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Vegetation, climate and fire dynamics of Upper Montane Forest and Campos de Altitude during the Holocene in southeastern Brazil

Dissertation

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Submitted by

Maria Carolina Guarinello de Oliveira Portes

From Curitiba (Brazil)

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Thesis committee

Prof. Dr. Hermann Behling (Department of Palynology and Climate Dynamics / A.-v.-H. Institute for Plant Sciences)

Prof. Dr. Erwin Bergmeier (Department of Vegetation and Phytodiversity Analysis/ A.-v.-H. Institute for Plant Sciences)

Dr. Sonia Fontana (Department of Palynology and Climate Dynamics / A.-v.-H. Institute for Plant Sciences)

Members of the examination committee

Prof. Dr. Hermann Behling
(Department of Palynology and Climate Dynamics / A.-v.-H. Institute for Plant Sciences)

Prof. Dr. Erwin Bergmeier
(Department of Vegetation and Phytodiversity Analysis/ A.-v.-H. Institute for Plant Sciences)

PD Dr. Dirk Gansert
(Department of Ecology and Ecosystem Research/ A.-v.-H. Institute for Plant Sciences)

Prof. Alexander Schmidt
(Department of Exobiology/Evolution of Landplants & Development of Terrestrial Ecosystems)

Dr. Michaela Dippold
(Department of Biogeochemistry of Agroecosystems/ Institute of Soil Science)

Dr. Ina Meier
(Department of Ecology and Ecosystem Research/ A.-v.-H. Institute for Plant Sciences)

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If things are unattainable… well

that's not enough reason not to want them…

How sad the path would be if it wasn't for

the presence of the distant stars!

Mario Quintana

**30/07/1906 – †5/05/1994*

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Summary

The Atlantic Forest biome is well known as one of the mostly biodiversity regions on earth, hosting high species endemism and species/area ratio. It stretches around 1,300,000 km^2 along the Brazilian coast between latitudes 3^o and 33º S and longitudes 35^o and 57º E. Due to the increase of human impact through the intensification of land-use and consequent broad landscape replacement along the centuries, only 10-15% of the Atlantic Forest biome remains in a natural or semi-natural state, being considered one of the most priority areas for conservation. It encompasses a wide variation of climates and geomorphologies, resulting in a complex mosaic of different ecosystems. Among them, the *Araucaria* forest, upper montane Atlantic rain forest (cloud forest) and the campos de altitude (high elevation grassland) occur on the Brazilian coastal highlands, which extends for about 1000 km parallel to the coastline from southern to southeastern Brazil. The *Araucaria* forest distribution is related to humid and relative cold climatic conditions, between 400 and 1400 m a.s.l. in southern Brazil and in smaller fragments at altitudes between 1400 and 1800 m a.s.l. in southeastern Brazil. Currently, it has been reduced to *c*. 7% of its original distribution. The upper montane Atlantic rain forest spread in the upper slopes of the Brazilian coastal highlands of southern and southeastern Brazil, normally above around 1100 m a.s.l. in the south and above around 1500 m a.s.l. in the southeast, mainly occupying the concavities and protected sites. The campos de altitude is a typical open vegetation, restricted to small areas on the summits of the higher peaks and plateaux.

Palaeoecological studies demonstrated that, although the mosaic of these ecosystems has prevailed along the Holocene, the perpetuation of campos de altitude is very fragile. The grassland vegetation expands under colder and dry climate conditions and seems to be fire adapted suggesting that the current area of campos de altitude is larger than the modern climate alone would dictate, especially in warmer, lower elevation sites. Moreover, climate changes studies suggest a warmer and wetter climate during the 21st century which it is likely to intensify the upward movement of the Atlantic Forest at the expense of open ecosystems like the campos de altitude.

In this research, the past and present relationship of the mosaic of campos de altitude and upper montane forests (*Araucaria* forest and upper montane Atlantic rain forest) are explored through palynological analyses. Foremost, the currently correlation between vegetation cover and pollen production was investigated. It was observed that arboreal taxa are over-represented in campos the altitude assemblage and that the campos de altitude pollen assemblage represents a much larger source area than the forest pollen assemblage, which is comprised of more local taxa. Afterwards, a record of the last almost 10,000 years was analysed. This study showed that, although upper montane forest taxa have been in the broader region of the study site throughout the Holocene, the forest vegetation has spread mostly in Late Holocene. Until around 1350 cal yr BP campos de altitude vegetation was much more widespread. Overall, the results demonstrated that increase in temperature and precipitation throughout the Holocene favoured the upward expansion of the forest. Furthermore, the research indicated that fire was presented before human arrival in southeastern Brazil, implying an adaptation of open vegetation to frequent fire. Latter, the dynamics of the vegetation on the last seven centuries was investigated. The outcomes revealed that anthropogenic disturbances such as fire, livestock grazing and logging have played a clear role in driving grassland-forest relationships in southeastern Brazilian highlands.

Based on the outcomes of this research, the maintenance of the mosaic of forest-grassland in the current and projected climate trends depends on an active disturbance management and a changed in conservation focus from forest to non-forest habitats.

Resumo

O bioma Mata Atlântica é mundialmente reconhecido como uma das regiões de maior diversidade biológica do planeta, abrigando elevada riqueza de espécies e um elevado número de espécies endêmicas, se estendendo por cerca de 1.300.000 km$_2$ ao longo da costa brasileira, entre as latitudes 3$_o$ e 33$_o$ S e longitudes 35$_o$ e 57$_o$ L. Como resultado do incremento das atividades humanas de uso da terra e, consequentemente, de ampla modificação da paisagem ao longo dos séculos, cerca de apenas 10-15% do bioma Mata Atlântica ainda se encontra em estado natural ou próximo ao natural, sendo considerados áreas prioritárias para conservação.

Devido à grande variedade climática e geomorfológica, o bioma Mata Atlântica é um complexo mosaico de diferentes ecossistemas. Dentre estes, a floresta com Araucária (Floresta Ombrófila Mista), a floresta nebular (Floresta Ombrófila Densa Altomontana) e os campos de altitude ocupam as médias e altas altitudes da Serra do Mar, que se estende por cerca de 1000 km paralela à costa, do sul ao sudeste brasileiro. A distribuição da floresta com Araucária está relacionada ao clima úmido e relativamente frio, entre 400 e 1400 m s.n.m. no sul do Brasil e em fragmentos menores entre as altitudes de 1400 a 1800 m s.n.m. no Sudeste. Atualmente, está reduzida a não mais do que 7% da sua distribuição original. A floresta nebular se estende nas encostas do alto da Serra do mar, normalmente acima de 1100 m s.n.m. no Sul e acima de 1500 m s.n.m. no sudeste do Brasil, nos pequenos vales e sítios protegidos. Os campos de altitude são uma vegetação tipicamente herbácea, restrita aos cumes e picos da serra e aos platôs mais elevados.

Estudos paleoecológicos demonstraram que, apesar deste mosaico de ecossistemas ter persistido durante o Holoceno, a perpetuação dos campos de altitude é muito frágil. Como a vegetação campestre se expande em condições climáticas mais frias e secas e parece ser adaptada ao fogo, sugere-se que a presente área de campos de altitude é maior do que esperada sobre as condições climáticas atuais, especialmente em locais mais quentes em altitudes mais baixas. Além disso, estudos de mudanças climáticas preveem um clima mais quente e úmido durante o século 21, que provavelmente irá

intensificar a migração da floresta atlântica para maiores altitudes, em detrimento da vegetação campestre.

Nesta pesquisa, as relações passadas e presentes do mosaico de campos de altitude e florestas altomontanas (floresta com Araucária e floresta Atlântica nebular) são exploradas por meio de análises palinológicas. Inicialmente, foi investigada a correlação atual entre cobertura vegetal e produção de pólen. Observou-se que os taxa arbóreos são superestimados no conjunto de pólen de campos de altitude, constituindo uma área muito maior de captação de pólen do que no conjunto de pólen arbóreos. Sendo assim, o conjunto de pólen que caracteriza a vegetação de campos de altitude apresenta uma grande proporção de taxa de vegetação arbórea. Posteriormente, um sedimento de quase 10.000 anos foi analisado, demonstrando que, apesar dos taxa representantes da floresta altomontana estarem presentes na região de estudo durante todo o Holoceno, a vegetação florestal expandiu majoritariamente durante o Holoceno Tardio. Até cerca de 1350 cal a AP, a vegetação de campos de altitude ocupava áreas mais extensas. Em geral, os resultados demonstraram que o aumento de temperatura e precipitação ao longo do Holoceno favoreceram a migração da floresta para altitudes mais elevadas. Além disso, a pesquisa indicou que o fogo já estava presente na região antes da chegada dos primeiros humanos no Sudeste do Brasil, implicando na adaptação da vegetação campestre ao fogo. Por último analisou-se a dinâmica da vegetação nos últimos sete séculos. Os resultados indicaram que interferências antropogênicas como fogo, pastoreio e exploração madeireira desempenharam um importante papel na relação campos-floresta na Serra do Mar do Sudeste do Brasil.

Com base nestes estudos, sugere-se que a manutenção do mosaico de campos de altitude e floresta no clima presente e futuro depende tanto de um manejo ativo quanto da mudança de foco da conservação de ambientes florestais para ambientes campestres.

Outline and content of the chapters

This research was developed during the period of April 2015 to March 2019 at the Department of Palynology and Climate Dynamics of the University of Göttingen, Germany and the results are herein presented in chapters.

Chapter 1 provides a general background information about the Atlantic Rain Forest Domain and the methods applied to produce the data.

Chapter 2 presents the manuscript of the relationship between modern pollen rain and vegetation cover along an elevational gradient in the Serra dos Órgãos National Park, southeastern Brazil.

Chapter 3 provides the manuscript of the vegetation, climate and fire dynamics in the Serra dos Órgãos Mountains of Rio de Janeiro State, southeastern Brazil, during the Holocene.

Chapter 4 presents the manuscript of human and climate as designers of the landscape in Serra da Bocaina National Park, southeastern Brazil, over the last seven centuries.

Chapter 5 synthesizes the most important outcomes and provide a short outlook and perspective.

This thesis is entirely my own original work based on the manuscripts presented in chapters 2-4, and I have not used any sources other than those identified as references. The three manuscripts are a collaborative work and the authors have been identified in the beginning of each chapter. One of the manuscripts has been already published, other is in press with journal pre-proof available online and the third is in review, as indicated in the beginning of each chapter.

CHAPTER 1

1 The Atlantic Rain Forest Domain

The Atlantic rain forest is one of the most diverse biome in the world and one of the most imperilled biodiversity hotspots on earth (Myers et al., 2000; Cunha and Guedes, 2013). Its domain extends for 1,300,000 km2 of coastal and eastern Brazil, stretching from 3° N latitude to almost 34° S, according to Brazilian federal law 11428/2006 and federal decree 6660/2008 (Fig. 1a).

Since it spreads over a variety of physiographic elements with different geomorphology, geology, soils and climate, it encompasses a mosaic of different ecosystems, including shoreline forests, lower, middle and upper montane rainforest, deciduous and semi-deciduous forests, *Araucaria* forest and campos de altitude (high elevation grass- and shrublands). As a result, the Atlantic rain forest presents high species endemism and species/area ratio (Meyers et al., 2000). Around 20,000 species of plants, almost 1000 species of birds, more than 450 species of amphibians, 310 species of reptiles, 350 species of fresh water fishes and 270 species of mammals are catalogued in its domain besides several to be registered yet (Cunha and Guedes, 2013).

Unfortunately, due to centuries of exploitation specially because of its strategic position along the coast, only 10-15% of the Atlantic Forest biome remains in a natural or semi-natural state (Fundação SOS Mata Atlântica/ INPE, 2017) (Fig. 1b). While more intense occupation and deforestation occurred since the European colonization, starting *c.* 1500 AD, the history of human occupation along the Brazilian coastline started with the migration of Amerindians from north to south arriving in southeastern Brazil about 10,000 years ago (Figuti et al., 2004).

Amerindians settled originally along the coast, but migrations and cultural transitions led a greatly increased human footprint in inland forests by 1800 yr BP (Noelli, 2008). By the time Portuguese settlers arrived in Brazil beginning in 1500 AD, centuries of swidden agriculture had altered much of the lowland forest, but the low population densities and primitive technologies of the Amerindians left some forest areas untouched and most cultivated areas were in some stage of recovery at any given time (Dean, 1995; Drummond, 1997). The first Portuguese settlements mainly established around Rio de Janeiro state, starting the more intense exploitation of the forest (Noelli, 2008). Currently, around 72% of Brazilian population live in the Atlantic rain forest region resulting in the fragmentation and loss of habitats.

Nevertheless, small fragments of Atlantic forest are still presented, mostly isolated from each other (Ribeiro et al., 2009). Due to the complexity of the relief, few and continuous larger fragments are found in montane areas particularly in southeastern Brazil inside protected areas (Ribeiro et al., 2009; Cunha and Guedes, 2013). Although national and states parks englobe only about 2.5% of this biome, protected areas are important tool to preserve the remaining Atlantic forest and must be strategic planned for maximize its effectiveness (Cunha and Guedes, 2013). In this context, palaeoecological studies can provide a foundation for better understanding the vegetation dynamics and, hence, contribute to develop management strategies for the perpetuation of the Atlantic forest biome.

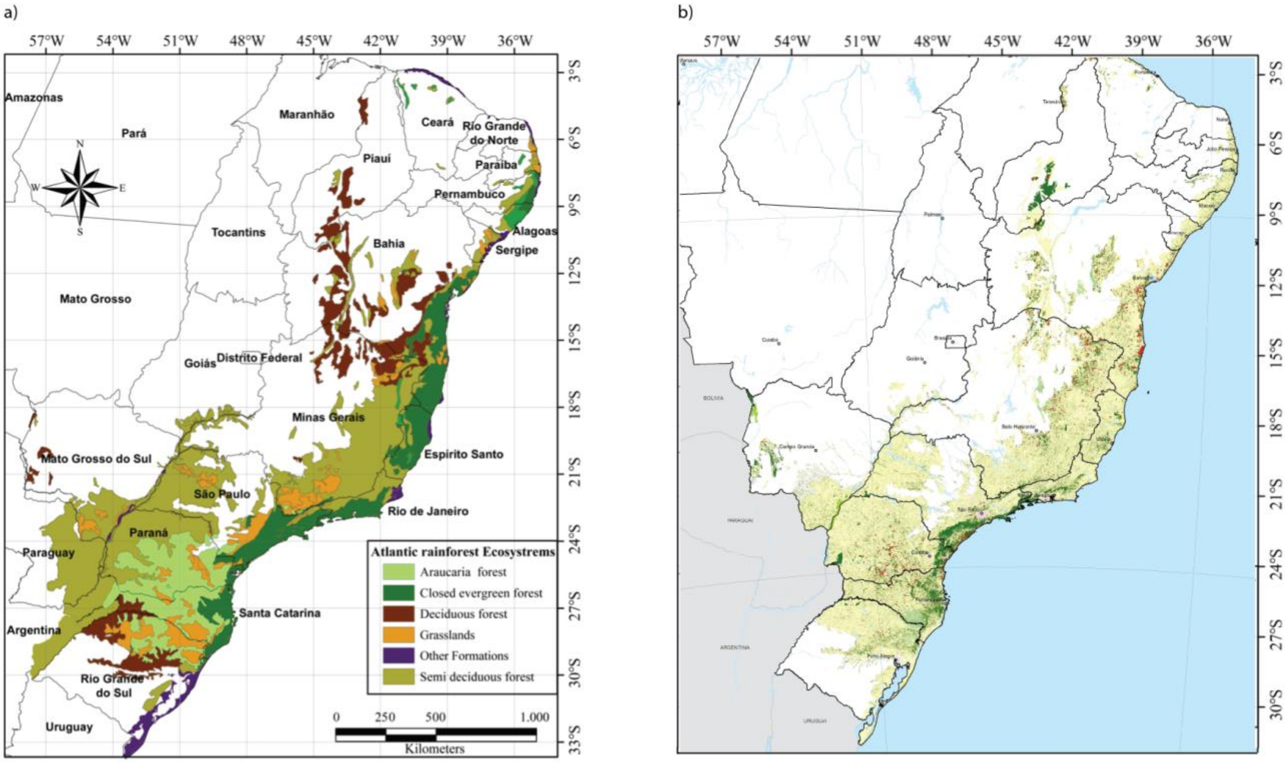
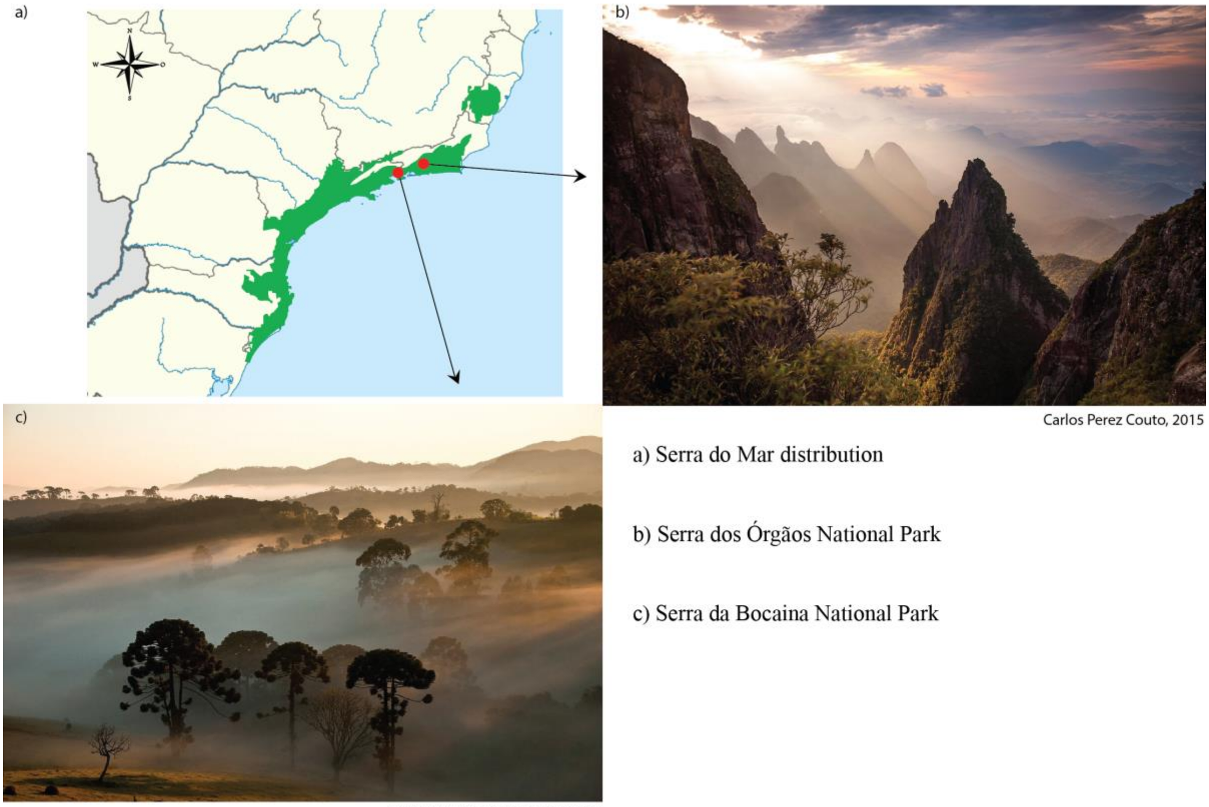


