/Sh	B	0.17	0.001	51
Tiliaceae	Tr/Sh	A	0.03	0.018	9		Begonia	Tr/Sh	B	0.12	0.001	35
Brasicaceae	Hb	A	0.03	0.021	5		Proteaceae	Tr/Sh	B	0.11	0.004	46

Liliaceae.type	Hb	A	0.03	0.018	5		Ochnaceae	Tr/Sh	B	0.10	0.001	24
Weinmannia	Tr/Sh	B	0.89	0.001	304		Clusia	Tr/Sh	B	0.09	0.001	23
Myrsine	Tr/Sh	B	0.72	0.001	369		Pera	Tr/Sh	B	0.08	0.001	19
Myrtaceae	Tr/Sh	B	0.70	0.001	378		Onagraceae	Tr/Sh	B	0.07	0.001	20
Euphorbiaceae	Tr/Sh	B	0.67	0.001	349		Slonaea.type	Tr/Sh	B	0.07	0.001	20
Ilex	Tr/Sh	B	0.66	0.001	246		Alestroemeria	Hb	B	0.07	0.005	26
Moraceae/Urticaceae	Tr/Sh	B	0.63	0.001	292		Gunnera	Hb	B	0.06	0.002	15
Symplocos	Tr/Sh	B	0.58	0.001	184		Apocynaceae	Tr/Sh	B	0.06	0.008	20
Arecaceae	Tr/Sh	B	0.53	0.001	231		Rhamnus.type	Tr/Sh	B	0.05	0.003	16
Sapindaceae	Tr/Sh	B	0.53	0.001	183		Gallesia	Tr/Sh	B	0.05	0.001	13
Fabaceae	Tr/Sh	B	0.50	0.001	338		Phyllanthus.type	Tr/Sh	B	0.05	0.001	13
Clethra	Tr/Sh	B	0.49	0.001	167		Bromeliaceae	Tr/Sh	B	0.05	0.013	15
Xyris	Hb	B	0.49	0.001	270		Salix.type	Tr/Sh	B	0.04	0.007	14
Celtis	Tr/Sh	B	0.47	0.001	277		Ternstroemia brasiliensis	Tr/Sh	B	0.04	0.003	11
Drimys brasiliensis	Tr/Sh	B	0.43	0.001	132		Hippiastrum	Hb	B	0.04	0.003	10
Araucaria angustifolia	Tr/Sh	B	0.41	0.001	217		Cactaceae	Tr/Sh	B	0.04	0.011	9
Podocarpus	Tr/Sh	B	0.39	0.001	264		Clematis.doica	Tr/Sh	B	0.04	0.016	9
Ericaceae	Tr/Sh	B	0.39	0.001	136		Cassuarina	Tr/Sh	B	0.02	0.042	6
Cecropia	Tr/Sh	B	0.36	0.001	94							

Table 2: List of selected taxa based on IndVal for 2 major clusters A and B. Tr/Sh – Tree/Shrubs; Hb - Herbs

At next level, both clusters A and B were subdivided into smaller groups. The cluster A was divided into 3 subgroups (A.1, A.2 and A.3) and cluster B into other 5 subgroups (B.1, B.2, B.3, B.4 and B.5). The cluster A.1 is formed by all 39 samples of site SFA between 25500 and 0 cal yrs BP, 1 sample (3500-4000 cal yrs BP) of SMar and 8 samples between 15500 and 11500 cal yrs BP of site SCG. The IndVal index ranging from 0.13 to 0.64, shows 3 taxa of tree/shrubs (Convolvaceae, Rubiaceae and Tiliaceae) and 3 of herbs (Amaranthaceae, Caryophyllaceae and Poaceae) as the most important for this group definition. Despite the balanced number of indicators, the average abundance of herbs (Amaranthaceae – 1.25 %, Caryophyllaceae - 0.19 % and Poaceae - 76.29 %) is higher than tree/shrubs (Convolvaceae – 0.68%, Rubiaceae – 1.56 % and Tiliaceae – 0.7 %). The cluster A.2 is formed by 55 samples of site CDS between 49500 and 15500 cal yrs BP. For this group, the IndVal index which varies between 0.09 and 0.44, showed 5 types of herbs that are in average most abundant (Eriocaulaceae – 2.48 %, *Plantago* – 5.46 %, Apiaceae - 15.33 %, Asteraceae - 20.46 % and Brasicacecae 0.18%) and 2 of tree/shrubs that occur in small proportions (Boraginaceae - 0.1% and *Podocarpus* - 0.48) as the most important for its

characterization. The cluster A.3 ifs formed by the largest number of sites, 8 in total, covering different time periods. It encompasses 2 samples from SDB for period between 9500 and 8000 cal yrs BP, 4 from Ita between 40500 and 25000 cal yrs BP, 10 from Botu comprising the period between 36500 and 22000 cal yrs BP and the top samples between 500 and 0 cal yrs BP, 18 samples from Ara between time period 18500 and 5000 cal yrs BP, all 8 samples from SFP for period between 6500 and 0 cal yrs BP, 7 samples from SMar for period 3500 and 0 cal yrs BP and 23 samples from RdCa covering the period between 17000 and 3500 cal yrs BP. Moreover, A.3 has the smallest IndVal index within major group A varying between 0.05 and 0.12. The smallest taxa abundance average is noticed here, being characterized by 6 type of herbs (Oxalis – 0.176 %, Lamiaceae – 0.319 %, Ranunculus – 0.14 %, Hypericum – 0.42%, Liliaceae – 0.03 % and Securidaca – 0.03%) and 1 type of tree/shrubs (Thymelaeaceae – 0.31 %).

The first subdivision of major cluster B is formed only samples from Ciama site that are in total 61 pollen samples covering the period between 45000 and 0 cal yrs BP. The taxa of tree/shrubs Sapindaceae and Ochnaceae are pointed out as the most representative for this group both with IndVal of 0.36 and low average abundance of 1.28 and 0.17 %, respectively. The subgroup B.2 encompasses the largest number of samples, in total 89, from 8 different sites. Six samples of them are from SDB site from periods between 11000 and 9500, 4500 and between 1500 and 0cal yes BP. Other ten samples are from site Ita covering period between 14000 and 9000 cal yrs BP, eighteen are from SCG from11500 cal yrs BP up to the present. The 4 most recent samples from Ara covering the time between 4500 and 0 cal yrs BP, 21 from SBV for the time window between 20500 and 12500 cal yrs BP and a second period covered from 4500 to 0 cal yrs BP. The 6 oldest samples from Tabu for the period between 13000 and 10500 cal yrs BP, all 16 from MDI site since 13000 cal yrs BP up to present and the 8 most recent from CDS for the period between 4000 and 0 cal yrs BP. The IndVal evidenced that 4 taxa of tree/shrubs (Ericaceae, Fabaceae, *Stryax* and *Cassurarina*) with index ranging from 0.06 to 0.28, average abundance between 0.014 and 1.63 % and 3 taxa of herbs (*Xyris*, Iridaceae and *Gunnera*) with index between 0.07 and 0.38 and average abundance between 0.035 and 2.3 % as the most significant for this group. The cluster B.3 is formed by all 11 samples from the site PG that cover period between 6500 and 0 cal yrs BP. This group presents the longest list of relevant taxa according to IndVal index, a total 30 taxa being 27 from tree/shrubs and 3 from herbs (table 3) varying from 0.13 up to 1 while the pollen abundance average range from 0.09 up to

39.9 %. The subdivision B.4 is composed by 31 pollen samples from 5 different sites, being 1 from SDB for the time window between 7500 – 7000 cal yrs BP, 4 from Ita 2 for period between 4500 and 3500 cal yrs BP and 2 others for the period between 8000 and 6500 cal yrs BP, 8 samples from SBV covering a period between 11000 and 4500 cal yrs BP, 12 pollen samples are from Tabu covering the period between 10000 and 4000 cal yrs BP and finally the 7 most recent samples from RdCa for the period between 3500 cal yrs BP and the present. For this subgroup, 5 taxa of tree/shrubs types (*Drimys brasiliensis*, *Weinmannia*, *Gordonia*, *Ilex*, *Clethra* and *Griselinia ruscifolia*) are highlighted by IndVal as the most important ones which IndVal index are 0.49, 0.45, 0.40, 0.33, 0.32 and 0.30, respectively and their pollen abundances vary between 0.08 and 46.3 %. The last cluster achieved from major group B is B.5 which is formed by 52 pollen samples from 5 different sites. The site SDB has 10 samples grouped as in this cluster, being 5 between 7000 and 4500 cal yrs BP and other 5 between 4000 and 1500 cal yrs BP. Ita contributes with more 6 samples being 1 from time window 5000 – 4500 and 5 covering the most recent period between 3000 cal yrs BP to present. The site SDO has all of 25 samples assigned to this last group, while Botu has 3 covering the period between 6000 and 500 cal yrs BP and the most recent 8 samples from Tabu cover the time from 4000 up to the present. The IndVal calculated for the group B.5 varies between 0.06 and 0.58. Moreover, it showed 16 taxa as the most important for this group characterization, which 14 are taxa from tree/shrubs that have average abundance ranging from 0.009 up to 7.9 % and 2 are from herbs that have average abundance of 0.04 and 0.02 %.