Figure 1: a) Atlantic rain forest domain with associated ecosystems (RBMA, 1999, after Rodrigues et al., 2016; b) Atlantic rain forest remain (Fundação SOS Mata Atlântica/ INPE, 2017).

2 Study Sites

The study sites are located inside two national parks in the upper slopes of the Brazilian coast highlands (Serra do Mar) in southeastern Brazil. The first study site is in the Serra dos Órgãos National Park, where the modern pollen rain and a sediment core of about 10,000 years were analysed. In the second study site, the Serra da Bocaina National Park, a sediment core of about 650 years was collected (Fig. 2).



Carlos Perez Couto, 2015

a) Serra do Mar distribution

b) Serra dos Órgãos National Park

c) Serra da Bocaina National Park

Henris Luiz Cordeiro Rocha, 2012

Fig. 2. Location of the study sites.

3 Geomorphology

The Serra do Mar (Brazilian coastal highlands) uplift is related to tectonic events resulting from the western Gondwana breakup and the opening of the South Atlantic Ocean throughout the Cretaceous, followed by reactivation of Proterozoic shear zones and uplift during the Late Cenozoic (Hiruma et al., 2010; Siqueira Ribeiro et al., 2011). As a rule, it follows a NE-SW orientation parallel to the coastline, extending for *c*. 1000 km along the Brazilian coastline from southern to northeastern Brazil, since north of Santa Catarina State (26_{o} S) to north of

Rio de Janeiro State (21$_{o}$ S) (Almeida and Carneiro, 1998; Riccomini et al., 1989). The basement rocks mainly consist of Late Proterozoic granite and granitic gneisses and the plateau are remnant erosional surface, mostly underlain by decomposed Proterozoic gneisses and granites (Ab´Saber, 2003; Hiruma et al., 2010).

Due to its great extension, the Serra do Mar is locally identified by different terms, being the Serra dos Órgãos the central part in Rio de Janeiro state and Serra da Bocaina the region at the border of São Paulo and Rio de Janeiro states. The Serra dos Órgãos presents sharply steep, reaching 2263 m a.s.l. almost without flat surfaces (ICMBio, 2008). In the Serra da Bocaina, the landscape is overall characterized by rounded mountaintops interrupted with valleys, interspersed with scattered inselberg formations, probably caused by repeated cycles of tropical/wet morphoclimatic processes punctuated by drier periods over the last few million years (Ab´Saber, 2003; Safford and Martinelli, 2000).

4 Climate

The climate in Serra do Mar is categorized as tropical humid with seasonal precipitation, with the bulk of precipitation falling during summer (November to April), ranging from 1000 to more than 2500 mm. A dry season occurs in winter (June to August), when precipitation is less than 50 mm (Nimer, 1977; IBAMA, 2002; ICMBio, 2008). Precipitation in southeastern Brazil is connected to the South American Monsoon System (SAMS), which results in higher austral summer insolation and a more southerly position of the Intertropical Convergence Zone in summer (Bernal et al., 2016). The seasonality of precipitation is mainly controlled by the South Atlantic Convergence Zone (SACZ) between São Paulo and Rio de Janeiro (Flantua et al., 2016). Furthermore, orographic effects play an important role to increase rainfall amounts in the middle and upper part of the Serra do Mar and to hold a frequent orographic fog covering upper montane forests and campos de altitude at the treeline (Safford, 1999). The highest precipitation amounts of Brazil are registered in upper montane forests of the Serra do Mar of São Paulo, where annual rainfall totals may exceed 5000 mm (Safford, 1999) (Fig. 3).

At the highest elevations, frost is common in the winter months, especially in high elevation basins. In the upper elevations of Serra do Mar, mean maxima during the warmest month may reach *c*. 20 °C whilst mean minima during the coldest month may drop as low as *c*. 3.5 °C in the campos de altitude. On the plateau, the temperature ranges from 29 to -4 °C and the annual average temperature is 17 °C, with mild, wet summers and cool, dry to moist winters (IBAMA, 2002; Nimer, 1977).

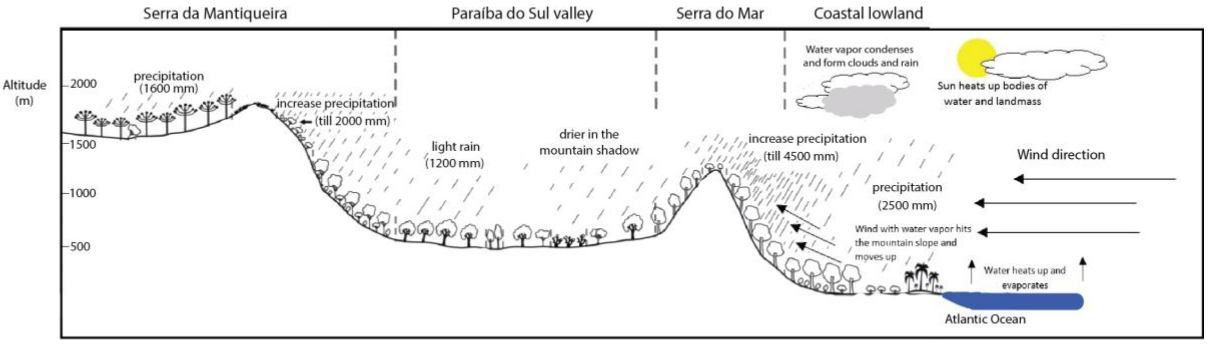


Fig. 3. Schematic profile of the Serra do Mar at the boarder of São Paulo and Rio de Janeiro states (after Hueck, 1966).

5 Vegetation

As described before, the Atlantic Rain Forest Biome encompasses a large range of ecosystems due to the diversity of physiographic elements compounding the region where it spreads over. In the study sites, the vegetation typologies of interest are *Araucaria* forest, montane rain forest, upper montane rain forest (cloud forest) and campos de altitude (high elevation grassland).

5.1 Araucaria forest

Araucaria forest occurs between 400 and 1400 m a.s.l. in southern Brazil and in smaller fragments at altitudes between 1400 and 1800 m a.s.l. in southeastern. It spreads over humid climate without dry season, with average mean temperature around 15 $_{o}$C and 3-6 months lower than 15 $_{o}$C. Its physiognomy is marked by the presence of *Araucaria angustifolia* in the upper canopy. Important species of the *Araucaria* forest are *Araucaria angustifolia, Podocarpus lamberttii* and *Drimys brasiliensis*. The families Myrtaceae, Lauraceae, Fabaceae, Melastomataceae are common together with the tree ferns *Dicksonia sellowiana*

(Dicksoniaceae) and *Alsophila capensis* (Cyatheaceae) (IBAMA, 2002; IBGE, 2012). Apiaceae, Piperaceae and Rubiaceae characterize the forest shrub layer (IBAMA, 2002).

Fig. 4. *Araucaria* forest and campos de altitude at the study site in Serra da Bocaina National Park.

5.2 *Montane rain forest*

Montane formation normally covers depth soils from *c*. 700 to *c*. 1600 m a.s.l. on. It usually presents three strata, within the canopy reaching 25-30 m height. Common tree families are Myrtaceae, Lauraceae, Melastomataceae, Fabaceae, Rubiaceae, Euphorbiaceae and shrubs from the families Piperaceae and Loranthaceae, besides Araceae, Pteridophyta, Begnoniaceae, Orchidaceae and Bromeliaceae. The palm *Euterpe edulis*, together with *Chusquea* and tree ferns are common in the understory (Pardo et al., 2007; ICMBio, 2008). Its distribution is related to warm and humid climate, without dry season and average mean temperature between 22-25 $_o$C (IBGE, 2002).

Fig. 5. Atlantic montane forest in Serra da Bocaina National Park.

5.3 Upper montane rain forest (cloud forest)

The upper montane forest occurs in general above 1500 m a.s.l. in small fragments close to the mountain summits. Due to the permanent presence of fog, high humidity, low temperatures, strong winds and shallow soils, it is characterized by twisted and dwarfed trees and shrubs distributed in only one strata less than 10 m height (Portes, 2001; IBAMA, 2002). The most frequent families are Myrtaceae, Proteaceae, Melastomataceae and Malphigiaceae (ICMBio, 2008). Important tree genera include *Myrsine*, *Clethra*, *Piptocarpha*, *Myrceugenia*, *Daphnopsis*, *Roupala*, *Weinmannia*, *Symplocos*, *Ilex* and *Ocotea* (IBAMA, 2000; Portes, 2001; Behling and Safford, 2010). The most salient feature is the abundance and diversity of epiphytes and mosses as a result of the high air humidity (Falkenberg and Voltolini, 1995; Safford, 1999).

Fig. 6. Interior of the upper montane rain forest.

5.4 *Campos de altitude*

The vegetation of campos de altitude occupies the summits and the upper mountain slopes above around 1500 m a.s.l., covering hilltops and convex slopes as well as poorly-drained valley bottoms in exposed surfaces (Safford, 1999; IBAMA, 2002; Hiruma et al., 2010). It is rich in endemic species, predominantly characterized by non-arboreal species (Martinelli and Bandeira, 1989). It is dominated by tall bunchgrasses (*Cortaderia*), montane bamboo (*Chusquea*) and heterogeneous mixture of sclerophyllous shrubs, particularly *Baccharis*, *Escallonia*, the families Asteraceae, Ericaceae, Melastomataceae and Myrtaceae. Frequent herbs are *Eryngium*, *Paepalanthus*, *Plantago* and *Xyris* (Behling and Safford, 2010). Temperatures can reach 35 ºC in summer with mean temperatures between 16 and 22 °C and frost during winter. Annual precipitation average is around 1800 mm. Albeit always humid mostly due to low evapotranspiration, a dry season of three months occurs in the southeastern mountains during winter (Nimer, 1977; Safford, 1999; Overbeck et al., 2007).

Fig. 7. Vegetation of the upper slopes of Serra dos Órgãos: rock outcrop, rock vegetation, campos de altitude and upper montane forest canopy.

6 Methodology

6.1 Fieldwork

For conducting this research, three fieldwork excursions were carried out on the Brazilian coastal highlands in southeastern Brazil. In February 2015, with the assistance of a Russian corer, one peat record was extruded in the upper montane Atlantic rain forest in the Serra dos Órgãos National Park and other sedimentological record was extracted in the Serra da Bocaina National Park from a swampy area. Each 50 cm length section was sealed with split PVC tubes and wrapped with plastic film before stored under cool (*c.* 4 $_{o}$C) and dark conditions (Fig. 8a).

In October 2015, 23 Behling pollen traps were installed along an elevational gradient in the Serra dos Órgãos National Park, being collected after one year, in October 2016 (Fig. 8b).

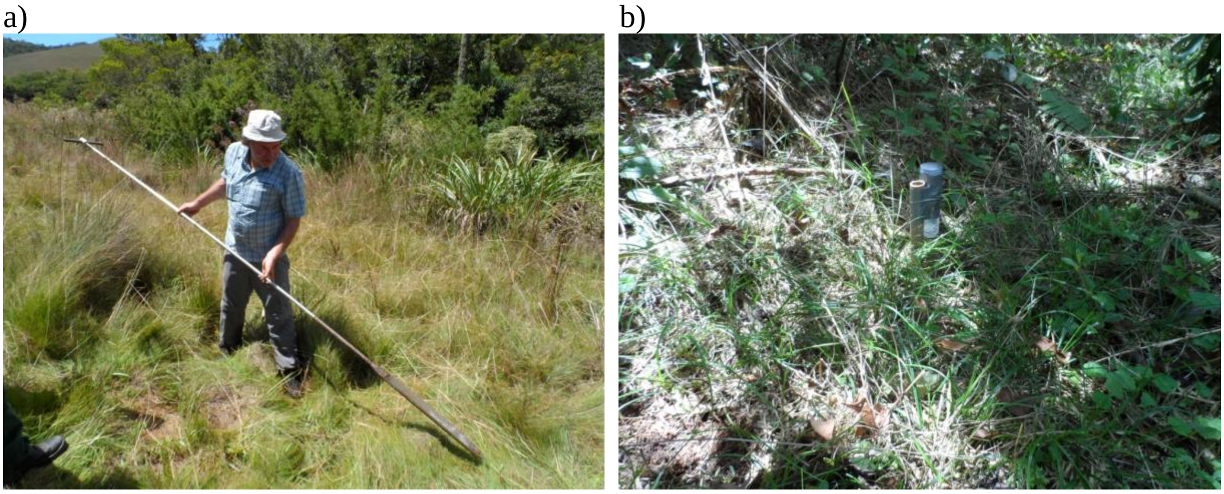


Fig. 8. a) Collecting the sediment in the Serra da Bocaina National Park, b) Installing the pollen traps in the Serra dos Órgãos National Park.

6.2 *Core chronology*

In total, nine subsamples were taken from the cores and sent to radiocarbon dating through Accelerator Mass Spectrometry (AMS). Four samples were sent to Laboratory at National Taiwan University (NTUAMS) and five samples to the AMS Poznan Radiocarbon Laboratory (LAMS). The resulting ages were converted into calibrated calendar years before present (cal yr BP) with R-package Clam 2.2 (Blaauw, 2010) in R-Studio (R-Studio Team, 2016, 2019) using the South Hemisphere calibration curve SHCal13.14C and postbomb curve SH 1-2. Calib 7.1 (Stuiver et al., 2019) was used for calculating the medians probability.

6.3 *Pollen and spore analysis*

Pollen and spores, unlike other organic material, are preserved for long periods of time due to their sporopollenin-wall structures (Birks and Birks, 1980). Their specific morphological characteristics allow the identification in accordance to their plant source and the association to a vegetation type (Birks and Birks, 1980; Faegri and Iversen, 1989). As a result, it is possible to reconstruct past vegetation dynamics by distinguishing and counting pollen and spores grains. Furthermore, modern pollen can also be analysed for better understanding of the relationship between pollen rain and vegetation.