Taxa	Type	cluster	IndVal	p-value	freq		Taxa	Type	cluster	IndVal	p-value	freq
Convulvaceae	Tr/Sh	A.1	0.65	0.001	37		Malpighiaceae	Tr/Sh	B.3	0.47	0.001	15
Rubiaceae	Tr/Sh	A.1	0.38	0.001	198		Amaryllis	Hb	B.3	0.47	0.001	19
Amaranthaceae	Hb	A.1	0.27	0.001	253		Tetrorchidium rubriveium	Tr/Sh	B.3	0.42	0.001	51
Caryophyllaceae	Hb	A.1	0.20	0.001	48		Bromeliaceae	Tr/Sh	B.3	0.41	0.001	15
Poaceae	Hb	A.1	0.17	0.001	435		Arecaceae	Tr/Sh	B.3	0.38	0.001	231
Tiliaceae	Tr/Sh	A.1	0.14	0.003	9		Loranthaceae	Tr/Sh	B.3	0.37	0.001	81
							Phyllanthus	Tr/Sh	B.3	0.36	0.001	13
Euriocaulaceae	Hb	A.2	0.45	0.001	193		Euphorbiaceae	Tr/Sh	B.3	0.34	0.001	349
Plantago	Hb	A.2	0.33	0.001	323		Myrtaceae	Tr/Sh	B.3	0.34	0.001	378
Apiaceae	Hb	A.2	0.33	0.001	393		Piper	Tr/Sh	B.3	0.33	0.001	79
Boraginaceae	Tr/Sh	A.2	0.23	0.001	40		Araliaceae	Tr/Sh	B.3	0.31	0.001	71
Asteraceae	Hb	A.2	0.19	0.001	433		Celtis	Tr/Sh	B.3	0.29	0.001	277

Podocarpus	Tr/Sh	A.2	0.16	0.036	264		Sabiaceae	Tr/Sh	B.3	0.29	0.001	81
Brasicaceae	Hb	A.2	0.09	0.009	5		Araucaria angustifolia	Tr/Sh	B.3	0.28	0.001	217
							Anacardiaceae	Tr/Sh	B.3	0.26	0.002	83
Oxalis	Hb	A.3	0.12	0.019	81		Myrsine	Tr/Sh	B.3	0.25	0.001	369
Lamiaceae	Hb	A.3	0.12	0.036	122		Onagraceae	Tr/Sh	B.3	0.24	0.001	20
Ranunculus	Hb	A.3	0.12	0.023	57		Solanaceae	Hb	B.3	0.19	0.009	159
Hypericum	Hb	A.3	0.11	0.012	11		Rutaceae	Tr/Sh	B.3	0.16	0.005	71
Thymelaeceae	Tr/Sh	A.3	0.10	0.01	16		Sapotaceae	Tr/Sh	B.3	0.14	0.003	32
Liliaceae	Hb	A.3	0.06	0.037	5							
Securidaca	Hb	A.3	0.05	0.047	9		Drimys brasiliensis	Tr/Sh	B.4	0.49	0.001	132
							Weinmannia	Tr/Sh	B.4	0.46	0.001	304
Sapindaceae	Tr/Sh	B.1	0.37	0.001	183		Gordonia	Tr/Sh	B.4	0.40	0.001	71
Ochnaceae	Tr/Sh	B.1	0.36	0.001	24		Ilex	Tr/Sh	B.4	0.34	0.001	246
							Clethra	Tr/Sh	B.4	0.32	0.001	167
Xyris	Hb	B.2	0.39	0.001	270		Griselinia ruscifolia	Tr/Sh	B.4	0.31	0.001	65
Ericaceae	Tr/Sh	B.2	0.28	0.001	136							
Fabaceae	Tr/Sh	B.2	0.17	0.017	338		Cecropia	Tr/Sh	B.5	0.59	0.001	94
Iridaceae	Hb	B.2	0.15	0.036	267		Trema	Tr/Sh	B.5	0.44	0.001	147
Stryax	Tr/Sh	B.2	0.13	0.017	79		Begonia	Tr/Sh	B.5	0.37	0.001	35
Gunnera	Hb	B.2	0.08	0.043	15		Moraceae.Urticaceae	Tr/Sh	B.5	0.35	0.001	292
Cassuarina	Tr/Sh	B.2	0.07	0.009	6		Symplocos	Tr/Sh	B.5	0.32	0.001	184
							Melastomataceae/ Combretaceae	Tr/Sh	B.5	0.30	0.001	303
Ternstroemia brasiliensis	Tr/Sh	B.3	1.00	0.001	11		Slonaea	Tr/Sh	B.5	0.27	0.002	20
Apocynaceae	Tr/Sh	B.3	0.86	0.001	20		Lamanonia speciosa	Tr/Sh	B.5	0.22	0.003	119
Clematis.doica	Tr/Sh	B.3	0.82	0.001	9		Pera	Tr/Sh	B.5	0.19	0.001	19
Malvaceae	Tr/Sh	B.3	0.76	0.001	86		Gallesia	Tr/Sh	B.5	0.12	0.005	13
Banara xylosma	Tr/Sh	B.3	0.75	0.001	57		Menispermaceae	Tr/Sh	B.5	0.12	0.006	6
Cactaceae	Tr/Sh	B.3	0.67	0.001	9		Proteaceae	Tr/Sh	B.5	0.08	0.04	46
Hyeronima	Tr/Sh	B.3	0.66	0.001	58		Linum	Hb	B.5	0.08	0.026	11
Clusia	Tr/Sh	B.3	0.65	0.001	23		Meliaceae	Tr/Sh	B.5	0.08	0.03	11
Hedyosmum	Tr/Sh	B.3	0.63	0.001	54		Notofagus	Tr/Sh	B.5	0.07	0.03	10
Hippiastrum	Hb	B.3	0.51	0.001	10		Drosera	Hb	B.5	0.06	0.023	5

Table 3: List of selected taxa based on IndVal for 8 clusters (A.1, A.2, A.3, B.1, B.2, B.3, B.4 and B.5) and further information. Tr/Sh – Tree/Shrubs; Hb - Herbs

4.4.2 *Principal curves – PC*

Principal curve (PC) is one-dimensional curve that pass through the middle of a multidimensional dataset and can thus explain a larger proportion of variance than the first axis in a principle component or correspondence analysis (Simpson and Birks,

2012). Therefore, PC explains 57 % of variance for 16 combined pollen dataset and similar amount (58 %) of explained variance is reached with 3 axes of principal components analysis.

The curve designed by PC shows oscillations through the samples. These variations are mainly related with the 2 major patterns identified, open and forested landscapes, for the 435 samples analyzed. The low values represent samples with dominance of herbs and while the peaks indicate more forested landscapes. A comparison between PC and abundance of Poaceae and *Weinmannia* (Fig. 3), the highest IndVal's among herbs and tree/shrubs, respectively, shows this correspondence once the low (high) amounts of Poaceae and the high (low) presence of *Weinmannia* are represented by peaks (base) noticed on PC.
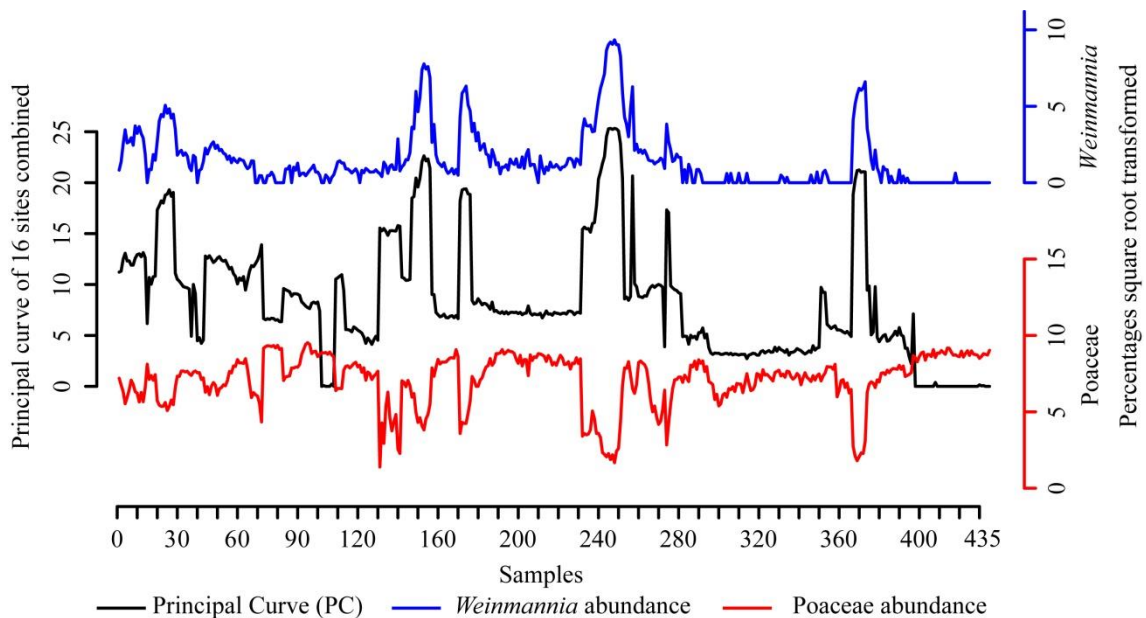
Figure 3 - Parallel comparison of Principal Curve (PC), *Weinmannia* and Poaceae abundances of 16 combined pollen records

4.4.3 Vegetation classification using pollen threshold

The vegetation classification performed by Rodrigues et al. (2016) starts with 2 major division using Poaceae as indicator for differentiation between more or less open landscapes. Applied to all 435 samples here studied, the major group identified as high Poaceae is observed for the 386 samples while the low Poaceae is noticed for the other 49 samples.

Within high Poaceae classification, the final cluster named HPGr is the most common occurring in 218 samples of 15 pollen records. At site CDS it covers 68 samples covering the period between 50000 up to 4500 cal yrs BP, moreover, this vegetation type is noticed for all samples of sites SFP (8 samples). SMar (8 samples), SFA (39 samples) covering periods of the last 6500, 4500 and 25500 cal yrs, respectively. For the other sites its occurrence ranges from 1 up to 22 samples from site to site and the only exception is observed for site Tabu which has no occurrence of this classification.

The classification HPST is noticed for 38 samples from 7 pollen records. Its presence is more prominent at sites SDB, Ita, Tabu and SBV where occurs 12, 9, 6 and 5 times covering time periods between 7500 and 1500 cal yrs BP, 8000 and 500 cal yrs BP, 13000 and 10000 cal yrs BP repeating at age bin 2501-3000 cal yrs BP and at different time intervals between 13500 and 3500 cal yrs BP.

The HPSW classification is the second most common group once it occurs at 128 samples from 12 pollen records. It is noticed in 46 samples of site Ciama between 45000 and 5000 cal yrs BP, 22 samples of site SDO between 13000 cal yrs BP and present, 12 samples of SBV between 12500 cal yrs BP and present, 11 of Ita occurring once at age bin 40001 – 40500 more frequent between 14000 and 8500 cal yrs BP and once more at age bin 500 – 0. The rest of HPSW observations are present between the early and the mid Holocene except by site SBV where it most notice during the last 3500 cal yrs BP.

The last subgroup of high Poaceae branch, HPPS, is observed only twice and for the same site. For age bins 4500 – 4001 and 1000 – 501 for Botu site, the vegetation was mainly formed by open vegetation with sparse tree/shrubs.

Within the major group of low Poaceae, the subdivision LPSF is the most common once it classified 38 samples from 6 sites. Its most frequency is observed at Tabu, where 19 samples from the last 10000 cal yrs were classified as LPSF, followed by 7 occurrences of the last 3500 cal yrs of RdCa, 5 between 9000 and 5000 cal yrs BP at SBV, 1 at PG for theage bins between 6000 - 5501 and 4 and 2 samples of the last 3000 and 100 cal yrs of sites Ciama and CDS, respectively.

The classification LPST is noticed at 11 samples of 3 sites. The higher number of occurrences is observed at site PG where it is noticed at 7 samples between 6500 cal yrs BP and the present, followed by 3 samples of MDI covering the period 12000 – 11500 cal yrs and 1 sample of Botu for the age bin 6000 – 5501.

Age Bins	SDO Sample	SDO Classif.	SDO Cluster	SDB Sample	SDB Classif.	SDB Cluster	Ita Sample	Ita Classif.	Ita Cluster	Botu Sample	Botu Classif.	Botu Cluster	SCG Sample	SCG Classif.	SCG Cluster	Ara Sample	Ara Classif.	Ara Cluster	PG Sample	PG Classif.	PG Cluster	SBV Sample	SBV Classif.	SBV Cluster	Ciama Sample	Ciama Classif.	Ciama Cluster	Tabu Sample	Tabu Classif.	Tabu Cluster	MDI Sample	MDI Classif.	MDI Cluster	CDS Sample	CDS Classif.	CDS Cluster	SFP Sample	SFP Classif.	SFP Cluster	Smar Sample	Smar Classif.	Smar Cluster	RdCa Sample	RdCa Classif.	RdCa Cluster	SFA Sample	SFA Classif.	SFA Cluster
0-500	1	HPSW	B.5	26	HPGr	B.2	45	HPSW	B.5	69	HPST	A.2	83	HPGr	B.2	109	HPGr	A.2	131	LPST	B.3	142	HPSW	B.2	171	LPSF	B.1	232	LPSF	B.5	258	HPSW	B.2	274	LPSF	B.2	351	HPGr	A.2	359	HPGr	A.2	367	LPSF	B.4	397	HPGr	A.1
501-1000	2	HPSW	B.5				46	HPST	B.5	70	HPPS	B.5	84	HPGr	B.2	110	HPSW	A.2							172	LPSF	B.1	233	LPSF	B.5	259	HPSW	B.2	275	LPSF	B.2	352	HPGr	A.2	360	HPGr	A.2	368	LPSF	B.4	398	HPGr	A.1
1001-1500				27	HPSW	B.2							85	HPGr	B.2	111	HPSW	A.2	132	LPST	B.3	143	HPSW	B.2				234	LPSF	B.5				276	HPSW	B.2	353	HPGr	A.2	361	HPGr	A.2	369	LPSF	B.4	399	HPGr	A.1
1501-2000	3	HPST	B.5	28	HPST	B.5	47	HPST	B.5				86	HPSW	B.2							144	HPSW	B.2				235	LPSF	B.5				277	HPSW	B.2	354	HPGr	A.2	362	HPGr	A.2	370	LPSF	B.4	400	HPGr	A.1
2001-2500	4	HPST	B.5	29	HPST	B.5	48	HPST	B.5				87	HPGr	B.2				133	LPST	B.3				173	LPSF	B.1	236	LPSF	B.5	260	HPSW	B.2	278	HPSW	B.2				363	HPGr	A.2	371	LPSF	B.4	401	HPGr	A.1
2501-3000	5	HPSW	B.5	30	HPST	B.5	49	HPST	B.5				88	HPSW	B.2				134	HPSW	B.3	145	HPSW	B.2	174	LPSF	B.1	237	HPST	B.5				279	HPSW	B.2				364	HPGr	A.2	372	LPSF	B.4			
3001-3500	6	HPSW	B.5	31	HPST	B.5							89	HPGr	B.2				135	HPGr	B.3	146	HPSW	B.2				238	LPSF	B.5	261	HPSW	B.2	280	HPSW	B.2	355	HPGr	A.2	365	HPGr	A.2	373	LPSF	B.4	402	HPGr	A.1
3501-4000	7	HPSW	B.5	32	HPST	B.5	50	HPST	B.4										136	LPST	B.3	147	HPST	B.2	175	HPST	B.1	239	LPSF	B.5				281	HPSW	B.2				366	HPGr	A.1	374	HPSW	A.2	403	HPGr	A.1
4001-4500	8	HPSW	B.5	33	HPST	B.2	51	HPPS	B.5	71	HPPS	B.5	90	HPSW	B.2	112	HPSW	A.2	137	LPST	B.3	148	HPSW	B.2	176	HPST	B.1	240	LPSF	B.4	262	HPSW	B.2				356	HPGr	A.2				375	HPSW	A.2	404	HPGr	A.1
4501-5000	9	HPSW	B.5	34	HPST	B.5	52	HPST	B.5										138	LPST	B.3	149	HPST	B.4				241	LPSF	B.4				282	HPGr	A.2	357	HPGr	A.2				376	HPSW	A.2	405	HPGr	A.1
5001-5500	10	HPSW	B.5	35	HPST	B.5										113	HPSW	A.2	139	HPGr	B.3	150	LPSF	B.4	177	HPSW	B.1	242	LPSF	B.4													377	HPGr	A.2	406	HPGr	A.1
5501-6000	11	HPSW	B.5	36	HPST	B.5				72	LPST	B.5	91	HPGr	B.2				140	LPSF	B.3	151	LPSF	B.4				243	LPSF	B.4	263	HPSW	B.2	283	HPGr	A.2							378	HPSW	A.2			
6001-6500	12	HPSW	B.5	37	HPST	B.5										114	HPGr	A.2	141	LPST	B.3				178	HPST	B.1	244	LPSF	B.4				284	HPGr	A.2	358	HPGr	A.2				379	HPGr	A.2			
6501-7000	13	HPSW	B.5	38	HPST	B.5	53	HPST	B.4				92	HPGr	B.2							152	LPSF	B.4	179	HPSW	B.1	245	LPSF	B.4	264	HPSW	B.2	285	HPSW	A.2							380	HPGr	A.2	407	HPGr	A.1
7001-7500	14	HPSW	B.5	39	HPST	B.4							93	HPGr	B.2	115	HPGr	A.2							180	HPSW	B.1	246	LPSF	B.4																		
7501-8000	15	HPSW	B.5				54	HPST	B.4													153	LPSF	B.4	181	HPSW	B.1	247	LPSF	B.4	265	HPSW	B.2	286	HPGr	A.2							381	HPGr	A.2	408	HPGr	A.1
8001-8500	16	HPSW	B.5	40	HPGr	A.2							94	HPGr	B.2	116	HPGr	A.2							182	HPSW	B.1	248	LPSF	B.4	266	HPSW	B.2	287	HPGr	A.2												
8501-9000	17	HPSW	B.5				55	HPSW	B.2				95	HPGr	B.2	117	HPGr	A.2				154	LPSF	B.4				249	LPSF	B.4				288	HPGr	A.2							382	HPSW	A.2			
9001-9500	18	HPSW	B.5	41	HPGr	A.2	56	HPSW	B.2				96	HPGr	B.2	118	HPGr	A.2										250	LPSF	B.4	267	HPSW	B.2	289	HPGr	A.2							383	HPGr	A.2			
9501-10000	19	HPSW	B.5	42	HPGr	B.2	57	HPSW	B.2				97	HPGr	B.2	119	HPGr	A.2				155	HPST	B.4				251	LPSF	B.4				290	HPGr	A.2												
10001-10500	20	HPSW	B.5	43	HPSW	B.2	58	HPSW	B.2				98	HPSW	B.2	120	HPGr	A.2							183	HPSW	B.1	252	HPST	B.2	268	HPSW	B.2	291	HPGr	A.2							384	HPGr	A.2			
10501-11000	21	HPSW	B.5	44	HPSW	B.2							99	HPGr	B.2							156	HPST	B.4				253	HPST	B.2	269	LPST	B.2	292	HPGr	A.2							385	HPGr	A.2	409	HPGr	A.1
11001-11500	22	HPGr	B.5				59	HPSW	B.2				100	HPGr	B.2										184	HPSW	B.1	254	HPST	B.2	270	LPST	B.2	293	HPGr	A.2							386	HPGr	A.2	410	HPGr	A.1
11501-12000	23	HPSW	B.5				60	HPSW	B.2				101	HPGr	A.1	121	HPGr	A.2							185	HPSW	B.1	255	HPSW	B.2	271	LPST	B.2	294	HPGr	A.2							387	HPGr	A.2	411	HPGr	A.1