6.3.1 Processing modern samples

Pollen and spore assemblages were extracted from each Behling trap by centrifuging and sieving. Afterwards, *Lycopodium clavatum* was added as exotic marker to each sample and acetolysis was carried out to dissolve cellulose material and to stain the pollen residues. The pollen residue obtained was kept in distilled water until mounted in slides with glycerine.

6.3.2 Processing fossil samples

Standard pollen techniques were used to process the samples applying 40% hydrofluoric acid (HF) and acetolysis (Faegri and Iversen, 1989). Previously, *Lycopodium clavatum* was added to each subsample. The extracted pollen and spores were kept in distilled water and mounted in slides for pollen taxa identification and counting under a light microscope.

6.4 Charcoal analysis

Combining other proxies with pollen fossil analysis can provide more information about past deposition processes and occurring events in the catchment area (Birks and Birks, 1980). In the case of the vegetation of campos de altitude, the fire regime is closed related with the expansion and regression of the vegetation. To understand the past local fire regime and its influence on vegetation of the study areas, subsamples were prepared following the method developed by Rhodes (1998) and Stevenson and Haberle (2005). All charcoal particles >150 µm were counted and concentrations were calculated as particles cm^{-3}. Fire regime characteristics were identified using the software CharAnalysis (Higuera et al., 2009).

7 Late Quaternary Palaeoecology of Serra do Mar in Southeastern Brazil

7.1 Late Pleistocene

During the Last Glacial, from about 35,000 to 17,000 ^{14}C BP, the highlands of southeastern Brazil were primarily covered by grassland vegetation stretched from southernmost Brazil, indicating a cold and dry climate (Behling, 2002, 2007). During the Late Glacial, between

17,000 and 10,000 ^{14}C yr BP, *Araucaria* forest, upper montane and montane Atlantic rain forest species expanded toward mountains, but were still rare on landscape and probably grew only at lower elevations, indicating a somewhat warmer climate (Behling, 1997; Behling et al., 2007).

Palaeofires seem to have been quite abundant during Late Pleistocene (i.e. before arrival of man) in southeastern Brazil in oppose to southern Brazil. Contrariwise, pollen diversity of herb taxa was lower in the southeast than in the south, probably resulted from the high fire frequency (Behling, 1997, 2002; Behling et al., 2007).

7.2 Holocene

During Early Holocene, climate remained cold and campos de altitude vegetation continued to occupy most of the highlands in southeastern Brazil. The development of upper montane forest close to the mountain summits indicates a possibly warm and moist climate on the Atlantic facing slopes, however the low abundance of arboreal taxa suggests that the climate in the highland plateau and summits remained dry (Behling, 1997; Behling et al. 2007; Behling and Safford, 2010; Veríssimo et al. 2012; Portes et al., in review). Fire appear to have been frequent in the upper slopes covered by campos de altitude vegetation (Behling, 1997; Behling et al., 2007; Behling and Safford, 2010; Veríssimo et al., 2012; Portes et al., in review).

A decrease in fire frequency and change in vegetation indicate that Mid-Holocene was wetter than Early Holocene (Veríssimo et al., 2012). Nevertheless, campos de altitude remained the dominant vegetation at high elevations (Veríssimo et al., 2012; Portes et al., in review). From the Mid- to Late Holocene a warmer and moister climate established in southeastern Brazil, allowing the expansion of *Araucaria* forest and low montane forest on the slopes (Behling, 1997). Actually, several palynological data show a clear trend of increasing forest cover – and decreasing campos cover – at high elevations since around 5000 cal yr BP, with acceleration in this trend during the Late Holocene (Behling, 1997; Behling and Safford, 2010; Portes et al., in review). The last about 1000 years are the wettest period of the Holocene (Behling, 1995).

The shift to wetter conditions throughout the Holocene is also registered by palaeoclimate records. Oxygen isotope record data from the last 10,000 years at Botuverá Cave (27$_{o}$13’S, 49$_{o}$09’W, 230 m a.s.l.; Bernal et al., 2016) registered an increase in rainfall starting about 4000 years ago. The increase in summer precipitation during the Late Holocene is supported by studies of the SAMS (South American Monsoon System) over the last 2000 years, which show a strengthening monsoon during the Little Ice Age (LIA), resulting in a wetter period from *c*. 1400-1800 AD (Vuille et al., 2012).

First registers of human evidence in southeastern Brazil dated to since around 9000 years when Amerindians mainly migrated from north to south along the coast due to expansion of the population; since 1800 BP tupi tribes inhabited the coastal zone of Rio de Janeiro (Noelli, 2008). Although most of the settlements were in the coast, inland territory was possibly explored due to the nutritional importance of *Araucaria* seeds to Amerindians (Robinson et al., 2018). Dean (1995) suggests that the “islands” of *Araucaria* forest found in the southeastern highlands may not be totally natural. Albeit archaeological investigations give no evidence of Amerindians settlements in the topographically extremely abrupt slopes of Serra dos Órgãos, indigenous trails of hunter-gatherers crossed the mountains (Nehren et al., 2013). In the Serra da Bocaina, where landscape is characterized by rounded mountaintops interrupted with valleys, Amerindians slash and burn agriculture began at least 1500 years before the arrival of Europeans (Corrêa, 2006; Noelli, 2008).

Even if the landscape was impacted somehow by Amerindians practices, it was low compared to the degradation process that started with the European colonization in the mid of 16$_{th}$ century (Nehren et al., 2013). After the arrival of the first Europeans, the vegetation cover rapidly changed due to the several economic cycles of exploitation (1-selective cutting of brazilwood, 2-sugar cane, 3-gold, 4-coffee; Nehren, 2013). Hence, today the landscape is highly fragmented with remnants of the Atlantic forest specially on the slopes (Nehren et al., 2009).

8 Aims and Objectives

This research aims to comprehend the processes which resulted in the actual vegetation distribution in the higher elevations of the Brazilian coastal highlands. It also intends to provide a foundation for better understanding how the grassland component of the mosaic might be conserved under a future climate that will greatly favour forest expansion.

The following objectives have been addressed through this research:

- Reconstruct the vegetation dynamics within campos de altitude and forest vegetation in two different landscapes;
- Detect possible regional climate changes;
- Disentangle the influences of climate and humans on the changing status of the forest-grassland mosaic.

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CHAPTER 2

Pollen rain - vegetation relationship along an elevational gradient in the Serra dos Órgãos National Park, southeastern Brazil

Maria Carolina Guarinello de Oliveira Portes[1,2,3], Hugh DeForest Safford[4,5],
Vincent Montade[1,6], Hermann Behling[1]

[1] *University of Goettingen, Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Sciences, Germany*

[2] *Instituto Chico Mendes de Conservação de Biodiversidade (ICMBio), Brazil*

[3] *CNPq-Brazil Scholarship, Brazil*

[4] *USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA*

[5] *Department of Environmental Science and Policy, University of California, Davis, California, USA*

[6] *Université de Montpellier, Institut des Sciences de l'Evolution de Montpellier, CNRS, IRD, EPHE, France*

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Abstract

We analysed modern pollen deposition along an altitudinal gradient in the Brazilian southeastern coastal mountains between 1600 and 2200 m elevation in order to investigate the relationship between modern vegetation and pollen rain, within vegetation composed of montane and upper montane forest in a mosaic with campos de altitude (CDA). The results revealed that the CDA pollen assemblage represents a much larger source area than the forest pollen assemblage, which is comprised of more local taxa. Anemophilous pollen from vegetation at lower elevations is over-represented in the higher elevation pollen traps. Although arboreal taxa dominate the pollen assemblages – even in the grassland pollen traps – the composition of the pollen traps can be confidently related to the vegetation surrounding the collection site. To improve distinction between grassland and forest dominance in a complex environmental mosaic subject to temporal dynamism, we selected a suite of arboreal pollen taxa aiming to reduce the influence of over- and under-representation of some pollen taxa in such kind of environment. Our findings permit more robust interpretation of palaeo-ecological and -geographical relationships between forest and CDA and build a firmer foundation for understanding how future climatic change may impact montane vegetation in SE Brazil.

Key words: modern pollen rain, campos de altitude (high elevation grassland), upper montane forest, tropical mountains, tropical South America.

1 Introduction

The Atlantic Forest biome stretches along Brazil's east coast for more than 4000 km, with the Brazilian Highlands as its geographic backbone. The Atlantic Forest, which once covered as much as 1.3 million km^2, has been drastically reduced in area since European settlement in the 16th century (Fundação SOS Mata Atlântica/ INPE, 2017) and is considered one of the world's most threatened biomes as well as one of its most important biodiversity hotspots (Myers et al., 2000). Today, some of the largest remaining fragments of the Atlantic Forest are inside national and state protected areas found on the steep slopes of the Serra do Mar and

Serra da Mantiqueira in the states of Rio de Janeiro, Minas Gerais, and São Paulo (Ribeiro et al., 2009). Among the ecosystems covered by these protected areas, some of the most important are upper montane forest and campos de altitude (CDA, or named high elevation grasslands), due to their rarity in eastern Brazil and the high numbers of endemic species they support (Martinelli and Bandeira, 1989; Safford and Martinelli, 2000; Spehn et al., 2010). These ecosystems share the summits of eastern Brazil's highest mountains, with upper montane forest often occupying concavities and protected sites and campos de altitude covering mountaintops and convex slopes (Safford, 1999a). Their geographic relationship is dynamic, with forests dominating in the absence of disturbance and when and where climates are warmer and wetter, and campos dominating after fire and in colder and drier periods (Safford, 1999a, 2001; Portes et al., 2018).

Over the last two decades palaeoecological studies based on fossil pollen and charcoal records have been carried out in the southeastern Brazilian highlands in order to better understand past, current, and potential future trends in vegetation, climate, and disturbance, as well as to discern synergies between these factors in driving ecological conditions (e.g. Behling, 1995, 1997a, 1997b, 2007; Scheel-Ybert, 2001; Ledru et al., 2005; Behling et al., 2007; Behling and Safford, 2010; Veríssimo et al., 2012; Raczka et al., 2013; Portes et al., 2018). This work has also provided information important to improve the design of conservation and management strategies that aim for sustainability in the face of rapid global change. However, because pollen production, dispersal, and preservation vary widely among plant species, the relationship between pollen rain, local vegetation and environment is not straightforward, which limits the interpretation of the fossil pollen record (e.g. Prentice, 1988). Studies that relate modern vegetation and environment to pollen rain – especially studies carried out along elevational and ecological gradients – can help to better discern pollen production and dispersal patterns, as well as habitat and elevational relationships among species and ecological communities in order to improve interpretation of fossil pollen records (e.g. Bartlein et al., 2011; Cárdenas et al., 2014; Jantz et al., 2014; Markgraf et al., 2002; Montade et al., 2016; Niemann et al., 2010; Rodrigues et al., 2016; Schüler et al., 2014; Tonello et al., 2009; Weng et al., 2004).

Montade et al. (2019) recently developed the first modern pollen dataset for the full Atlantic Forest biome, describing regional vegetation and climate patterns. Based on this dataset, the authors were able to discern four broad "eco-physiognomies" from modern pollen samples, including northeastern Atlantic rain forest, semi-deciduous and riverine forests, lowland rain forest, and high elevation vegetation consisting of forests and grasslands. In the case of the high elevation vegetation group, the authors pointed out that the fine-spatial scale of intercalation of forest and grassland vegetation posed a challenge to further differentiation that only well-designed, local sampling could resolve. Due to the reduced number of modern pollen samples, several sampling methods had to be combined in this regional dataset. Nonetheless, different sampling methods can present different results which could explain this local scale limitation in differentiating vegetation physiognomies. Surface samples may be considered more representative of the pollen production as pollen rain composition commonly varies over 2 and 3 years as well as according to plant specific systems and changing in climatic conditions (Niemann et al., 2010; Montade et al., 2019). In contrast, pollen traps not only provide the representation and distribution patterns of pollen spectra but also the accumulation rates. Moreover, pollen traps present better pollen preservation, diminishing the difficulty and uncertainties in determination of pollen types and allowing to distinguish similar pollen that normally are classified together, and registering pollen with fragile exine that rarely appear in surface samples or in fossil records (Jantz et al., 2014).

The dynamic relationship between CDA and forest is of major ecological, conservation, and management interest in southeastern Brazil (Martinelli and Bandeira 1989; Safford, 1999a; 2001; Aximoff 2011; Portes et al., 2018). In order to understand how these ecosystems interact over space and time, we require a robust discrimination of their signal in the fossil pollen record, but to this point such a discrimination had been lacking. To fill this gap, we installed a series of pollen traps along a high elevation transect through areas dominated by montane forest, upper montane forest and CDA in Serra dos Órgãos National Park (PARNASO; Fig. 1). We used pollen traps rather than surface samples so as to better preserve fragile pollen types that rarely appear in soil surface samples, to diminish identification errors and to allow the calculation of pollen accumulation rates. Our principal purposes were to (1) investigate the relationship between the modern pollen assemblage and local modern vegetation cover; (2) try to better discriminate between grassland and forest dominance in a complex environmental mosaic subject to temporal dynamism; and (3) augment the modern pollen database of the Brazilian Atlantic Forest biome.

2 Environmental Settings

2.1 Study site

Our pollen traps were located along an elevational gradient in the Serra dos Órgãos, a subrange of the Serra do Mar, within PARNASO (Fig. 1). Founded in 1939 as the third national park in Brazil, PARNASO protects 20,024 ha of lower montane, montane and upper montane forest and campos de altitude of the Brazilian Atlantic Forest biome (ICMBio, 2008). The park is famous for its spectacular landscape and extraordinary levels of biodiversity. Ironically, it is found in one of the most densely populated areas of Brazil, less than 50 km from downtown Rio de Janeiro.

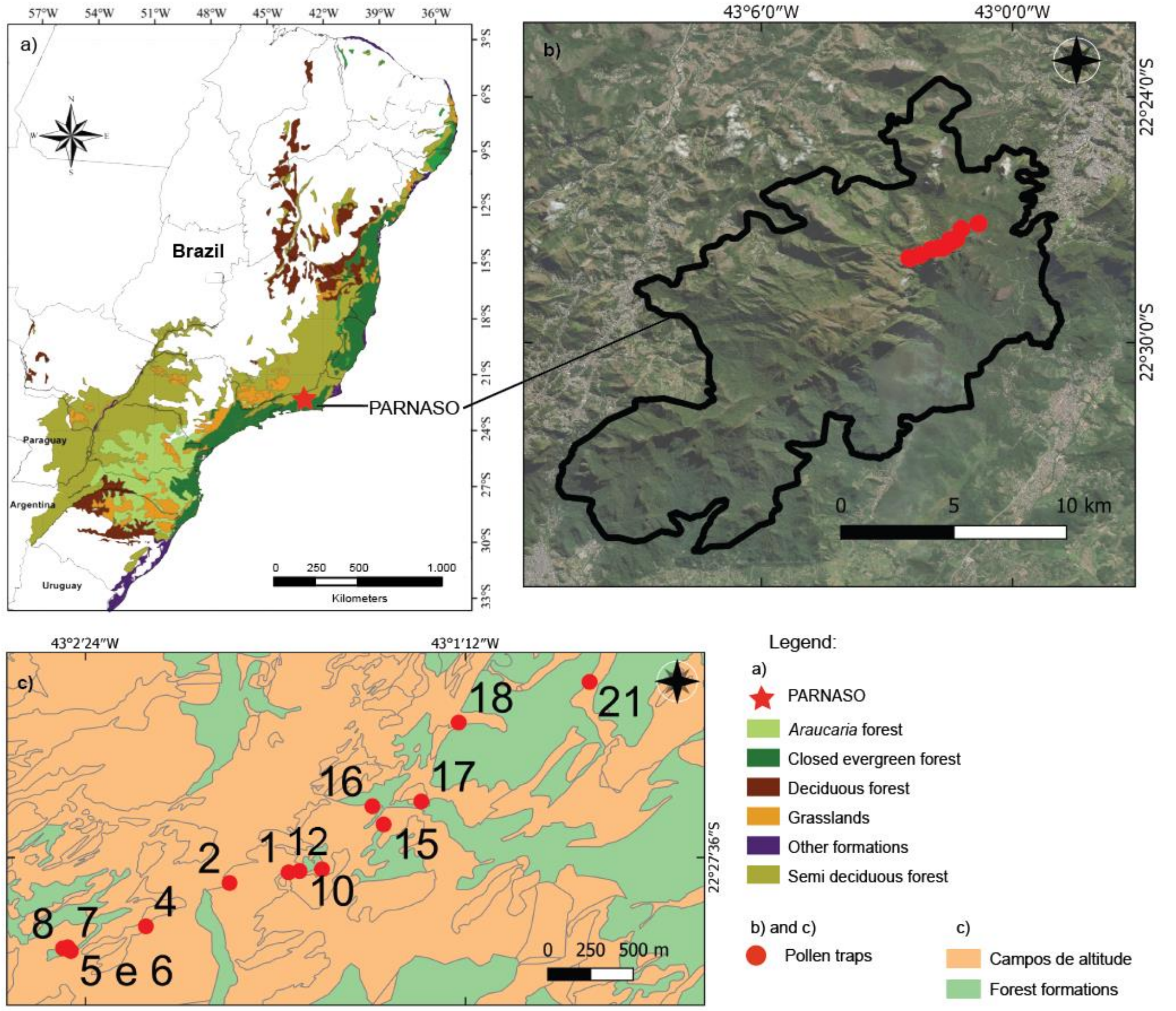


Fig. 1. Location of the study site and the pollen traps. a) national location of Parque Nacional da Serra dos Órgãos (PARNASO) (adapted from Fundação SOS Mata Atlântica/ INPE, 2017), b) regional location of PARNASO and c) location of the pollen traps collected in PARNASO.