110

Range																																	
12001-12500	24	HPSW	B.5	61	HPSW	B.2	102	HPGr	A.1				157	HPSW	B.2	186	HPSW	B.1	256	HPST	B.2	272	HPSW	B.2				388	HPGr	A.2	412	HPGr	A.1
12501-13000	25	HPSW	B.5	62	HPGr	B.2	103	HPGr	A.1	122	HPGr	A.2				187	HPSW	B.1	257	HPST	B.2	273	HPGr	B.2							413	HPGr	A.1
13001-13500				63	HPSW	B.2	104	HPGr	A.1	123	HPGr	A.2	158	HPST	B.2													389	HPGr	A.2			
13501-14000				64	HPSW	B.2	105	HPGr	A.1							188	HPSW	B.1							295	HPGr	A.2	390	HPGr	A.2	414	HPGr	A.1
14001-14500							106	HPGr	A.1	124	HPGr	A.2	159	HPSW	B.2													391	HPGr	A.2			
14501-15000							107	HPGr	A.1	125	HPGr	A.2	160	HPSW	B.2	189	HPSW	B.1										392	HPGr	A.2	415	HPGr	A.1
15001-15500							108	HPGr	A.1	126	HPGr	A.2	161	HPSW	B.2	190	HPSW	B.1										393	HPGr	A.2	416	HPGr	A.1
15501-16000										127	HPGr	A.2	162	HPSW	B.2	191	HPGr	B.1							296	HPGr	A.2	394	HPGr	A.2			
16001-16500													163	HPSW	B.2	192	HPSW	B.1										395	HPGr	A.2	417	HPGr	A.1
16501-17000										128	HPGr	A.2	164	HPGr	B.2													396	HPGr	A.2	418	HPGr	A.1
17001-17500										129	HPGr	A.2	165	HPGr	B.2										297	HPGr	A.2				419	HPGr	A.1
17501-18000													166	HPGr	B.2																420	HPGr	A.1
18001-18500										130	HPGr	A.2	167	HPGr	B.2																421	HPGr	A.1
18501-19000													168	HPGr	B.2	193	HPSW	B.1							298	HPGr	A.2				422	HPGr	A.1
19001-19500																															423	HPGr	A.1
19501-20000													169	HPGr	B.2										299	HPGr	A.2				424	HPGr	A.1
20001-20500													170	HPGr	B.2																425	HPGr	A.1
20501-21000																194	HPSW	B.1													426	HPGr	A.1
21001-21500																									300	HPGr	A.2				427	HPGr	A.1
21501-22000																															428	HPGr	A.1
22001-22500				73	HPGr	A.2										195	HPGr	B.1							301	HPGr	A.2				429	HPGr	A.1
22501-23000																196	HPSW	B.1													430	HPGr	A.1
23001-23500																197	HPSW	B.1													431	HPGr	A.1
23501-24000				74	HPGr	A.2										198	HPSW	B.1							302	HPGr	A.2				432	HPGr	A.1
24001-24500																									303	HPGr	A.2				433	HPGr	A.1
24501-25000																199	HPSW	B.1							304	HPGr	A.2				434	HPGr	A.1
25001-25500				65	HPGr	A.2										200	HPSW	B.1							305	HPGr	A.2				435	HPGr	A.1
25501-26000																									306	HPGr	A.2						
26001-26500																201	HPSW	B.1							307	HPGr	A.2						

Range				
26501-27000			202 HPSW B.1	308 HPGr A.2
27001-27500			203 HPGr B.1	309 HPGr A.2
27501-28000			204 HPSW B.1	310 HPGr A.2
28001-28500		75 HPGr A.2	205 HPSW B.1	311 HPGr A.2
28501-29000			206 HPSW B.1	312 HPGr A.2
29001-29500		76 HPGr A.2	207 HPSW B.1	313 HPGr A.2
29501-30000			208 HPSW B.1	314 HPGr A.2
30001-30500		77 HPGr A.2	209 HPGr B.1	315 HPGr A.2
30501-31000				316 HPGr A.2
31001-31500		78 HPGr A.2		317 HPGr A.2
31501-32000		79 HPGr A.2	210 HPGr B.1	318 HPGr A.2
32001-32500				319 HPGr A.2
32501-33000			211 HPSW B.1	320 HPGr A.2
33001-33500			212 HPSW B.1	321 HPGr A.2
33501-34000		80 HPGr A.2		322 HPGr A.2
34001-34500	66 HPGr A.2		213 HPGr B.1	323 HPGr A.2
34501-35000		81 HPGr A.2	214 HPSW B.1	
35001-35500				324 HPGr A.2
35501-36000		82 HPGr A.2	215 HPGr B.1	325 HPGr A.2
36001-36500			216 HPSW B.1	326 HPGr A.2
36501-37000				327 HPGr A.2
37001-37500			217 HPSW B.1	328 HPGr A.2
37501-38000			218 HPSW B.1	329 HPGr A.2
38001-38500	67 HPGr A.2		219 HPSW B.1	330 HPGr A.2
38501-39000			220 HPSW B.1	331 HPGr A.2
39001-39500			221 HPGr B.1	
39501-40000			222 HPSW B.1	332 HPGr A.2
40001-40500	68 HPSW A.2			333 HPGr A.2
40501-41000			223 HPSW B.1	334 HPGr A.2

Age bin																																									
41001-41500																					224	HPSW	B.1					335	HPGr	A.2												
41501-42000																					225	HPSW	B.1					336	HPGr	A.2												
42001-42500																					226	HPSW	B.1					337	HPGr	A.2												
42501-43000																					227	HPSW	B.1					338	HPGr	A.2												
43001-43500																					228	HPSW	B.1																		
43501-44000																					229	HPSW	B.1					339	HPGr	A.2												
44001-44500																					230	HPSW	B.1					340	HPGr	A.2												
44501-45000																					231	HPSW	B.1					341	HPGr	A.2												
45001-45500																												342	HPGr	A.2												
45501-46000																												343	HPGr	A.2												
46001-46500																												344	HPGr	A.2												
46501-47000																												345	HPGr	A.2												
47001-47500																												346	HPGr	A.2												
47501-48000																												347	HPGr	A.2												
48001-48500																												348	HPGr	A.2												
48501-49000																												349	HPGr	A.2												
49001-49500																												350	HPGr	A.2												

Table 4: Samples number, classification (classif.) and cluster (clust.) of all 435 pollen samples in their respective age bins for each of 16 sites.