In the Serra dos Órgãos, basement rocks are mostly Late Proterozoic granite and granitoid gneisses. Topographic relief is associated with late Cenozoic reactivation of faults that originally arose during the opening of the Atlantic Ocean in the late Mesozoic (Machado Filho et al., 1983). Soils in the study area are generally shallow, poorly developed, acidic and highly organic with a deep litter layer (Falkenberg and Voltolini, 1995). As a rule, the Serra dos Órgãos follows a SW-NE orientation parallel to the coastline (Riccomini et al., 1989; Safford, 1999a; ICMBio, 2008).

2.2 *Climate*

In the broader region, the climate is mostly controlled by the South Atlantic Convergence Zone (SACZ), with most precipitation falling between November and April (Safford, 1999a). Although the climate for the region has been classified as mesothermic with mild and wet summers and moderate winters without a marked dry season (ICMBio, 2008), a winter dry season (months with <50 mm precipitation) of two to three months occurs most years in the southeastern Brazilian mountains (Nimer, 1977; Safford, 1999b). The annual average temperature at the nearest long-term meteorological station at Teresópolis (22°25.980'S, 42°58.980'W, 1100 m a.s.l.) is 17.6 $_{o}$C, ranging from 8.6 $_{o}$C (mean of the coldest month – July) to 27.2 $_{o}$C (mean of the warmest month – February). Mean average precipitation at Teresópolis is 1800 mm, with less than 40 mm in the driest month (July) and 270 mm in the wettest (January) (Hijmans et al., 2005). Orographic effects play an important role in modifying the Serra dos Órgãos climate, and elevations higher than Teresópolis are cooler, wetter, and characterized by frequent fog. PARNASO installed temperature data loggers at sites near our transect between September 2012 and February 2014 (C. Cronemberger, PARNASO, pers. comm.). In montane forest at 1600 m elevation (near pollen trap site 21), the mean overall temperature was 15.4 $_{o}$C, with an absolute maximum of 30.7 $_{o}$C and a minimum of 3.1 $_{o}$C. In upper montane forest at 2012 m elevation, mean, maximum and minimum temperatures were 12.7 $_{o}$C, 25.6 $_{o}$C, and 1 $_{o}$C, respectively. Temperatures in the campos de altitude at 1954 m elevation showed a similar mean temperature (12.5 $_{o}$C), but temperatures were more extreme due to the lack of trees and the valley bottom position: max = 27 $_{o}$C, min = -5.2 $_{o}$C).

Safford (unpub. data) measured -9.8 $_{o}$C during a July night in 1997 at this same campos de altitude site. Safford (1999b) measured soil temperatures from depths of >75 cm in deep soil pockets on the summit of Pedra do Sino and obtained an estimate of mean annual temperature of approximately 10.2 °C at 2260 m a.s.l.. Annual precipitation in the Serra dos Órgãos at 2000 m elevation is >2500 mm (Safford, 1999b).

2.3 Vegetation

The vegetation encountered at the study sites is classified as montane Atlantic rain forest (ARF), upper montane ARF, and campos de altitude (CDA) (ICMBio, 2008). Montane ARF occurs from *c.* 700 to *c.* 1600 m a.s.l. It typically presents three strata, within the canopy reaching 25-30 m height. Common overstory tree families include Myrtaceae, Lauraceae, Melastomataceae, Fabaceae, Solanaceae, Asteraceae, Rubiaceae, and Euphorbiaceae. Important epiphyte families include Orchidaceae, Bromeliaceae, Gesneriaceae and various ferns. The palm *Euterpe edulis*, tall *Chusquea* bamboos, and tree ferns are common in the midstory. Lianas are dominated by Asteraceae, Malpighiaceae, Fabaceae and Sapindaceae, and shrubs are represented by Rubiaceae, Melastomataceae, Piperaceae, and Begoniaceae, among many other families (Lima and Guedes-Bruni, 1997; Pardo et al., 2007; ICMBio, 2008).

Montane habitats grade gradually into upper montane habitats starting above 1300 m a.s.l., with upper montane ARF prevailing at elevations >1600 m a.s.l. (ICMBio, 2008). Due to the common presence of fog, constant winds and other microclimatic conditions, upper montane ARF is characterized by twisted and dwarfed trees and shrubs distributed usually in one stratum <10 m height. A salient feature is the abundance and diversity of epiphytes – especially Orchidaceae, Bromelicaeae, Cactaceae, ferns and mosses – as a result of the high air humidity (Falkenberg and Voltolini, 1995; Safford, 1999a). The most frequent tree and shrub families are Myrtaceae, Proteaceae, Melastomataceae and Malpighiaceae (ICMBio, 2008). Important tree genera include *Myrsine*, *Clethra*, *Piptocarpha*, *Myrceugenia*, *Daphnopsis*, *Roupala*, *Weinmannia*, *Symplocos*, *Ilex* and *Ocotea* (Behling and Safford, 2010; Gomes, 2015).

CDA vegetation dominates above 1800 m a.s.l., covering hilltops and convex slopes as well as poorly-drained valley bottoms that are affected by cold air drainage (Safford, 1999a;

ICMBio, 2008). The CDA is dominated by tall bunchgrasses and sedges (especially *Cortaderia* and *Machaerina*), montane bamboo (*Chusquea*) and a heterogeneous mixture of sclerophyllous shrubs, particularly from the genera *Baccharis* and *Escallonia,* and the families Asteraceae, Ericaceae, Melastomataceae and Myrtaceae. Frequent herbs are *Eryngium*, *Paepalanthus*, *Plantago* and *Xyris*, and lycopods and cool-weather bryophytes are widespread (Behling and Safford, 2010).

3 Material and Methods

3.1 Pollen trap design and sampling

For collection of the modern pollen assemblage of the mountain vegetation of PARNASO, 23 pollen traps were placed along a 4 km section of the Pedra do Sino trail, ranging from 1600 m to 2200 m a.s.l., between the coordinates 22$_{o}$26’53”S, 43$_{o}$00’28”W and 22$_{o}$27’53”S, 43$_{o}$02’28”W (Fig. 1). Each pollen trap was classified according to their respective local vegetation in the field (CDA, upper montane ARF and montane ARF). The trap model used was developed by Behling and formally described in Behling et al. (2001) and tested by Jantz et al. (2013). Each trap was installed about 10 cm above the soil surface in October, 2015 and collected in October, 2016 (Table 1).

3.2 Pollen analysis

The pollen grains were extracted from each trap as described in Jantz et al. (2013). Before processing, one tablet of *Lycopodium clavatum* spores (20,848± 1546, batch 3862) was added as exotic marker to each sample for influx calculation. Acetolysis was carried out to dissolve cellulose material and to stain the pollen residues. The pollen residue obtained was kept in distilled water until mounted in slides with glycerine for pollen analysis. Samples were counted to a minimum of 300 pollen grains and identification of pollen and spores was based on the reference collection of Brazil and Ecuador at the Department of Palynology and Climate Dynamics, University of Goettingen (Germany). Further support was obtained from literature and electronic pollen keys (Behling, 1993; Melhem et al., 2003; Bush and Weng, 2006; Neotropical Fossil Pollen Search Tool developed by Dr. Hermann Behling and Dr.

Chengyu Weng, unpublished). Nomenclature follows the Flora do Brasil 2020 (http://floradobrasil.jbjr.gov.br). Pollen percentages were calculated excluding aquatics, exotics, unidentified and spores. Pollen diagrams were plotted using the C2 software (Juggins, 2007) and clustered according to the habit and the ecology of the taxa.

Table 1. List of 23 pollen traps grouped by vegetation zone where each trap was installed, with their geographic coordinates and elevation. In black the recovered traps and in grey the unfounded ones.

Vegetation	Sample	Coordinate S	Coordinate W	Altitude (m)
Campos de altitude (CDA)	SOPT1	22o27’38.48”	43o01’45.66”	2188
	SOPT10	22o27’38.23”	43o01’43.57”	2180
	SOPT2	22o27’40.50”	43o01’56.86”	2169
	SOPT11	22°27'37.87"	43°01'36.44"	2148
	SOPT15	22o27’29.41”	43o01’27.66”	2128
	SOPT13	22°27'33.08"	43°01'43.46"	2126
	SOPT14	22°27'31.78"	43°01'40.81"	2115
	SOPT3	22°27'44.86"	43°02'4.27"	2107
	SOPT4	22o27’48.70”	43o02’12.70”	2086
Upper montane ARF	SOPT16	22o27’25.96”	43o01’29.78”	2157
	SOPT12	22o27’37.90”	43o01’39.36”	2134
	SOPT9	22°27'46.30"	43°02'6.97"	2113
	SOPT17	22o27’25.06”	43o01’20.53”	2031
	SOPT7	22o27’52.67”	43o02’27.52”	2013
	SOPT8	22o27’52.88”	43o02’28.39”	2008
	SOPT5	22o27’53.40”	43o02’26.91”	2003
	SOPT6	22o27’53.40”	43o02’26.91”	2003
	SOPT18	22o27’10.12”	43o01’13.44”	1923
Montane ARF	SOPT19	22°27'18.18"	43°01'3.40"	1844
	SOPT20	22°27'8.17"	43° 0'53.60"	1671
	SOPT21	22o27’02.41”	43o00’48.67”	1597
	SOPT22	22°26'54.49"	43°00'49.36"	1439
	SOPT23	22°26'53.27"	43°00'28.15"	1287

3.3 Vegetation cover analysis and multivariate analysis

The modern vegetation surrounding each pollen trap was analysed using the software QGIS (QGIS Developing Team, 2019) based on a Bing aerial image (2019) with support of geographical information from 2008 provided by PARNASO. We delimited buffers of 0.79

ha (50 m radius), 3.14 ha (100 m radius) and 78.6 ha (500 m radius) for each trap (see supplementary material) and identified the percentage of the area dominated by two different components: forest and CDA. The CDA component includes CDA *sensu stricto*, rock vegetation, and rock outcrops. A coefficient of correlation (r) was calculated between percentage values of vegetation cover and pollen data for the forest and CDA components within each of the buffer areas.

A correspondence analysis (CA) was applied with R-packages ADE4 (Dray and Dufour, 2007) and VEGAN (Orkansen et al., 2019) in R-Studio (R-Studio Team, 2016) to investigate correlations between pollen spectra from the pollen traps and the representative vegetation. We focused on the CDA and upper montane forest groups and excluded the montane forest group from the CA as it was characterized by only one sample (SOPT21). In order to reduce noise, the CA was performed with the major pollen taxa (with percentages ≥1% occurring in at least three samples). Percentage values were square-root transformed before performing the CA to stabilize the variance.

To better reconstruct the local changes of ARF in this mosaic of grassland and forest, we defined a group of most distinctive pollen taxa of upper montane ARF composed by *Weinmannia*, *Myrsine*, *Clethra* and Myrtaceae based on the results of the CA and considering pollen assemblages, habit and ecological features. We also considered the facility in distinguishing these taxa (important when comparing several sites involving different palynologists) as well as their abundance and well preservation in fossil samples.

This restricted group of ARF and the ARF group were passively projected on the first and second axes of the CA bi-plot.

4 Results

4.1 Modern pollen rain

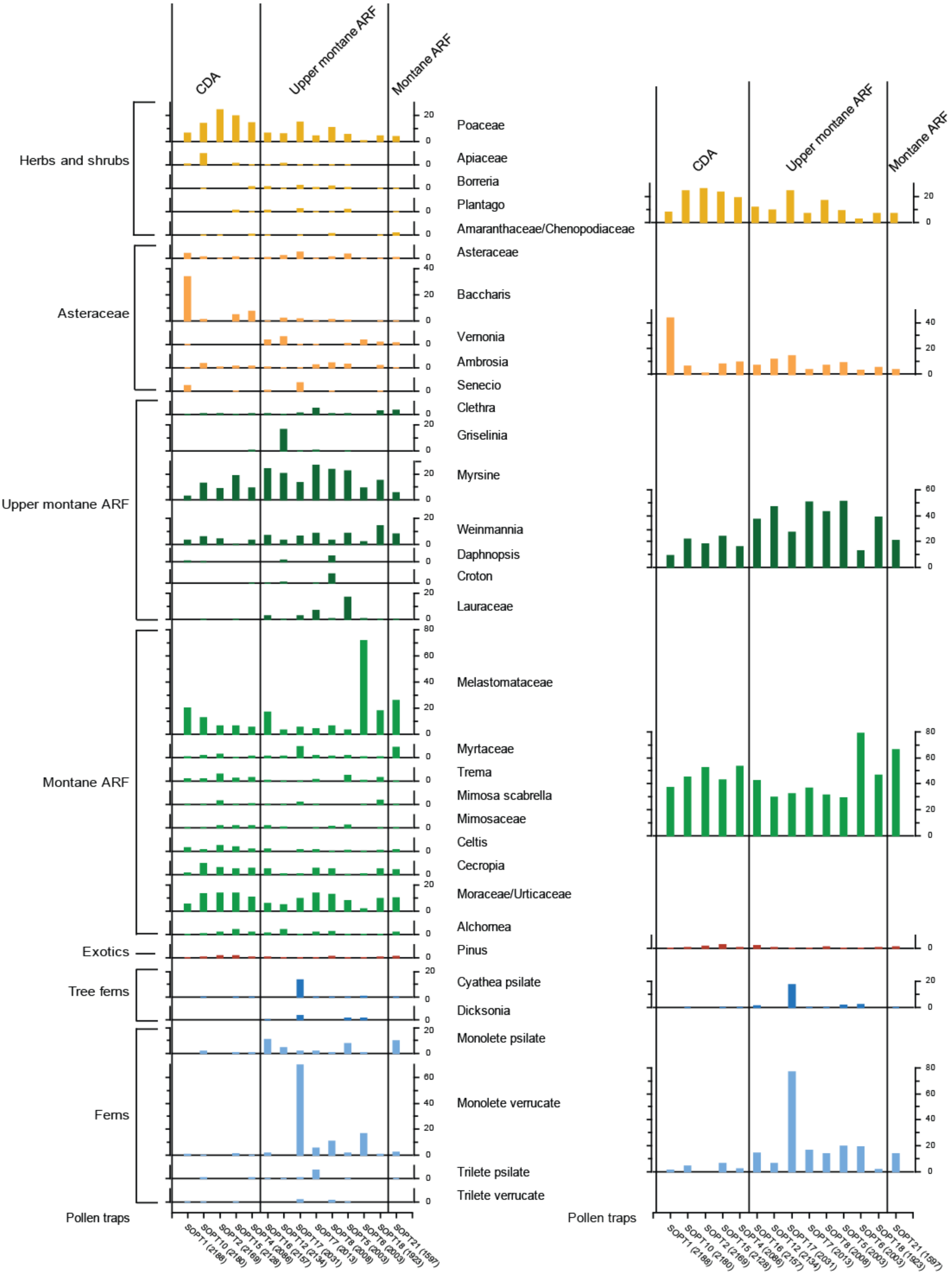
Of the original 23 pollen traps only 14 were recovered. A total of 98 pollen types and 24 spores were identified from the recovered traps. The most abundant and important taxa are displayed in the pollen diagrams (Figs. 2 and 3). A list of all palynomorphs identified can be found in the supplementary material. The pollen taxa were classified into the following ecological groups based on their habit and ecology: CDA including subgroups herbs and shrubs and Asteraceae; upper montane ARF; montane ARF; sub-aquatics, exotics, tree ferns and ferns. The separation of the groups follows Safford (1999a), Behling and Safford (2010), Gomes (2015) and Montade et al. (2019).