4.5 Discussion

4.5.1 Vegetation groups

The vegetation clusters and classifications here identified, although diffuse and did not evidenced temporal patterns, showed that for long periods and at many locations taxa of herbs extensively dominated the landscapes. Among the high diverse herbs composition, Poaceae largely dominated the samples once its high frequency at all environments of Brazil (Longhi-Wagner and Renvoize 2006; Rezende et al. 2008; Morrone et al. 2008) being observed in all 435 samples here studied. In fact, Poaceae is an indicator of open landscapes in Brazil however, the family encompasses several tribes and species that develop with different forests formations (Longhi-Wagner 2012) which may lead to misinterpretations. Such of problem may be strengthened by lack of detailed information once they were reduced to the same taxonomic level.

A solution can be a combined analysis with further taxa that can provide more information about vegetation features. Gosling et al. (2009) aiming to differentiate vegetation types from moist evergreen tropical forest, semi-deciduous dry tropical forest and wooded savannah using pollen records, observed that no one taxon could be used as a definitive indicator of any of the ecosystems and suggested an association of taxa would be important. This observation matches the analysis here conducted once IndVal applied to unconstrained cluster analysis revealed that open vegetation is not only characterized by Poaceae but, by a combination with other taxa such as Apiaceae, *Plantago*, Asteraceae and others. Moreover, exploring combination of taxa abundance thresholds provided reliable classifications for fossil pollen samples as achieved by Rodrigues et al. (2016) for surface assemblages.

The dominance of herbs occurred mainly at samples older than age bin 11501-12000 in response to stable climate condition and plant communities with water restriction and low temperatures. Behling et al. (2004) noticed that CDS and surrounding regions were mainly dominated by Apiceae genus *Eryngium* during the glacial period until the early Holocene which, corroborates with analysis here performed and pointed out this taxa type as the most representative for open vegetation characterization. The change from glacial to the Holocene shows that the open vegetation still largely dominating the landscapes however, some incursions of trees and shrubs start to play a role on landscape configurations. This interaction provided a new feature to the landscape, which became a mosaic of open and woodland vegetation. This configuration became stronger as South American monsoon intensified,

mainly from the mid Holocene onward when the number of vegetation turnovers became more frequent as well as noticed by Rodrigues et al. (submitted), who reported higher number of vegetation changes from the late Holocene due to climate changes. On the other hand, at sites such as SFP, SMar and SFA independently of grouping technique used, no changes is noticed which indicates location where climate still stable for a long period while based on cluster analysis changes on vegetation did not occur at sites SDO, Ara, PG, Ciama, MDI reflecting that cluster analysis may not clearly capture the vegetation variation in details.

4.5.2 *Cluster and taxa abundance classification threshold*

Both techniques for presented a good correspondence with each other concerning the identification of open vegetation features. All samples clustered in major group A, were classified as high Poaceae group and majority as HPGr. This indicates that open vegetation has a strong signal able to be captured by any technique. However, when applied to samples with more diverse composition, the classification based on threshold was more sensible in capturing incursion of tropical of subtropical tree/shrubs taxa. This level of sensibility using cluster analysis would be achieved by splitting the samples into even more subgroups. Using silhouette width to estimate the best number of clusters (Rousseeuw 1987; Borcard et al. 2011), only 5 were pointed out as the best. This number is not realistic and would generalize even more cluster weakly differentiated. Thus we subjectively selected 8 groups which gave a good view of pollen spectra by representing the main structures, further divisions were tested and they did not provide new information or better detailed groups.

Despite, some drawbacks on cluster analysis here performed, it is a strong tool for pat vegetation patterns identification. Huntley (1989) mapped the vegetation patterns of Europe for the last 13000 cal yrs based on cluster results. The author noticed that the dominant patterns in the maps also change through time, indicating important changes in palaeoenvironmental conditions and in the alignment of major environmental gradients. We also tried to find patterns on time and space, however they could not be achieved. The pollen samples were explored on principal components analysis (PCA) and well separated the similar samples, however it failed on identification of temporal patterns. An analysis of different vegetation types of Atlantic rainforest using pollen records performed by Ledru et al. (2015) showed that the replacement of open vegetation in southern Brazil by *Araucaria* since the beginning of the Holocene, began from local patches of vegetation, probably from refugia, and were not spatially uniform. This explains why sites geographically close to each other

present diverse pollen composition such as CDS and SFP that are 70 km apart. An explanation for such of diverse results may be aligned to combination of factors rather than only climate. The landforms variation is one of the most important elements for plants community of tropical forests within the Atlantic rainforest region (Berg and Oliveira Filho 1999) once the it can change soil drainage and nutrient availability on local scales (Wright, 2002), which may explain close location with different pollen compositions. The occurrence of acid and nutrient-poor soils has been systematically described along the Atlantic rain forest (Leitão Filho 1993). Guilherme et al. (2012) analyzed the relation of Atlantic rainforest trees with soil and relief features and observed that higher plant diversity and density is related with moderately developed, drained and acid soil. Moreover, the authors noticed that, soil profile and relief features can determine preferences for niche occupation and can also rule the spatial distribution of tree species rather than nutrient content.

4.6 Conclusion

The southern and southeastern portions of Brazilian environments presented dynamic changes on vegetation composition. We showed that, there are no strong evidences of temporal patterns on vegetation dominance, despite few examples. Whatever view is taken of the changes during the period considered, it is clear that the most striking changes in broadscale vegetation patterns in southern and southeastern Brazil are between open and forested formations. The dominant vegetation type is composed by herbs, mainly Poaceae that occurs in different types at different ecoregions. The classification that explores pollen thresholds and clusters analysis worked well on identification of past vegetation patterns. The first one seems to be more sensible to small changes, while cluster complemented the analysis here performed by informing what taxa are the most relevant for identification of vegetation types time-to-time. For further studies, we suggest a compilation of more pollen records and a combination of all techniques here used in order to capture small pollen variation signals avoiding generalizations.

4.7 References

Anderson P.M., Bartlein P.J., Brubaker L.B., Gajewski K., Ritchie J.C., 1989. Modern analogs of late-Quaternary pollen spectra from the western interior of North America. J. Biogeogr. 16: 573–96.

Anderson N.J., Bugmann H., Dearing J.A., Gaillard M.J., 2006. Linking palaeoenvironmental data and models to understand the past and predict the future. TRENDS in Ecology and Evolution, 21: 696 - 704.

Behling H., 2002. South and Southeast Brazilian grasslands during Late Quaternary times: a synthesis. Palaeogeography, Palaeoclimatology, Palaeoecology. 177: 19-27.

Behling H., 1997. Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology. 129:407-422.

Behling H., Hooghiemstra H., 2001. Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons, in: Markgraf, V. (Eds.), Interhemispheric Climate Linkages, Academic Press, pp. 307-323.

Behling H., Lichte M., 1997. Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. Quat. Res. 48:348-358.

Behling H., Pillar V.D., Orlóci L., Bauermann S.G., 2004. Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southernBrazil. Palaeogeogr Palaeoclimatol Palaeoecol, 203:277–297.

Berg. van den E., Oliveira Filho A.T., 1999. Spatial partitioning among tree species within an area of tropical montane gallery forest in south-eastern Brazil. Flora, 194: 249-266.

Birks H. J. B., Birks, H. H. (1980). Quaternary Palaeoecology. Edward Arnold, London.

Birks H.J.B., Heiri O., Seppä H., Bjune, A.E., 2010. Strengths and Weaknesses of Quantitative Climate Reconstructions Based on Late-Quaternary Biological Proxies. The Open Ecology Journal, 3:68-110.

Birks, H.J.B., Seppä, H., 2004. Pollen-based reconstructions of late-Quaternary climate in Europe - progress, problems, and pitfalls. Acta Palaeobotanica, 44:317-34.
Boldrini, I.I., 2009. Biodiversidade dos Campos do Planalto das Araucárias. Ministério do Meio Ambiente, Brasília.

Borcard D., Gillet F., Legendre P., 2011, Numerical ecology with R. Springer, New York

Brewer S., Guiot J., Barboni. D., 2007. Pollen Data as Climate Proxies. Encyclopedia of Quaternary Science, 4: 2498-2510.

Davis M.B., 2000. Palynology after Y2K— understanding the source area of pollen in sediments. Annu. Rev. Earth Planet. Sci. 28:1–18.

De'ath G., 1999. A New Technique for Indirect and Direct Gradient Analysis. Ecological Society of America. 80(7): 2237-2253.