According to their respective local vegetation and elevation, the pollen sampling sites were separated into three ecological zones: CDA, upper montane ARF, and montane ARF (Table 1). Each zone is typified by a characteristic pollen assemblage composition and abundance. Overall, arboreal taxa predominate in the pollen rain, even in samples taken from CDA vegetation. The five most abundant taxa in all pollen spectra are *Myrsine*, Melastomataceae, Poaceae, Moraceae/Urticaceae and *Weinmannia*. Asteraceae, Myrtaceae, *Cecropia* and *Alchornea* were present in all samples, along with the introduced taxon *Pinus*.

4.1.1 Campos de altitude (5 samples)

Although this vegetation zone is characterized principally by herbs, shrubs and Asteraceae, forest pollen types are up to 65% of all pollen; that is, pollen from the CDA ecological group only contributed an average of 35% of the pollen collected in the traps. In this vegetation type, pollen of Poaceae (16%) and *Baccharis* (*c.*10%, separated from other Asteraceae pollen types due to its relatively high number of small and long echini (Behling, 1993)) are the best indicators. Pollen taxa of upper montane ARF (*Myrsine* >10%, *Weinmannia c.* 4% and *Clethra* 1%) and montane ARF (Moraceae/Urticaceae *c.* 12%, Melastomataceae *c.* 10%, *Cecropia* 5%, *Celtis c.* 3%, Myrtaceae 2%, and *Alchornea c.* 2%) are also abundant. There is high variability among samples for some pollen taxa. For example, *Baccharis* represents *c.* 34% and Melastomataceae *c.* 20% in sample SOPT1 and Cyperaceae almost 12% in SOPT2. Although *Eryngium* type 2 is generally rare, it occurs at a high percentage in a single sample (SOPT10 >9%). *Mimosa scabrella* reaches *c.* 3% in SOPT2 with average of *c.* 1% in this zone. Spores of tree ferns are almost absent in CDA, the average sum of other spores reaches 3% while the exotic *Pinus* is about 1% in this zone.

Pollen influx is very low in traps in CDA, the mean value is <2000 pollen grains cm$_{-2}$, varying from 920 to 3055 pollen grains cm$_{-2}$. In the CDA zone, the sum of characteristic CDA taxa produces an average influx of *c.* 700 pollen grains cm$_{-2}$, while upper montane ARF average influx is 335 pollen grains cm$_{-2}$ and the montane ARF average is 945 pollen grains cm$_{-2}$.



A) Taxa (%)

B) Subgroups (%)

Fig. 2. Percentage diagram of main taxa per groups sorted by vegetation types and altitude.

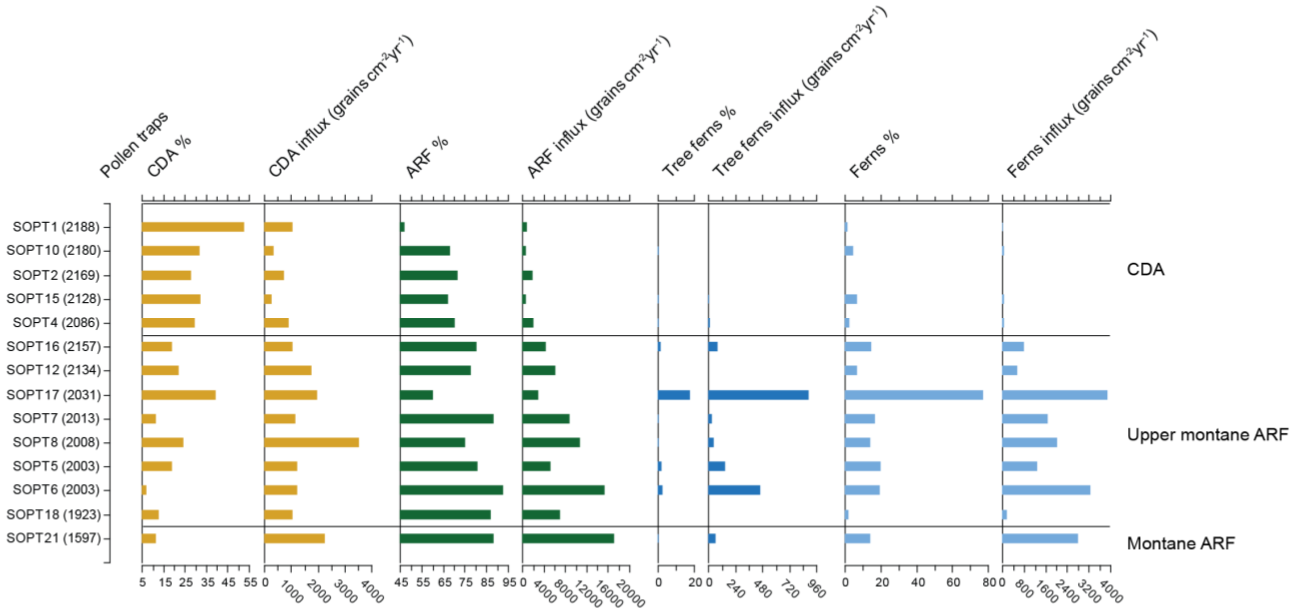


Fig. 3. Percentage and influx diagram of groups sorted by vegetation types and altitude.

4.1.2 Upper montane ARF (8 samples) and montane ARF (1 sample)

Upper montane vegetation is well represented by its pollen assemblage. The upper montane/montane ARF zone (they are combined here due to similar pollen spectra and the existence of only one sample in the montane ARF zone) is characterized by higher spore sums than the CDA zone. *Myrsine*, *Weinmannia*, Lauraceae, *Griselinia* and *Clethra* are the most important upper montane ARF indicator taxa with averages of *c.* 18%, 7%, 4%, 2% and *c.* 2%, respectively. The main montane ARF pollen taxa are Melastomataceae 18%, Moraceae/Urticaceae 9%, *Cecropia* c. 3% and Myrtaceae 3%. Pollen traps from SOPT17 and SOPT18 have higher values of *Mimosa scabrella*, 2% and 4% respectively, and Melastomataceae represents 72% of all pollen in the trap SOPT6. Pollen types from the CDA ecological group contribute about 19% of all pollen in the ARF zone, mainly from Poaceae (*c.* 7%), *Vernonia* (*c.* 2%) and other Asteraceae types (*c.* 2%). Two outlying samples are SOPT6 (7% CDA pollen) and SOPT17 (*c.* 40% CDA pollen). The average for tree ferns reaches *c.* 3%, but SOPT17 shows very high values: *Cyathea* with 14% and *Dicksonia* with *c.* 4%. The group of sub-aquatic taxa is represented by *c.* 2% and exotics by *c.* 1% pollen.

Regarding pollen influx in these zones, the average sum is 10,400 pollen grains cm-2, varying from 5000 in SOPT17 to 20,000 in SOPT21. The influx of taxa from the upper montane ARF ecological group ranges from 1400 to 6250 pollen grains cm-2 and taxa correlated with the montane ARF ecological group range from 1700 to 13,000 pollen grains cm^{-2}. Pollen influx from the CDA ecological group averages 1700 pollen grains cm^{-2}.

4.2 Vegetation cover and multivariate analysis

Table 2 shows the percentage of CDA and forest vegetation surrounding each pollen trap using spatial buffers of 50 m radius (0.79 ha total area), 100 m radius (3.14 ha) and 500 m (78.6 ha) radius, combined with pollen percentage of the CDA and ARF ecological groups. Applying a smaller buffer would have been interesting if the satellite image presented higher resolution however, with the resolution available, the surrounded vegetation was the same as in the pollen traps classification. Pollen traps installed in CDA are mostly surrounded by CDA vegetation (mean = >70% CDA vegetation) in all sizes of buffer, although the percentage of forest vegetation is higher at the 500 m radius. With buffer at 50 m, the highest % of forest is shown in SOPT10 (*c*. 30%) and with buffer at 100 m both SOPT10 and SOPT15 reach *c*. 16%. On the other hand, the area surrounding the pollen traps in upper montane forest only averaged 55% of forest in the small buffer (excluding SOPT21) and <70% in the two larger buffers. The one recovered trap installed in montane forest (SOPT21) at lower altitude is dominated by forest vegetation at all buffer sizes, although the 78.6 ha buffer included a number of patches of open canopy where rock and herbaceous vegetation dominated (see supplementary material). The correlation coefficient (r) between the pollen assemblages and the respective vegetation groups dropped as buffer size increased. The coefficients for the CDA group are 0.63 for 50 m radius, 0.48 for 100 m and 0.36 for 500 m radius, while in the ARF group the coefficients are 0.60, 0.49 and 0.39 for 50, 100 and 500 m radius, respectively (Fig. 4).

A preliminary correspondence analysis using 13 samples clearly separated a group that includes all samples from SOPT6 (supplementary material). This sample is characterized by a high value of Melastomataceae (>70%) due to a local signal. We therefore considered this sample as an outlier and performed a new CA with 12 samples to provide an understanding of the relationships among pollen assemblages and vegetation groups (Fig. 5). The first two axes explain 54.6% of the total variation. Axis 1 clearly separates CDA from forest pollen trap samples (Fig. 5a). The most robust CDA indicators include *Baccharis (*displaced upward along ordination Axis 2 by its strong association with sample SOPT1), Melastomataceae, and

Poaceae, as well the woody genera (trees and lianas) *Celtis*, *Trema*, and *Cecropia*, all of which are pioneer taxa in disturbed forest (Fig. 5b). Mimosaceae, *Alchornea*, and Moraceae/Urticaceae (also largely pioneer/secondary taxa) are located very close to the Axis 1 origin line and are not very robust indicators of CDA sites as they occur in all vegetation groups (see Fig. 2). Indicators of forest habitats have a stronger signal in the ordination. The most robust forest indicators according to the results of the CA are Lauraceae, *Vernonia*, *Plantago* and *Borreria* (excluding Lauraceae, they are weedy, mostly herbaceous genera, *Plantago* is cosmopolitan and *Vernonia* and *Borreria* are found mostly in warm, tropical habitats), followed by the upper montane forest taxa *Myrsine*, *Clethra*, *Weinmannia*, and Myrtaceae (Fig. 5b).

Table 2. Percentages of total vegetation cover comprised by campos (CDA) and forest (ARF) vegetation within areas of 0.79 ha (50 m radius), 3.14 ha (100 m radius) and 78.6 ha (500 m radius) surrounding each pollen trap, and pollen % of CDA group and ARF group in each pollen trap. Table organized by vegetation type found at the pollen trap site.

Sample	Buffer 50 m		Buffer 100 m		Buffer 500 m		Pollen	
	Campos	Forest	Campos	Forest	Campos	Forest	CDA	ARF
CDA (mean)	93.2	6.8	93.2	6.8	80.8	16.07	34.98	65.02
SOPT1	100.00	0.00	97.89	1.97	81.61	14.85	52.98	47.02
SOPT10	70.95	29.05	84.29	15.60	81.20	15.39	31.83	68.17
SOPT2	100.00	0.00	99.90	0.00	84.29	12.29	28.04	71.96
SOPT15	95.26	4.74	83.93	16.17	78.30	22.60	32.45	67.55
SOPT4	100.00	0.00	100.08	0.00	78.66	15.19	29.59	70.41
ARF (mean)	40.6	59.4	63.8	36.2	66.0	34.0	18.73	81.27
SOPT16	48.44	51.56	44.93	55.08	72.62	29.38	19.38	80.63
SOPT12	74.60	25.40	75.95	24.03	77.87	16.07	22.16	77.84
SOPT17	49.25	50.75	71.61	28.28	64.01	38.44	39.54	60.46
SOPT7	54.91	45.09	79.26	20.78	78.90	21.04	11.75	88.25
SOPT8	32.75	67.25	77.67	22.40	79.08	20.79	24.67	75.33
SOPT5	52.20	47.80	79.87	20.06	79.48	20.46	18.95	81.05
SOPT6	52.20	47.80	79.87	20.06	79.48	20.46	7.36	92.64
SOPT18	0.99	99.01	64.79	35.37	45.06	57.50	13.07	86.93
SOPT21	0.00	100.00	0.40	99.60	18.36	81.66	11.68	88.32

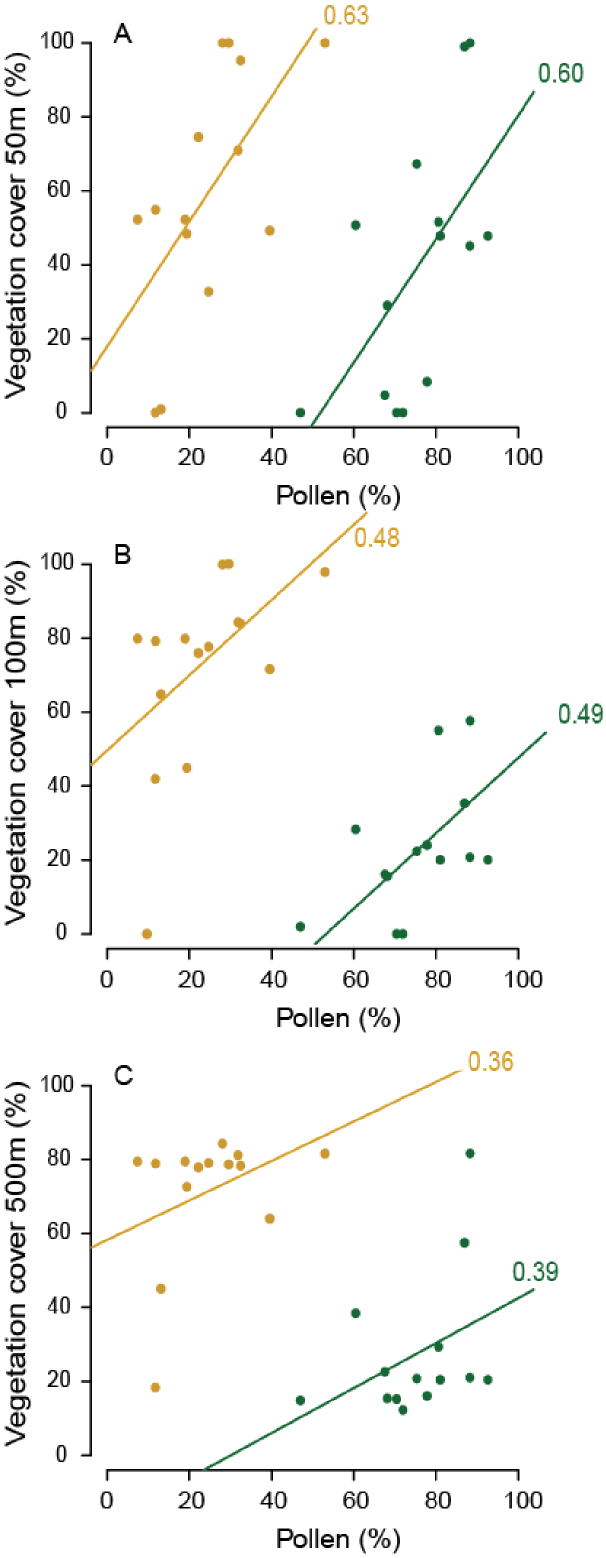


Fig. 4. Correlation coefficient (r) between pollen group and modern vegetation for spatial buffers of 50, 100 and 500 m radius. Pollen traps of CDA are in orange and ARF in green.

To present an assemblage approach whereby associations of pollen taxa are better indicative of a particular vegetation type, we defined a restricted group representing the ARF. For this restricted group of forest habitat, we considered several aspects to select the taxa. We only considered arboreal pollen taxa. Although evidenced as robust indicators based on the CA (Fig. 5b), we for example excluded *Plantago*, *Vernonia* and *Borreria* which represent mostly herbaceous genera and which can also be characteristic of CDA. Among the arboreal pollen taxa, we excluded taxa which are abundant in CDA pollen traps, e.g. *Celtis*, *Alchornea*, *Trema*, *Cecropia*, Mimosaceae, Moraceae/Urticaceae (Fig. 2 and 5b). Their high relative abundances in CDA pollen traps is certainly due to high pollen productivity of these taxa (Gosling et al., 2009; Jantz et al., 2013; Schüler et al., 2014) and their occurrence as dwarfed trees in or near CDA habitats. The representativeness of the taxa in fossil records was also considered for the selection of taxa. For example, although Lauraceae is one of the best indicators of forest in modern pollen rain (Fig. 2 and 5b), this pollen taxon is generally not well preserved in the fossil pollen records due to its thin exine (Behling, 1993) and it was excluded from the restricted forest group. We finally settled our choice on

Weinmannia, *Myrsine*, *Clethra* and Myrtaceae, which are good indicators of upper montane ARF since they are morphologically distinct arboreal pollen taxa and easily distinguished, they are significantly more abundant in upper montane forest than in CDA (Figures 2 and 5b) and they are generally well preserved and abundant in fossil pollen records (Behling, 1997a; Behling et al., 2007; Behling and Safford, 2010; Niemann et al., 2010; Veríssimo et al., 2012).