Dufrêne M., Legendre P., 1997. Species assemblages and indicator species: the need for a flexible
asymmetrical approach. Ecological Monographs, 67:345–366.

Gavin D.G., Oswald W.W., Wahl E., Williams J.W., 2003. A statistical approach for evaluating distance metrics and analog assignments for pollen records. Quat. Res., 60:356–67.

Giesecke T., Bennett K.D., Birks H.J.B., Bjune A.E., Bozilova E., Feurdean A., Finsinger W., Froyd C., Pokorný P., Rösch M., Seppä H., Tonkov S., Valsecchi V., Wolters S., 2011. The pace of Holocene vegetation change e testing for synchronous developments. Quaternary Science Reviews. 30(19–20): 2805–2814.

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

Gosz J.R., 1992. Gradient Analysis of Ecological Change in Time and Space: Implications for Forest Management. Ecological Applications, 2: 248-261.

Guilherme F.A.G., Ferreira T.O., Assis M.A., Torrado P.V., Morellato L.P.C., 2012. Soil profile, relief features and their relation to structure and distribution of Brazilian Atlantic rain forest trees. Scientia Agricola, 69(1): 61-69.

Hastie T., Stuetzle, W., 1989. Principal Curves. Journal of American Statistical Association. 84: 502-516.

Hogg, A.G., 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.H., 2013. SHCal13 Southern Hemisphere Calibration, 0-50,000 Years cal BP. Radiocarbon. 55(4): 1-15.

Huntley B., 1990. European vegetation history : palaeovegetation maps from pollen data - 13 000 yr BP to presente. Journal of Quaternary science, 5(2):103-122.

Huntley B., WEBB, T. III., 1989. Migration: species' response to climatic variations caused by changes in the earth's orbit. Lournal of Biogeography, 16: 5-19.

IBGE - Fundação Instituto Brasileiro de Geografia e Estatística, 1995. Zoneamento ambiental e agroecológico do Estado de Goiás: região nordeste. Rio de Janeiro: IBGE/Divisão de Geociências do Centro-Oeste. (Estudos e pesquisas em geociências, n. 3).

Ledru M.P., Salgado-Laboriau M.L., Lorscheitter M.L., 1998. Vegetation dynamics in southern and central Brazil during the last 10,000 yr B.P. Review of Palaeobotany and Palynology, 99:131-142.

Ledru M-P., Montade V., Blanchard G., Hély C., 2015 Long-term Spatial Changes in the Distribution of the Brazilian Atlantic Forest. Biotropica, 0(0):1–11.

Legendre, P., Birks, H.J.B., 2012. Clustering and partitioning. in: Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (Eds.), Tracking environmental change using lake sediments: Data Handling and Numerical Techniques. Dordrecht: Springer, pp. 167-200.

Leitão Filho, H.F. ,1993. Atlantic Rainforest Ecology in Cubatão. Editora UNESP, São Paulo, SP, Brazil.

Longhi-Wagner H.M., 2012. Poaceae: an overview with reference to Brazil. Rodriguésia, 63:89–100.

Longhi-Wagner H.M., Renvoize, S.A., 2006. Poaceae. In: Barbosa, M.R.V., Sothers, C., Mayo. S., Gamarra Rojas, C.F.L, Mesquita, A.C. (eds) Checklist das plantas do nordeste brasileiro. Brasília, pp 91–97.

Maechler M., Rousseeuw P., Struyf A., Hubert M., 2005. Cluster Analysis Basics and Extensions; unpublished.

Mazier F., Broström A., Bragée P., Fredh D., Stenberg L., Thiere G., Sugita S., Hammarlund D., 2015. Two hundred years of land-use change in the South Swedish Uplands: comparison of historical map-based estimates with a pollen-based reconstruction using the landscape reconstruction algorithm. Vegetation History and Archaeobotany, 24: 555-570.

Morrone O., Zuloaga F.O., Longhi-Wagner H.M., et al., 2008. Poaceae. In: Zuloaga FO, Morrone O, Belgrano MJ, Smol JP (eds) Cata´logo de las plantas vasculares del Cono Sur (Argentina, sur de Brasil, Chile, Paraguay y Uruguay). Springer, Saint Louis, pp 705–1,063

Nakagawa T., Tarasov P.E., Nishida K., Gotanda K., Yasuda, Y. 2002. Quantitative pollen-based climate reconstruction in central Japan: application to surface and Late Quaternary spectra. Quaternary Science Reviews, 21: 2099–2113.

Nimer E., 1989. Climatologia do Brasil. Fundacão Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Oksanen J., Blanchet F.G., Kindt R, Legendre P, O'Hara B, Simpson G.L, Solymos P., Stevens M.H.H., Wagner, H., 2010. vegan: Community ecology package. R package Version 1.17-3.

Oliveira J.M., V.D. Oliveira, J.M. & V.D. Pillar., 2004. Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. Community Ecology 5(2): 197-202.

Overpeck J.T., 1985. A pollen study of a late Quaternary peat bog, south-central Adirondack Mountains, New York. Geol. Soc. Am. Bull., 96:145–54.

Overpeck, G.E., Muller, S.C., Fidelis, A., Pfadenhauer, J., Pillar, V.D., Blanco, C.C., Boldrini, I., Both, R., Forneck, E.D., 2007. Brazil's neglected biome: the South Brazilian Campos. Perspectives in Plant Ecology, Evolution and Systematics. 9, 101-116.

Prentice, I.C., 1980. Multidimensional scaling as a research tool in Quaternary palynology: A review of theory and methods. Review of Palaeobotany and Palynology. 31, 71-104.

Prentice, I.C., Webb, T., 1986. Pollen percentages, tree abundance and the Fagerlind effect. Journal of Quaternary Science 1 (1): 35–43.

Ramsey, C.B., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon. 51(1), 337–60.

Ramsey, C.B., Lee, S., 2013. Recent and Planned Developments of the Program Oxcal. Radiocarbon. 55(2-3), 720-730.

R Core Team, 2012. R: A language and environment for statistical computing. Vienna: R foundation for statistical computing. Available at: http://www.R-project.org/

RBMA – Reserva da Biosfera da Mata Atlântica, 1999. Caderno n° 15 Mata Atlântica: Ciência, conservação e políticas. Workshop científico, São Paulo.

Rezende, A.V., Walter, B.M.T., Fagg, C.W. ,et al., 2008. Flora vascular do bioma cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: ecologia e flora. Embrapa, Braília, pp 1,028–1,059.

Roberts D.W., 2010. labdsv: Ordination and multivariate analysis for ecology. R package Version 1:4-1.

Rodrigues J.M., Behling H., Giesecke T., 2016. Differentiating vegetation types from eastern South American ecosystems based on modern and subfossil pollen samples - evaluating modern analogues. Vegetation History Archaeobotany, 25: 387-403.

Rousseeuw P.J., 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. J Comput Appl Math, 20:53–65

Safford, H.D., 1999. Brazilian páramos II. Macro- and mesoclimate of the campos de altitude and affinities with high mountain climates of the tropical Andes and Costa Rica. The Journal of Biogeography. 26, 739-760.

Sant'Anna Neto, J.L., Nery, J.T., 2005. Variabilidade e mudanças climáticas no Brasil e seus impactos, in: Souza, G.R.G., Suguio, K., Oliveira, M.A.S., Oliveira, P.L. (Eds.), Quaternário do Brasil. Ribeirão Preto: Holos Editora, pp 28–50.

Simpson G.L.. 2007. Analogue methods in palaeoecology: using the analogue package. J Stat Softw, 22:1–29

Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991. Classificação da vegetação brasileira adaptada a um sistema universal. IBGE, Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro.

Wahl E.R., 2004. A general framework for determining cutoff values to select pollen analogs with dissimilarity metrics in the modern analog technique. Review of Palaeobotany and Palynology, 128:263-280.

Willis K.J., Birks H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science, 314:1261-5.

Woodward F.I., Williams B.G., 1987. Climate and plant distribution at global and local scales. Vegetatio. 69:189-197.

Wright S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia, 130: 1-14.

Chapter 5

Synthesis

The chapters of this dissertation contribute to an enhanced knowledge of Quaternary palaeoecology of the Altantic rainforest biome. The integrated analyses of studied sites, together with the comprehensive overview of broader patterns in vegetation provide important information for a more comprehensive view on large-scale vegetation changes resulted of either human actions or climate changes. Furthermore, the correct application of exploratory approaches, commonly used in tropical palynology, supported a broader understanding of the magnitude of complex mechanisms that drive vegetation through time, thus providing background for planning strategies for conservation in scenarios of current and future climate changes. In the following sections, main research outcomes of this thesis are synthesized. Further topics for researches are adressed as well as an outline is given to general conclusions and implications.

5.1 Main research outcomes

5.1.1 Late Holocene vegetation, climate, human impact at Atlantic rainforest

The late Holocene environmental history of Atlanic rainforest and associated ecosystems was the main topic of the chapters 2 of this thesis. This palaeoecological study helped to elucidate important questions about natural and human induced vegetation changes. The palaeoenvironmental records of most of the sites revealed a trend of forest expansion from 3000 cal yrs BP onward that were reversed at most of sites due exclusively human land-use.

One of the most important issues in palynology is to acquire surface pollen data capable to represent the natural vegetation without the human footprints. Based on principle of uniformitarism (Birks and Birks 1980), the relationship between surface pollen samples, representing the local vegetation composition, with the present environment would be used to explore fossil pollen samples, thus reconstructing the past environment conditions. However, in conditions of human modified landscape, these pollen records may not represent the natural vegetation conditions and even in well-preserved vegetation, the pollen assemblages may be biased by dispersed pollen from large areas of modified vegetation.

Regarding the scenario of intense vegetation modificatioin noticed at Atlantic rainforest, before any try of use its surface pollen as modern analogues, it should be previously analysed

in terms of reliability to represent the main vegetation features in order to avoid biased analysis. Thus, the analysis of pre-colonization assemblages of Atlantic rainforest, period when certainly no human impacts were present, revealed that pollen samples from the natural vegetation are able to represent the main environment and environmental characteristics.

Several supervised and unsupervised techniques such as multivariate regression trees, biomisation, cluster analysis, ordination techniques and others (Rousseeuw 1987; Prentice et al. 1992, 1996; Borcard et al. 2011; Simpson and Birks 2012; Felde et al.2014) were used to capture the latent structure of pollen samples, however most of them produced groups not meaningful highlight the complexity of our data hampering clear differentiation between sites cause by low taxonomic resolution resulted of harmonization procedure. The achievement of reasonable vegetation differentiation was achived by handling an appropriate ordination technique (principal component analysis - PCA) combined with key taxa threshold. We observed, in terms of taxonomical and geographical coherence, two major gradients varying from from open grassland to forest as well as that from subtropical to tropical vegetation types. Combining PCA with indicator taxa such as Poaceae, *Weinmannia*, Arecaceae, Melastoataceae and *Cecropia*, pre-colonization assemblages were splited into 7 groups coherent with natural environmental variation.

Comparing the pre-colonization assemblages with the 3000 BP assemblages, it is noticed that the environment gradient is stronger for the older sample than for the pre-colonization as evidenced by long taxa vector indicators except by *Araucaria angustifolia*. On the other hand, as observed for pre-colonization assemblages PCA, the PCA for 3000 BP assemblages separates in the first principal component tropical and subtropical sites and the second axis shows the gradient between open subtropical vegetation and forest dominated sites. Furtherrmore, it is known that since the beginning of late Holocene, Araucaria forest continuously expanded and replaced open landscapes (Behling et al. 2004) due to moisture increasing as revelaed by oxygen isotopes from Botuverá cave (Wang et al. 2007).

The comparison of the pre-colonization with modern assemblages showed that the vegetation shifted from forested to grass dominated landscape while few sites presented opposite trend. Most of surface pollen assemblages still able to distinguish between open and forested landscapes on the other hand the gradient associated with temperature enabling the classification into tropical and subtropical vegetation types is not as easily detected in the modern assemblages due to a strong decrease in Weinmannia, which is the main indicator of subtropical forest. A quantitative measurement based on squared chord dissimilarity showed that in average, the transition 3000 BP - pre-colonization and pre-colonization – modern

assemblages are equivalent, which mean that 3000 years of natural changes was reproduced in intensity within 500 years of human actions. Moreover, despite of intense land use and induced vegetation change, modern pollen assemblages capture some aspects of the gradient in natural vegetation and may thus be useful as modern analogues. However, at some locations the vegetation is strongly altered with a loss of characteristic species affecting the pollen composition. Therefore, a careful selection of sites for modern analogue analyses is recommended. A dataset of pre-colonization pollen samples is preferable in terms of modern analogues.

5.1.2   *The natural vegetation changes during the Holocene*

The chapter 3 explores the main periods of vegetation changes through the Holocene by a parallel analysis of 19 pollen records from southeastern and southern Brazil. This palaeoecological study revealed the main periods simultaneous vegetation changes during the complex palaecological history of Brazilian ecosystems, highlighting its connections with climatic system.

The history of Brazilian vegetation reported by several studies that explored pollen, charcoal and others palaeoecological records show with high confidence local abrupt, smooth or stepwise vegetation changes (e.g. Behling et al. 2004, Pessenda et al. 2005 and Enters et al. 2010). The clearest portray of vegetation history in Brazil concerns the Araucaria forest in southern region, where grasslands largely dominated the landscapes since the glacial period until around 4000 years BP, when, as consequence of wetter climate, formations rich of *Araucaria angustifolia* and other species replaced grasses dominated ecosystems (e.g. Behling et al. 2004 and Jeske-Pieruschka et al. 2012). Furthermore, a comparative analysis of 27 Brazilian pollen diagrams conducted by Rodrigues et al. (2016), evidences a synoptic shift of many pollen records from 3000 years BP to conditions prior to colonizers impacts, mainly at those sites located at subtropical region. Despite the human impacts, there is an agreement that the climate was the main driver of the changes noticed along the Holocene, since according to Giesecke et al. (2011) it is the only mechanism capable to cause synchronous changes on vegetation on subcontinental scale.

Thus, aiming to test the synchronicity of vegetation changes at South and Southeastern Brazil during the Holocene, we combined 19 pollen diagrams from different ecosystems based on consistent age depths model built on Bayesian approach performed in Oxcal. In sequence, the pollen composition changes were accessed by handling 2 splitting techniques -

binary and optimal - associated to 2 variation criteria - sum of squares and information content - performed in Psimpoll. Then, we combined the probability distribution of each event in an accumulated probability distribution curve, which resulted in peaks indicating potential synchronous vegetation changes in at least five periods 8900, 5900, 2800, 1200 and 550 cal yrs BP. Furthermore, the sites located at southern positions experienced more cycles of changes than others, mainly during the late Holocene. The main variations on pollen spectra were captured by both PC (Principal Curve) and rate of change analysis that well represented the main periods of change. In general, the early Holocene was a stable period, and later on the mid-Holocene the changes have started and intensified around 2800 cal yrs BP with other pulses later, agreeing with other researches carried out at other regions of South America indicating connections with continental climate patterns associated to South American monsoon.

The periods of either stability or change of vegetation changes of southern and southeastern Brazil observed in this study are consistent with Holocene patterns detected for South America. Whitlock et al. (2006), for example, analyzed pollen and charcoal records from Argentinian Andes and noticed that the period between 11400 and 6000 cal yrs BP was characterized by open *Nothophagus* forest/shrubland as result of dry climate. From the mid-Holocene onward the climate became moister allowing progressive increase of *Austrocedrus* at studied region resulting in the current mixed *Notophagus*/*Austrocedrus* forest. In Patagonia, Iglesias et al. (2014) noticed from 5 pollen records that steppe vegetation had been progressively replaced since the late glacial/early Holocene until 5000 cal yrs BP by *Nothofagus* forest reflecting cold and dry climate, thereafter due to moisture increasing, the *Austrocedrus chilensis* started to spread. Northward, at Colombian Amazonia rainforest-savanna ecotone, Behling and Hooghiemstra (2000) studied a pollen record of Laguna Loma Linda and noticed three remarkable phases on vegetation history. Between 8700 and 6000 uncal yrs BP the authors noticed that vegetation was dominated by grass savanna with rare forest taxa indicators reflecting a climate dry with strong seasonality. Moreover, the authors noticed that during the period from mid-Holocene to 2300 uncal yrs BP the rainforest expanded along the water sources in consequence of increasing in precipitation while the remaining grass savanna of the hills became more wooded. From 2300 uncal yrs BP to the present, savanna grasses expanded again due to clear influence of human impacts. A pollen compilation from southeastern and southern Brazil investigated by Behling (1998) showed that during the early and mid-Holocene the highlands were dominated by Campos vegetation suggesting a warm and dry climate, and during the late Holocene a very humid climate

establishes allowing the Araucaria and tropical forests expansion mainly around at 1000 uncal yrs BP. For the same region, Ledru et al. (1998) analyzed 11 pollen diagrams covering the last 10000 years and observed three different stages on palaeovegetation history. Between 10000 and 7000 yrs BP (12000 – 8000 cal yrs BP), arid conditions was predominant and in consequence the landscapes were mainly dominated by non-arboreal pollen, whereas the arboreal elements were more evident at sites located at valleys. Later, between 7000 and 4000 yrs BP (8000 – 4500 cal yrs BP), in consequence of moister climate, occurred the expansion of swamp vegetation and gallery forests and thereafter, from 4000 yrs BP (4500 cal yrs BP) to the present, the humidity still increasing resulting in a broad vegetation development mainly represented by cerrado, semi-deciduous and Araucaria forest.