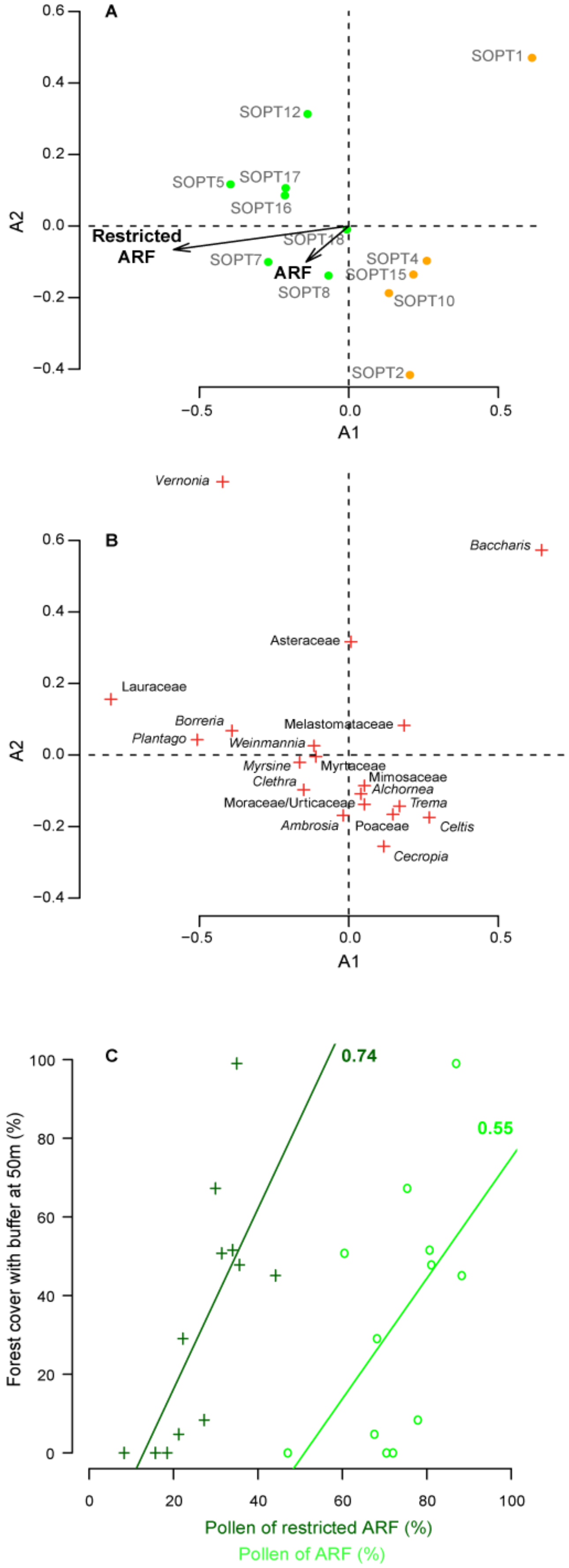


Fig. 5. Correspondence Analysis (CA) for axes 1 and 2 using pollen taxa ≥1% in at least three samples. A - distribution of pollen traps (CDA in orange and ARF in green) with the projection of the ARF restricted group and ARF group, B - distribution of pollen taxa, C –correlation between ARF restricted group and forest vegetation cover with buffer at 50 m (dark green) and correlation between ARF and forest vegetation cover with buffer at 50 m (light green).

The correlation between the restricted ARF group and the forest vegetation cover at 50 m (r=0.74) shows a higher correlation than the correlation calculated between the ARF group and forest vegetation cover at 50 m (r=0.55) in figure 5c. We also try to select taxa to better discriminate CDA, however this was discarded because this group is mostly composed of Poaceae which pollen grains are extremely difficult to be identified to species or genera level due to the rather uniform morphology, and may be over-represented in some fossil records according to the study site (e.g. Gosling et al., 2009).

5 Interpretation and Discussion

The pollen rain collected by our traps permitted a relatively robust discrimination of campos de altitude (CDA) and upper montane forest (ARF) habitats, even though there was notable overlap between the pollen assemblages. With respect to the CDA, our pollen trap data show that the pollen taxa most indicative of the CDA environment are Poaceae and *Baccharis*. Other common taxa in the CDA pollen traps represent (mostly small tree/shrub) taxa shared with ARF, or pioneer or secondary tree/liana taxa associated with disturbed forest habitats at lower elevations. The upper montane ARF pollen traps were characterized by a suite of taxa that are common to all eastern and southern Brazilian studies of mountain forests (e.g. Portes et al., 2001; Koehler et al., 2002; Sheer and Mocochinski, 2009; Gomes; 2015). These include, most prominently, Melastomataceae, *Myrsine*, and *Weinmannia*, but also *Clethra*, *Symplocos*, *Drimys*, *Croton*, Myrtaceae, *Ilex*, and the tree ferns *Cyathea* and *Dicksonia*. In addition, as pollen traps allow better pollen preservation than surface samples, we recorded a high percentage of Lauraceae, which, although very characteristic of upper montane ARF, have thin exine therefore are not commonly found in fossil pollen records (see also Cardenás et al., 2019).

These results are strikingly similar to those of Montade et al. (2019), who carried out a broad geographic meta-analysis of 125 modern pollen samples across the Atlantic Forest biome. Montade et al. (2019) also found high levels of pollen taxa overlap between neighbouring high elevation vegetation types, including campos de altitude, *Araucaria* forest, and upper montane Atlantic Forest. They ascribed at least some of this palynological concordance to the mosaic pattern of habitats that characterizes the higher Brazilian mountains (Safford, 1999a), where patches of grassland and forests occur in such close proximity that typical pollen sampling methods cannot discern a completely "clean" pollen signature from either habitat. We found the same pattern of pollen "pollution" happening between our CDA and ARF traps. This was especially pronounced in the CDA traps, where upper montane ARF taxa comprised almost 2/3 of the captured pollen. This was due to at least three factors. First, the Brazilian Highlands do not reach the elevations of climatic treeline (Safford, 1999b), therefore the presence and distribution of high-elevation páramo-like grasslands is driven by local-scale environmental and disturbance gradients that lead to a very fine-grained intercalation of grassland and forest patches (Safford, 1999a, 2001). Second, many taxa from the upper montane ARF – such as the prodigious pollen producers *Myrsine* and *Weinmannia*, as well as various species of Myrtaceae, Melastomataceae, *Croton*, *Drimys*, *Clethra*, and *Symplocos* – occur as shrubs or small scattered trees in the campos de altitude (Safford, 2007). These are usually interpreted as either remnants of burned forest stands, or pioneers of forest expansion. Third, CDA vegetation is characterized by a much lower pollen production and accumulation rate than the montane or upper montane ARF. The same pattern was recognized by Bush (2000) in a study of páramo vs treeline forests in Central America and by Gosling at al. (2009) in an ecotonal area of tropical forest, semi-deciduous forest and savannah in Colombia. Even though Poaceae is wind-pollinated, most of the genera in the CDA require a pollen vector (*c.* 71% are insect-pollinated and 5% bird or bat pollinated according to Safford, 2007), and such taxa are always under-represented in the pollen rain. There are also relatively few wind-pollinated taxa in the ARF, but a number of pioneer or secondary forest taxa are anemophilous – examples include Moraceae/Urticaceae, *Cecropia*, *Trema*, *Celtis*, and *Alchornea* – and their high levels of pollen production, combined with the often up-slope nature of mountain winds, lead to over-representation of these montane taxa in many higher elevation pollen rain studies in the neotropics (e.g. Weng et al., 2004; Niemann et al., 2010; Urrego et al., 2011; Montade et al., 2019). The relative paucity of CDA pollen in the lower elevation forest traps is driven probably by the combination of predominantly upslope winds with the very high local production of pollen in ARF, which masks the downslope movement of CDA pollen (see also Bush, 2000; Schüler et al., 2014).

Another important difference between the CDA and ARF pollen assemblages is the size of the pollen source area. Pollen samples from open areas dominated by Poaceae and subject to high influence of wind transport will necessarily represent larger geographic areas than samples from close canopy forests, where local pollen production strongly dominates (Tauber, 1967; Schüler et al., 2014). This explains why, although our ARF traps were found mostly in forest patches surrounded by CDA vegetation (almost 64% of vegetation within 100 m of the ARF traps was CDA), they still recorded an average of >80% ARF pollen (Table 2). In some cases, forest pollen rain can be strongly influenced by individual trees beneath which the traps are located (Cheng et al., 2020; Niemann et al., 2010; Weng et al., 2004). One obvious case in our study is sample SOPT6, which registered >70% Melastomataceae pollen, while the adjacent sample SOPT5 (only 10 m distant) registered only 3% of this pollen type.

A few unexpected results are worth briefly mentioning. The low percentages of *Celtis* and *Trema* pollen in the lower montane sample SOPT21 – which are typically characteristic of lower montane ARF – are anomalous and may represent masking by Melastomataceae. SOPT21 also recorded a high percentage of *Weinmannia* which, although it produces large amounts of pollen and is usually over-represented in upper montane environments, is not normally present in lower elevation forest samples. In an arboreal floristic inventory of a montane forest in the PARNASO, Pardo et al. (2007) registered the occurrence of all the arboreal taxa we found in the pollen rain, except for *Weinmannia*. Cárdenas et al. (2019), studying the modern pollen-vegetation relationship in *Araucaria* forest in southern Brazil also remarked that although *Weinmannia* is normally cited as evidence of *Araucaria* forest, it is much more floristically important at higher elevations.

In order to develop a reasonably accurate process by which fossil pollen records might be used to better discriminate between grassland and forest habitats in such a complex environmental mosaic, we proposed a suite of distinctive upper montane ARF taxa composed of *Weinmannia, Myrsine, Clethra* and Myrtaceae. Calculated with more specific taxa than the pollen groups usually used to distinguish forest from CDA, this discrimination group excludes over-represented taxa (e.g. *Celtis, Cecropia,* Moraceae/Urticaceae as observed in the pollen traps) as well as under-represented taxa (e.g. Lauraceae in fossil samples). Within vegetation cover buffer at 50 m of the sampling site, it reflects better proportion of forest cover (Fig. 5c). We believe this group is more appropriate to discriminate vegetation change between forest habitats and CDA and can be applied to fossil pollen data in order to support palaeo records interpretation. However, as each region presents a different species occurrence pattern, its replication should be treated with caution. It can be transferred to historical pollen data for the given region or other CDA and forest mosaic in similar altitude and in the same mountain range in southeastern Brazil.

Moreover, data from a sediment core and a pollen trap from the same vegetation type may lead to slightly different results with regard to pollen diversity (Jantz et al., 2013) as the catchment area from which samples are taken may be different. For example, fossil samples from lake sediments represent a large source area and high proportions of Poaceae and Cyperaceae (Gosling et al., 2009). Sediments collect in the mosaic of CDA and forest in the Highlands from southeastern Brazil are basically peats but also bogs, within a more local catchment area (but probably also larger than the pollen trap source area) and the contribution of these taxa are quite well representative of local diversity. Application of our restricted ARF might be therefore more relevant for sites with local catchment area (e.g. peats and bogs) than for site with large source area (e.g. lakes). Other point to consider is that our study was based on 1 year of pollen rain, and probably there is variability in pollen productivity according to changes in climatic conditions through the years. A long-term investigation with pollen traps could be interesting to verify this possible variation.

6 Conclusion

Our study of the modern pollen rain along an elevational gradient was focused on supporting palaeo-studies of vegetation and climate dynamics in southeastern Brazil by helping to refine the pollen taxa and spectra that most robustly differentiate CDA and forest habitats. Our assemblages indicated that vegetation distribution is closed related with altitude, even with occurrence of low montane taxa in higher elevations. Although arboreal taxa dominated all of our pollen assemblages, pollen traps located in CDA captured a characteristic mix of grass, herbs and shrub pollen. The results indicate that the CDA pollen spectra represent much larger geographic areas than forest pollen spectra, which sample local taxa more heavily. Nonetheless, the pollen assemblages accurately reflected the vegetation zone in which they were found, and we were able to specify a characteristic group of taxa for each elevation. Our results underlined that special care must be taken with pollen trap location, as samples can be strongly influenced by a few individual plants if they dominate the trap area. Pioneer tree and liana species with anemophilous pollen disperal dispersion produce copious pollen and were over-represented in CDA pollen traps from higher elevation, these included Melastomataceae, Moraceae/Urticaceae, *Cecropia*, *Trema* and *Celtis*. As found in other tropical montane studies as well, the main direction of wind-driven pollen dispersal seems to be uphill in our study area, although the low presence of CDA pollen in lower elevation forest traps is probably also influenced by masking due to high local pollen production in the study area forests. Finally, we proposed the use of a suite of distinctive taxa which more confidently differentiate CDA and forest habitats from pollen data. We believe that will prove useful to efforts to reconstruct and model climate and vegetation dynamics in such kind of specific environment, with important applications to conservation and management (e.g., developing the natural range of variation of CDA vs. forest areas as a function of landscape and climate) and climate and vegetation science (e.g., developing a more quantitative idea of the dependence of CDA vegetation on climate variability vs. natural disturbances like fire).

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9 Supplementary Material of Chapter 2

List of taxa identified in the pollen rain.

Taxa	Group	Vegetation
Poaceae	Herbs and shrubs	Campos de altitude (CDA)
Apiaceae		
Eryngium type 1		
Eryngium type 2		
Lamiaceae		
Fabaceae		
Borreria		
Ericaceae		
Plantago		
Amaranthaceae/Chenopodiaceae		
Malpighiaceae		
Valeriana		
Cactaceae *Rhipsalis*		
Cactaceae		
Amaryllis		
Menispermacaceae		
Malvaceae		
Verbena		
Scrophulariaceae		
Ochnaceae		
Polygonum		
Polygala		
Convolvulaceae		
Asteraceae	Asteraceae	
Baccharis		
Vernonia		
Ambrosia		
Senecio		

Taxa	Group	Vegetation
Cyperaceae	Sub-aquatics	Sub-aquatics
Hydrocotyle		
Xyris		
Typha		
Liliaceae		
Clethra	Upper Montane ARF	Atlantic rain forest (ARF)
Griselinia		
Myrsine		
Weinmannia		
Symplocos tenuifolia type		
Symplocos lanceolata type		
Hedyosmum		
Drimys		
Daphnopsis		
Croton		
Roupala		
Lauraceae		
Lamanonia		
Fuchsia		
Begonia		
Euphorbia		
Laplacea		
Struthanthus		
Podocarpus	Montane ARF	
Araucaria		
Mimosa scabrella		
Melastomataceae		
Melastomataceae (small)		
Flacourtiaceae		
Myrtaceae		
Ilex		

Taxa	Group	Vegetation
Mimosaceae	Montane ARF	Atlantic rain forest (ARF)
Mimosa (small)		
Schefflera		
Oreopanax		
Sebastiana commersoniana		
Sebastiana brasiliensis		
Piper		
Trema		
Celtis		
Schinus		
Zanthoxylum		
Meliosma		
Allophylus		
Luehea		
Pera		
Parapiptadenia		
Matayba		
Bignoniaceae		
Anacardiacceae		
Bauhinia		
Cordia		
Rubiaceae		
Rubiaceae *Bridelia*		
Lythraea		
Dodonea		
Solanaceae		
Prunus type		
Euterpe/Geonoma		
Cecropia		
Moraceae/Urticaceae		
Alchornea		

Taxa	Group	Vegetation
Sloanea	Montane ARF	Atlantic rain forest (ARF)
Schizolobium		
Rhamnus		
Tetrorchiolium		
Pinus	Exotics	Exotics
Casuarina		
Cyathea psilate	Tree ferns	Ferns
Cyathea reticulate		
Cyathea verrucate		
Dicksonia		
Lophosoria quadripinnata		
Lycopodium foveolate	Ferns	
Lycopodium clavatum		
Monolete psilate		
Monolete psilate large (> 40 µm)		
Monolete scabrate		
Monolete echinate		
Monolete verrucate		
Monolete verrucate large		
Osmunda		
Polypodiaceae		
Monolete with perispore type 2		
Pteris type		
Schizaea		
Trilete psilate		
Trilete verrucate		
Trilete scabrate		
Pteridophyta type 6		
Pteridophyta type 4		
Trilete with perispore		
Trilete striate		

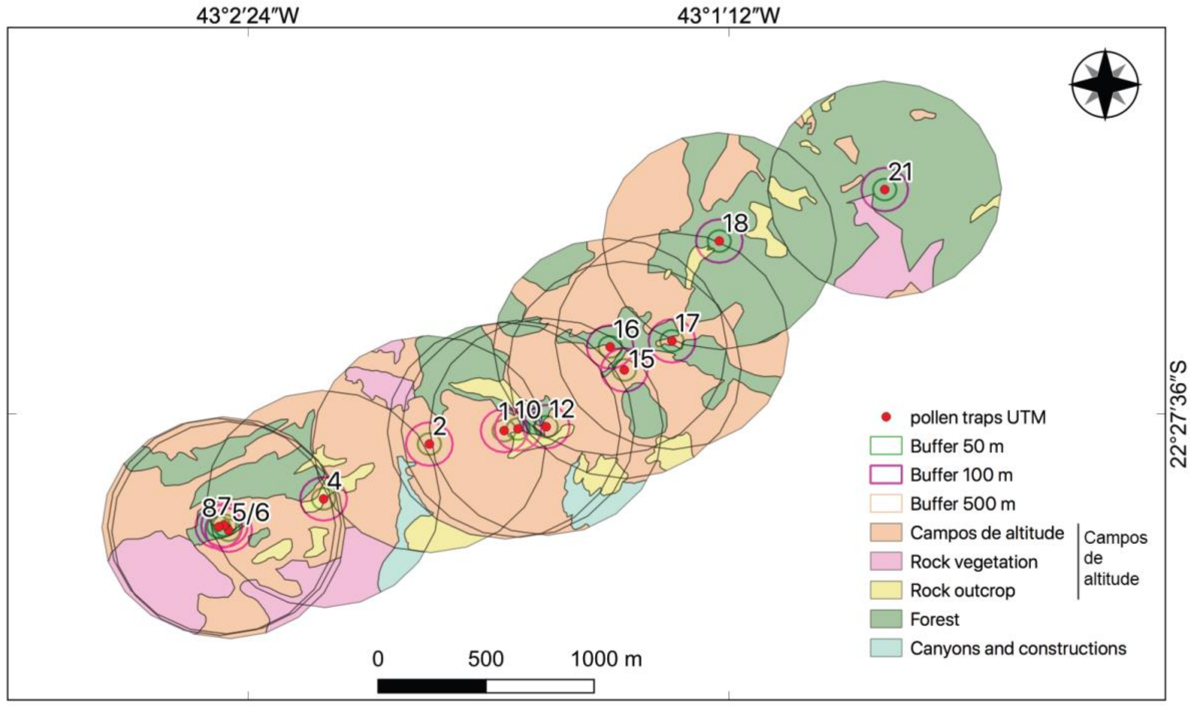

Figure: Interpretation of the vegetation surrounding each pollen trap and limit of the spatial buffers of 50 m radius (0.79 ha total area), 100 m radius (3.14 ha total area) and 500 m radius (78.6 ha total area).

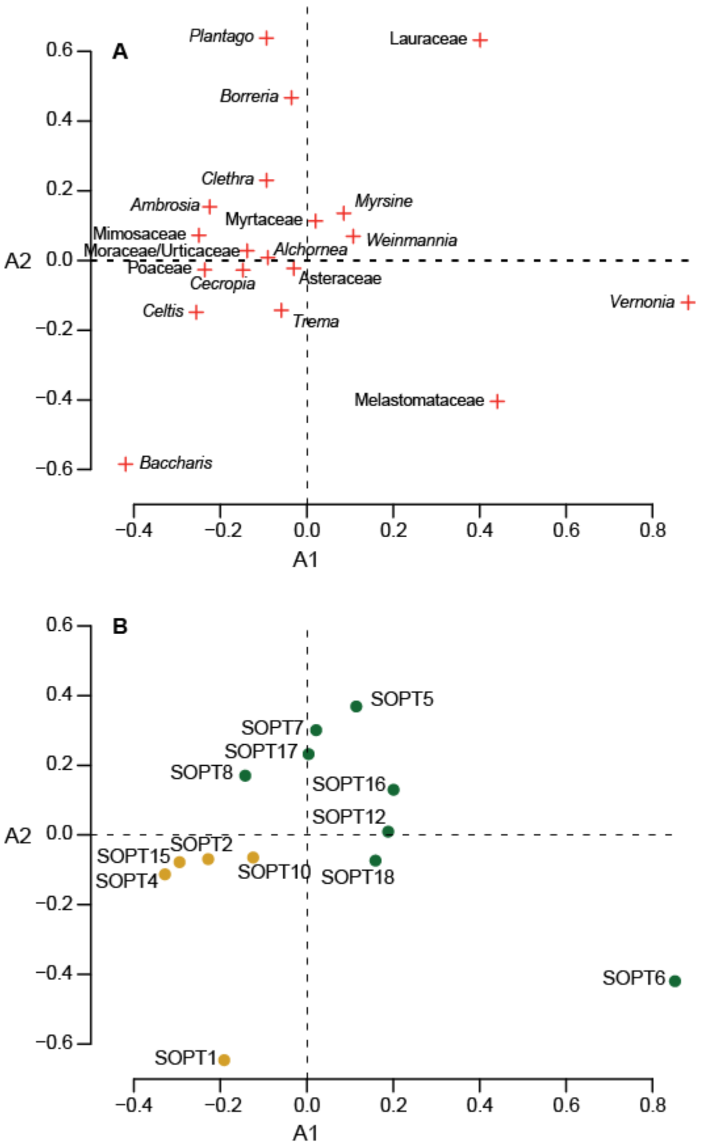

Figure: Correspondence Analysis (CA) for axes 1 and 2 using pollen taxa >1% in at least three samples, including sample SOPT6. A – distribution of pollen taxa, B - distribution of pollen traps.

CHAPTER 3

Holocene vegetation, climate and fire dynamics in the Serra dos Órgãos, Rio de Janeiro State, southeastern Brazil

Maria Carolina Guarinello de Oliveira Portes[a,b,c], Hermann Behling[a], Vincent Montade[a,d], Hugh Deforest Safford[e,f]

[a] *University of Goettingen, Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Sciences, Germany*

[b] *Instituto Chico Mendes de Conservação de Biodiversidade (ICMBio), Brazil*

[c] *CNPq-Brazil Scholarship, Brazil*

[d] *Université de Montpellier, Institut des Sciences de l’Evolution de Montpellier, CNRS, IRD, EPHE, France*

[e] *USDA Forest Service, Pacific Southwest Region, Vallejo, California,*

[f] *USA Department of Environmental Science and Policy, University of California, Davis, California, USA*

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Abstract

We analysed pollen and macro-charcoal from a sediment core representing the last 9840 cal yr BP, collected at 2003 m a.s.l. in a patch of upper montane Atlantic Rain Forest (UMARF) embedded in a campos de altitude (high elevation grassland) matrix in the Serra dos Órgãos National Park, southeastern Brazil. From 9840 to 4480 cal yr BP, campos de altitude (CDA) was the dominant vegetation at the site, indicating that the climate was relatively cool and dry. However, pollen data document that UMARF was near the core site throughout the recorded Holocene. Frequent and high magnitude fires occurred during the Early Holocene but became rarer in the Mid-Holocene after 4480 cal yr BP, when the climate became wetter. In the Mid-Holocene, UMARF and tree fern taxa became slightly more frequent at the site, but CDA vegetation continued to dominate most of the high mountain landscape. A climatic change to wetter and warmer conditions during the last 1350 cal yr BP is evidenced by an increase in UMARF and even lowland forest taxa in our core, as well as the near complete absence of fire after this date.

Key words: Southeastern Brazil, campos de altitude (high elevation grassland), upper montane Atlantic Rain Forest, climate and fire history, Holocene.

1 Introduction

The Brazilian coastal highlands (Serra do Mar) extend for *c.* 1000 km along the Brazilian coastline from southern to northeastern Brazil, from the north of Santa Catarina State (26_o S) to the north of Rio de Janeiro State (21_o S) in the Atlantic Forest domain. The Atlantic Forest is one of the world’s great tropical forest biomes, and once covered around 130 million ha of coastal and eastern Brazil, stretching *c.* 4000 km from 3° N latitude to almost 34° S (Ribeiro et al., 2009; Fundação SOS Mata Atlântica/ INPE, 2017). Due to the variability of environmental conditions (geomorphology/topography, geology, climate, soils, ecosystems) together with a large elevational range, the Atlantic Forest is one of the most diverse biomes in the world and is considered among the most important and most imperilled biodiversity hotspots on earth (Myers et al., 2000). Before European settlement, the Serra do Mar was clothed in dense rainforest for much of its length, with drier cerrado (Brazilian savanna) formations inland, and elfin "cloud forests" and orographic grasslands (campos de altitude) at higher elevations, mostly above 1500-1800 m a.s.l. At the highest elevations, cloud forests (here referred to as "upper montane Atlantic Rain Forest", or UMARF) tend to occupy topographic concavities and other protected sites, and campos de altitude (CDA) are more common on hilltops, plains, and convex slopes, or where waterlogging occurs (Safford, 1999a).

Climatic changes during the Late Quaternary greatly influenced the modern vegetation distribution. Present-day CDA is a vestigial vegetation type from colder and drier climates which reached its widest distribution during the Last Glacial and in particular the Last Glacial Maximum (25,000-17,000 yr BP) when forest vegetation was nearly completely absent in the higher mountains (Behling, 1997b; Behling and Safford, 2010). UMARF expansion began during the Late-glacial, indicating a shift to moister conditions (Behling, 1997b; Behling and Safford, 2010). A further increase in both temperature and precipitation in the Early to Mid-Holocene allowed the expansion of the Atlantic Rain Forest to higher elevations, markedly reducing the area occupied by CDA (Behling and Safford, 2010). Displacement of the Intertropical Convergence Zone (ITCZ) over northeastern Brazil might explain the Younger Dryas (YD) warming (second part of the YD period) documented in eastern Brazil, in contrast to the YD cooling in the North Hemisphere (Behling and Safford, 2010). A palaeoecological study carried out by Behling and Safford (2010) at 2130 m elevation in the Serra dos Órgãos (SDO core; Fig. 1c) recorded widespread CDA vegetation and drier climatic conditions until about 5600 cal yr BP. Thereafter a trend toward warmer and wetter conditions resulted in expansion of montane forest and contraction of campos. The last *c.* 1000 years were the wettest period during the whole Holocene (Behling and Safford, 2010).

Centuries of exploitation reduced the Atlantic Forest to a patchwork of small fragments in a natural or semi-natural state, covering today only *c.* 10% of its pre-Columbian area (Fundação SOS Mata Atlântica/ INPE, 2017). While more intense occupation and deforestation occurred after European colonization, starting *c.* 1500 AD, the history of human presence along the Brazilian coast started with the migration of Amerindians from the north, arriving in southeastern Brazil about 10,000 years ago (Figuti et al., 2004). Although mostly settled along the coast, these populations also occupied inland forests by around 1800 yr BP (Noelli, 2008). Evidence is strong that Amerindian practices had important impacts on forest structure and composition before the arrival of Europeans (Portes et al., 2018). The first Portuguese settlements were mainly established in Rio de Janeiro state, beginning a period of more intense exploitation of the forest. Today, the southeast is the most populated region of Brazil, but it ironically supports some of the most important remnants of the Atlantic Forest, due to the steep topography and complex relief of montane areas in the region.

Most of the large forest remnants in southeastern Brazil are found in protected areas. One of the most important is the Serra dos Órgãos National Park (PARNASO). Located in the northernmost part of the Serra do Mar, PARNASO protects montane rainforest stands and an important complex of UMARF and CDA on a high plateau that supports many rare and endangered species (Martinelli and Bandeira, 1989). As the climate becomes warmer and wetter, upward migration is expected and the reduction of available habitat for high mountain taxa is a strong possibility (Rull et al., 2009; Vegas-Vilarúbia et al., 2011). Understanding the temporal relationships between climate and vegetation is essential for conservation in the face of climate change, and palaeoecological studies can help to reveal which species and ecosystems may need human intervention to persist (Behling and Pillar, 2007; Overbeck et al., 2015; Barnosky et al., 2017). Although the Brazilian highlands have been the object of palaeoecological investigations for more than two decades (e.g., Behling 1995, 1997a, 1997b, 2007; Scheel-Ybert, 2001; Ledru et al., 2005; Behling et al., 2007; Behling and Safford, 2010; Veríssimo et al., 2012; Raczka et al., 2013; Portes et al., 2018; Behling et al., 2020), much more remains to be learned about how montane vegetation in this region is influenced by climate, fire and human impacts over the long term.

Here we report results from a multi-proxy study that analysed temporal vegetation dynamics in a forest patch currently occupied by UMARF and surrounded by CDA vegetation, located near the SDO core sampled by Behling and Safford (2010). Overall, our goal was to better understand temporal dynamics between forest and grassland vegetation in a highly heterogeneous landscape characterized by high biodiversity and high species turnover. Our specific research questions were (1) how did climatic change and fire interact at this montane forest site to influence vegetation composition and dynamics during the Holocene?; and (2) how did Holocene vegetation dynamics differ in this forest patch as compared to the CDA vegetation sampled in the nearby SDO core (Behling and Safford 2010)?

2 Environmental Settings

The study site is located at 2003 m a.s.l., at latitude 22$_{o}$27’53.49” S and longitude 43$_{o}$2’27.04” W in the Serra dos Órgãos National Park (PARNASO), Rio de Janeiro State, southeastern Brazil (Fig. 1). The southeast facing site is characterized by a 2.2 ha patch of upper montane Atlantic Rain Forest (UMARF) bordered by campos de altitude (CDA) in the Serra dos Órgãos, a subrange of the Serra do Mar (Brazilian coastal highlands), about *c*. 90 km from the Atlantic Ocean. Geologic substrate in the study area is Upper Proterozoic granite and granitoid gneiss, uplifted to its present elevation by Cenozoic tectonism associated with widening of the Atlantic Ocean (Riccomini et al., 1989). The Serra dos Órgãos follows a largely NE-SW orientation parallel to the coast. Soils at the study site are generally shallow, poorly developed, acidic and highly organic with high amounts of litter (Falkenberg and Voltolini, 1995).

In the region, the climate is mostly controlled by the South Atlantic Convergence Zone (SACZ) with most precipitation falling between November and April (Safford, 1999a; Vuille et al., 2012). The climate for the region has been generally defined as mesothermic with mild and wet summers and moderate winters without a well-defined dry season (Nimer, 1977; ICMBio, 2008). The nearest long-term meteorological station is found at Teresópolis (22°25.980' S, 42°58.980' W) at 1100 m a.s.l., where mean annual temperature is 17.6 $_{o}$C (July mean = 8.6 $_{o}$C, February mean = 27.2 $_{o}$C), and mean annual average precipitation is 1800 mm (Hijmans et al., 2005). Our field site is 900 m higher and there is considerable orographic enhancement of precipitation, resulting in a winter without dry season. PARNASO installed temperature data loggers near the study site in September 2012. Between September 17, 2012 and February 2, 2014, the mean overall temperature was 12.7 $_{o}$C, the maximum was 25.6 $_{o}$C and the minimum was 1 $_{o}$C (C. Cronemberger, PARNASO, pers. comm.). Temperatures in the nearby CDA in the Vale das Antas proper (the study site is in forest slightly above the valley bottom) showed a similar mean temperature (12.5 $_{o}$C), but temperatures were more extreme due to the lack of trees and the valley bottom position: max = 27 $_{o}$C, min = -5.2 $_{o}$C). Safford (unpub. data) also measured winter temperatures in the Vale das Antas campos, in July 1997 a minimum of -9.8 $_{o}$C was measured, which is the lowest for the Serra dos Órgãos. From regressions against elevation, Safford (1999a,b; Behling and Safford, 2010), estimated precipitation at 2000 m elevation in the Serra dos Órgãos study site to be between 2500 and 3000 mm annually.

In the Serra dos Órgãos, CDA vegetation occurs above 1800-2000 m elevation, depending on substrate, topography, slope aspect, and history of disturbance (Safford 1999a). CDA is most common on hilltops and convex slopes, and also dominates poorly-drained valley bottoms (Safford, 1999a; see Fig. 1). Below 1800-2000 m elevation UMARF is the dominant vegetation which gradually replaces tall montane forest above about 1500 m a.s.l., while above these elevations UMRAF becomes more and more restricted to protected sites.