In this way, comparing the palaeocological period of vegetation changes above mentioned with the results here achieved, it is possible to infer that broad synchronous vegetation changes may happen during the Holocene not only in Southern and southeasterhn Brazil but in large areas of in South America.

5.1.3 *Vegetation classification during the late Quaternary of south and southeast Brazil*

The chapter 4 shows the classification based on combination of indicator taxa threshold and cluster of bins of 500 cal yrs of entire pollen spectra of 16 sites. The main objective of this study is to built a clear portray of how vegetation was at different locations of south and southeast Brazil. To carry out this study, we rebuilt the chronology for all 16 sites in order to allow harmonic comparison. Moreover, uncontrained cluster analysis and pollen classification proposed by Rodrigues et al. (2016) was applied and evaluated by using IndVal index.

The results showed that for long periods, open vegetation features extensively dominated the the lndscapes. Based on cluster analysis, 190 out 435 pollen samples were assigned to the major group A, which is mainly characterized by high frequency of herbs such as Apiaceae, *Plantago*, Asteraceae, Poaceae and others being these 4 taxa the most abundant and important for this group accorditg to IndVal index. The rest of 245 samples were classified into group B which is mainly represented by trees/shrubs such as *Weinmannia*, *Myrsine*, Myrtaceae, Euphorbiaceae, *Ilex*, Moraceae/Urticaceae, *Symplocos*, Arecaceae, Sapindaceae and Fabaceae, those the highest IndVal and high frequency ranging from 183 up to 378 occurrences. The further divisions were applied to both major groups and it is noticed that subgroups A.1, A.2 and A.3 were consistently caracaterized by dominance of herbs occurring on dispersed pollen samples across the time. While the subgroups B.1, B.2, B.3, B.4

and B.5 represented the vegetation with different inncursions of subtropical and tropical forest.

The pollen classification using combination of taxa thresholds revealed more detailed pollen variation, once it identified small changes within long series variations. The major classification (high Poaceae - HP) was observed in superior nnuber than in cluster, from 435 pollen samples 386 were classified as HP and the rest 49 samples as low Poaceae (LP). The lower classification HPGr, although occurring on several pollen samples, has a great correspondence with the cluster A.1, A.2 and A.3 while the other subdivisions of high Poaceae (HPPS, HPSW, HPST) did not find a strong correspondence with any other group identified in cluster analysis the same is observed for the subgroups o low Poaceae (LPST and LPSF).

Using principal curve (PC) analysis on all 435 pollen samples, it as noticed that this technique is capable to capture the oscillation between open and forested landscape, comparing it with the Poaceae and *Weinmannia*, both with the best IndVal index for herbs and tree/shrubs, respectively, it is noticed that high (low) amounts of Poaceae and low (high) of *Weinmannia* make the PC reach small (big) values.

Although no strong time pattern is detected, the use of techniques here performed showed as a good strategy for detection of vegetation main features through time. An improvement for future studies would be the integration of both technique, cluster and classification, which may provide strong details about vegetation time-to-time,.

5.2   Open questions, uncertainties and perspectives

The analyses carried out in this thesis aimed to contribute in understanding the environmental patterns through the Holocene of southern and southeastern Brazil. Moreover, these studies leave open doors for questions and uncertainties for further studies on the subject.

The analysis here carried showed that there is a need in linking the different techniques of data analysis in order to explore the existing data in a more quantitative way.

Although the data, after proper treatment, reflected very well the natural vegetation conditions by grouping coherent vegetation types, the surface pollen still lack taxonomical precision, once there are several cases of pollen taxa that could not be identified in more detailed level and contamination by exotic taxa. Nevertheless, the study of surface pollen is an important step towards a better interpretation of fossil pollen records identifying the patterns and processes during the Holocene. Furthermore, a better spatial resolution would provide

more detailed information regarding vegetation transitions within short distances as well as its variations as consequence of different climate patterns. Ideal surface pollen net would involve dense collection of assemblages throughout the landscape with transects covering the ecotones where each individual plant species could be identified with all physiological details. Also, climate data, should be recorded to assess the modern pollen/vegetation/climate relationships on a more detailed scale which would make quantitative estimations about past climate conditions based on pollen data feasible. Moreover, despite the large deforestation, the remaining untouched vegetation patches still to provide confident information of natural vegetation.

Our knowledge of ecosystem dynamics and climate variability in the South America during the late Quaternary is limited by the reduced number of palaeoecological records available. These few palaeocological reconstructions report different vegetation variability, and the extent to which these proxies data and statistical calibration methods, need to be reconciled. In the same way, despite all data combination here performed, the understanding of how climatic extremes varied and impacted in the past ecosystems need more careful analysis. This assessment would be improved with extensive interdisciplinary networks of high-resolution multiproxy data. The lack of high-resolution records is one of the major issues as well as, the lack of better dating for some diagrams. The lower resolution, identified in some sites, hampers detailed vegetation changes identification through the time. We observed that within few centuries or millennia significant changes can happen on landscape due human or natural changes, thus a high recods resolution would help to skip such misinterpretations. Similarly, the reduced number of radiocarbon dating hampers the achievement of exact or most likely period of occurrence of an event, thus the most number of radiocarbon dates as possible, provided a further better time control of vegetation changes or extreme events captured by pollen records. The results achieved from improved data quality will surely allow a more elaborate comparison of South American palaeo-archives providing a more elaborate and applicable knowledge for conservation and management issues.

The need for an expansion of palaeoecological investigations in the Atlantic rainforest is strengthened by current and future global climate changes scenarios. The climate changes predictions are built on dense dataset of observations, which highlight the relevance of palaeoclimate studies that can provide a robust source of information for calibration and calibrate and validation of climatic models used to predict different scenarios. However, the relevance of palaeocological and palaeoclimate researches should not be underestimated once they enable us to gain valuable insight into the ability of our ecosystems and climate systems

to change. The acquisition of further palaeoecological data will certainly increase our knowledge about patterns and processes that help to understand the underlying mechanisms of *why* ecosystems changed in this way or the other and *how* these changes happen. It can help to predict ecosystem response in future climate and conservation scenarios, but moreover it also shows us nature as it is, and should be conserved in all its complexity and beauty.

5.3   References

Behling H (1998) Late Quaternary vegetational and climatic changes in Brazil. Review of Palaeobotany and Palynology, 99:143-156.

Behling H, Hooghiemstra H (2000) Holocene Amazon rain forest - savanna dynamics and climatic implications: high resolution pollen record Laguna Loma Linda in eastern Colombia. Journal of Quaternary Sciences, 15: 687-695.

Behling H, Pillar VD, Orlóci L, Bauermann SG (2004) Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogeogr Palaeoclimatol Palaeoecol, 203:277–297.

Birks HJB, Birks HH (1980) Quaternary palaeoecology. Arnold, London

Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Springer, New York

Felde VA, Peglar SM, Bjune AE, Grytnes J-A, Birks HJB (2014) The relationship between vegetation composition, vegetation zones and modern pollen assemblages in Setesdal, southern Norway. Holocene, 4:1–17

Iglesias V, Whtilock C, Markgraf V, Bianchi MM (2014) Postglacial history of the Patagonia forest/steppe ecotone (41-43ºS). Quaternary Sciences Reviews. 94:120-135.

Jeske-Pieruschka V, Pillar VD, De Oliveira MAT, Behling H (2012). New insights into vegetation, climate and fire history of southern Brazil revealed by a 40,000 year environmental record from the State Park Serra do Tabuleiro. Vegetation History Archaeobotany, 22:299-314.

Ledru M-P, Salgado-Labouriau ML, Lorscheitter ML (1998) Vegetation dynamics in southern and central Brazil during the last 10,000 yr B.P. Review of Palaeobotany and Playnology, 99:131-142.

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biomemodel based on plant physiology and dominance, soil properties and climate. J Biogeogr, 19:117–134

Prentice IC, Guiot J, Huntley B, Jolly D, Cheddadi R (1996) Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. Clim Dyn, 12:185–194

Rousseeuw PJ (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. J Comput Appl Math, 20:53–65

Simpson GL, Birks HJB (2012) Statistical learning in palaeolimnology. In: Birks HJB, Lotter AF, Juggins S, Smol JP (eds) Tracking environmental change using lake sediments: data handling and numerical techniques. Springer, Dordrecht, pp 249–327

Wang XF, Auler AS, Edwards RL, Cheng H, Ito E, WangYJ, Kong XG, Solheid M, (2007) Millennial-scale precipitation changes in southern Brazil over the past 90,000 years. Geophysical Research Letters. 34.

Whitlock C, Bianchi MM, Barthlein PJ, Markgraf V, Marlon J, Walsh M, McCoy N, (2006) Postglacial vegetation, climate, and fires history along the east side of the Andes (lat 41-42.5ºS), Argentina, Quaternary Research, 66:187-301.