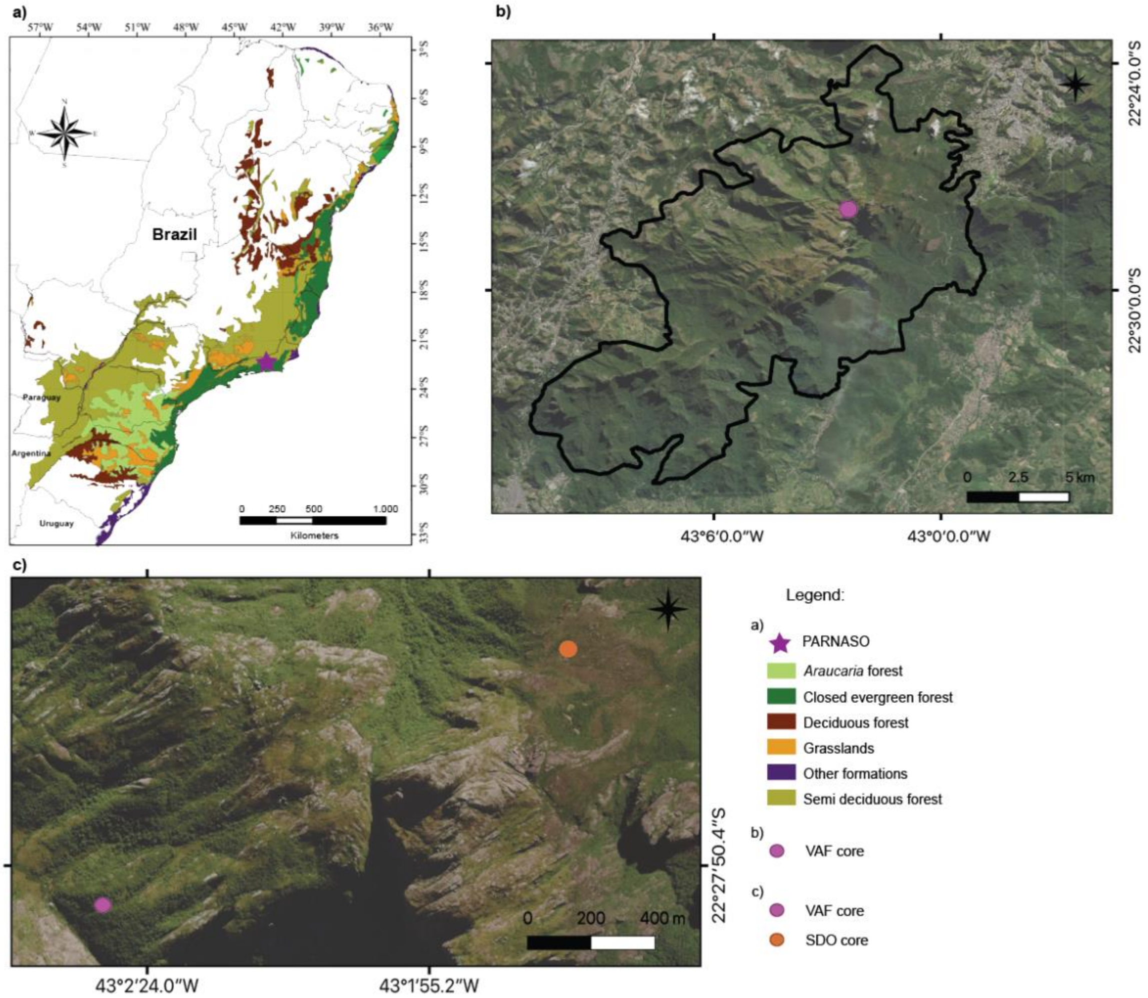

Fig. 1. Location of PARNASO and Vale das Antas Forest (VAF) core. a) national location of PARNASO (adapted from Fundação SOS Mata Atlântica/ INPE, 2017), b) location of VAF core in PARNASO and c) distance and vegetation type of VAF core (in UMARF) and SDO core (in CDA) from Behling and Safford (2010).

The CDA is dominated by graminoids, in PARNASO especially by the giant bunchgrass *Cortaderia modesta*, montane bamboo (*Chusquea pinifolia*), and the large sedge *Machaerina ensifolia*. Frequent herb genera include *Eryngium* (Apiaceae) *Paepalanthus*, *Plantago* and

Xyris (Behling and Safford, 2010). A high number of sclerophyllous shrub taxa is found in the CDA, as well as smaller trees, often in some stage of succession moving toward (after fire or livestock incursion) or away from grassland (long-term lack of disturbance). More open habitats tend to support more woody taxa from Asteraceae (e.g., *Baccharis,* which is a good indicator of campos vegetation). Certain woody taxa from genera such as *Croton* and a number of genera from Myrtaceae (*Myrceugenia, Gomidesia*) and Ericaceae (*Gaylussacia*) are also more common in campos habitat. However, most woody taxa in the campos are forest taxa and their density is higher near forest borders. The UMARF is formed by twisted and dwarfed trees and shrubs distributed largely in one stratum normally less than 10 m height. Due to high air humidity and frequent fog there is high abundance and diversity of epiphytes and mosses on tree trunks and branches, rocks and soil (Falkenberg and Voltolini, 1995; Safford, 1999a; Portes et al., 2001). Important tree genera include *Myrsine*, *Weinmannia*, *Clethra*, *Daphnopsis*, *Roupala*, *Symplocos*, *Tibouchina*, *Ilex*, *Ocotea*, and a number of genera from Myrtaceae (Behling and Safford, 2010; Gomes, 2015). Tree ferns of various species are common, as well as epiphytes such as bromeliads and orchids. The grassland-forest ecotone, where scattered trees/open forest cover and understory species co-dominate, is marked by very high habitat heterogeneity. Many herbaceous species from Rubiaceae are especially common in these situations, likewise shrubs of Myrtaceae and Melastomataceae.

Our study site consists of an island of UMARF surrounded by CDA vegetation, located in a protected site facing southeast at 2003 m a.s.l. (Fig. 1), around about 1.5 km from the of the higher located SDO core site at 2130 m a.s.l. (Behling and Safford, 2010).

3 Material and Methods

3.1 Sediment core sampling and dating

In February 2015, an 88 cm-long core was collected in an undisturbed area of UMARF in the Vale das Antas (“Tapir Valley”) and herein called VAF (Vale das Antas Forest). From a base of bedrock, two sections of 50 cm length were extruded onsite using a Russian Corer, wrapped in plastic film and stored under cool (*c*. 4 $_{o}$C) and dark conditions. Six organic bulk sediment samples were collected along the sediment for radiocarbon dating. Two samples were analysed at the Accelerator Mass Spectrometry (AMS) Laboratory at National Taiwan University (NTUAMS) and four samples at the AMS Poznan Radiocarbon Laboratory (LAMS) (Table 2). An HCl test on several core samples was negative and excludes the possibility of a carbon reservoir effect. The age-depth model was performed with R-package Clam 2.2 (Blaauw, 2010) in R-Studio (R-Studio Team, 2016) using the South Hemisphere calibration curve SHCal13.14C and postbomb curve SH 1-2. Calib 7.1 was used for calculating the median probability (Stuiver et al., 2019).

3.2 *Palynological analysis*

In total 44 subsamples (0.25 cm_3) in 2 cm intervals were taken along the core for analysing palynomorphs. Standard pollen techniques were used to process the samples applying 40% hydrofluoric acid (HF) and acetolysis (Faegri and Iversen, 1989). The marker *Lycopodium clavatum* (20848±1546, batch 1031) was added to each subsample to determine the pollen concentration (grains cm_{-3}) and pollen accumulation rate (grains cm_{-2} yr_{-1}) (Stockmarr, 1971). The residue obtained was kept in distilled water and mounted in slides with glycerine for palynomorph analysis under a light microscope. A minimum of 300 pollen grains was counted per sample. Pollen and spores were identified based on the Brazil reference collection of the Department of Palynology and Climate Dynamics at the University of Goettingen, and with support of literature and electronic pollen keys (Behling, 1993; Melhem et al., 2003; Neotropical Fossil Pollen Search Tool developed by Dr. Hermann Behling and Dr. Chengyu Weng [unpublished]). Nomenclature is based on Flora do Brasil 2020 (http://floradobrasil.jbjr.gov.br).

Pollen and spore percentage were calculated from the pollen sum, including herbs, shrubs, trees, unknowns and excluding ferns, mosses, fungal and Non Pollen Palynomorphs (NPPs). The groups were separated following Behling and Safford (2010) for further comparison: campos de altitude (CDA), upper montane Atlantic Rain Forest (UMARF), other Atlantic Rain Forest (OARF), lowland Atlantic Rain Forest (LARF), ferns (tree ferns and ferns), mosses, fungal spores and NPPs. The pollen diagram was performed with C2 (Juggins, 2007) and portrays the most important taxa based on frequency and dominance. TILIA and TILIAGRAPH were applied to determine pollen assemblage zones based on the stratigraphic constrained cluster analysis of the pollen sum by CONISS (Grimm, 1987).

3.3 *Macro-charcoal analysis*

For analysing the past fire regime and its influence on vegetation, macro-charcoal particles (>150 µm) were counted in a total of 176 subsamples of 0.5 cm^3 continuously extracted from the core at 0.5 cm resolution. Samples were prepared following the method of Stevenson and Haberle (2005, adapted from Rhodes (1998)) which is a procedure that greatly limits particle fragmentation. 6% H_2O_2 was added to remove organic material in the sediment and samples were gently wet-sieved, retaining particles >125 µm. Concentrations were determined as particles cm^{-3}. Fire regime characteristics were identified using the software CharAnalysis (Higuera, 2009). The data were interpolated to the median temporal resolution (42 years) to obtain the charcoal accumulation rate (CHAR particles cm^{-2} yr^{-1}). A window of 1000-year locally weighted regression was applied to separate background ($C_{background}$) and peak components (C_{peaks}) (Higuera et al., 2010). A Gaussian mixture model was used to identify the C_{noise} distribution. The 99th percentile of the C_{noise} distribution was used to define thresholds. Poisson minimum-count was used to eliminate the peaks from statistically insignificant counts. We used a window of 1000 years to estimate the distribution of fire frequencies. Peak magnitude as an estimate of total charcoal deposition per fire event was used to reflect fuel consumption per fire and/or fire size (Biagioni et al., 2015; Higuera et al., 2010).

3.4 *Loss on ignition*

To estimate the organic matter and carbonate content in the sediment, 0.5 cm^3 subsamples were continuously extracted from the sediment and immediately weighed. The samples were dried at 105 ^oC for 24 h, dried and combusted at 550 ^oC during 4 h. Afterward the samples were dried again and OM% was calculated following the method described in Heiri et al. (2001).

4 Results

4.1 *Stratigraphy, chronology and accumulation rate*

The 88 cm-long core mostly consists of black organic material on a rocky subsurface. A detailed description is given in Table 1.

Table 1. Stratigraphy of Vale das Antas core.

Depth (cm)	Description
0-20	Black organic material, rather compact and strongly decomposed, some rootless, roots and plant remains
20-41	Black organic material, compact and strongly decomposed, few root fragments
41-61	Black organic material, compact and strongly decomposed, few plant remains, little silty
61-84	Black organic material, compact and completely decomposed, fine sandy
84-88	Black organic material, compact and completely decomposed, few small yellow rocks
88-	Rocky subsurface

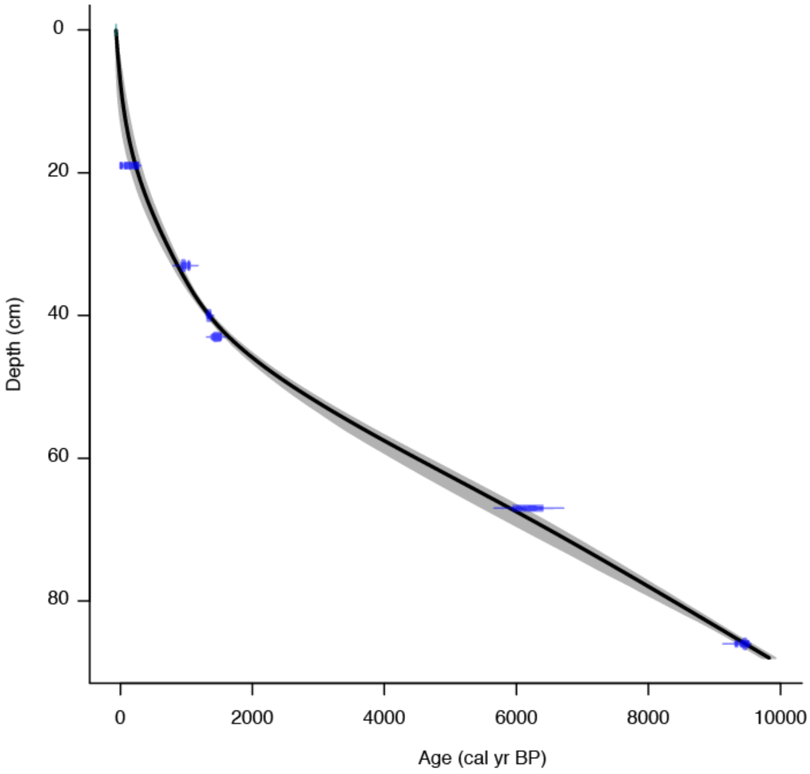

Fig. 2. Age-depth smoothing spline model for the Vale das Antas core.

Six AMS radiocarbon dates were used to construct the age-depth model (Table 2), spanning the period 9840 cal yr BP (calculated age for the lowermost sample at 88 cm) to the present. After testing several techniques, the data were best represented using a 0.3 smoothing spline (Fig. 2). Using this technique, the lowest accumulation rate is at 63 cm (203 yr/cm) while the highest accumulation rate is at present (8 yr/cm). Using interpolation, from the age-depth model the accumulation rate is 170 yr/cm from 88-67 cm core depth, 197 yr/cm from 66-43 cm, 40 yr/cm from 42-40 cm, 52 yr/cm between 39-33 cm, 59 yr/cm from 32-19 cm and 11 yr/cm from 31 to the surface. The median probability was calculated using the software Calib 7.1 (Table 2).

Loss-of-ignition analysis demonstrated that the sediment is organic, defined as having more than 12% organic carbon. Organic content is lowest in the bottom part of the core, c. 30% from 88-60 cm depth, while from 60-0 cm depth the average of organic matter is c. 38%.

Table 2. AMS radiocarbon dates from VAF core, calibrated age ranges at 95% confidence intervals.

Lab-code	Depth (cm)	Material dated	Date (^{14}C age BP)	Calendar Age (cal yr BP) 2σ	Median probability (cal yr BP)
Poz-106102	19	Organic bulk sediment	180±30	164 – 282 (46.1%) 56 – 123 (25%) -3 – 33 (13.4%) 132 – 157 (10.1%) 39 – 40 (0.1%)	152
Poz-106103	33	Organic bulk sediment	1115±30	927 – 996 (68.5%) 1013 – 1056 (26.4%)	969
Ntuams-2691	40	Organic bulk sediment	1511±9	1315 – 1369 (95%)	1343
Poz-106105	43	Organic bulk sediment	1610±30	1400 – 1531 (90.1%) 1378 – 1393 (4.7%)	1461
Poz-106106	67	Organic bulk sediment	5460±110	5982 – 6406 (92.2%) 5941 – 5974 (2.8%)	6196
Ntuams-2015	86	Organic bulk sediment	8465±44	9396 – 9529 (82.7%) 9308 – 9361 (11.3%) 9375 – 9382 (1%)	9455

4.2 *Palynological results*

The record is divided into three pollen zones based on the constrained cluster analyses by CONISS: VAF-I, VAF-II and VAF-III. A total of 94 pollen and 37 spore taxa were identified in the 44 samples (supplementary material). 12 pollen types remain unidentified. The percentage pollen diagram (Fig. 3a) shows the dominant and most important taxa grouped into: CDA, UMARF, OARF, LMARF and ferns. The summary diagram (Fig. 3b) shows the total percentage sum for each group: CDA, UMARF, OARF, LARF, tree ferns and spores and the sum of all Asteraceae types. Fig. 3b also includes the depth curves of: sedimentation rate (yr/cm), LOI (%), charcoal concentration (particles cm^{-3}), charcoal accumulation rate (particles cm^{-2} yr^{-1}), fire peaks and fire magnitude.

4.2.1 VAF-I (88-60 cm; 9840-4480 cal yr BP) – 14 samples

This zone is characterized by the dominance of CDA pollen, averaging 61% and ranging from 49% to 69%. Poaceae is the most dominant taxon (46%), followed by different Asteraceae types which represent almost 10% of the pollen sum in this zone. However, *Baccharis* shows its lowest values in the core in this zone (*c*. 2%). Other taxa characteristic for the CDA assemblages in VAF-I are Apiaceae (*c*. 2%), Cyperaceae (1%) and Fabaceae (1%).

The average sum of arboreal taxa represents 33% of the pollen spectra, and are dominated by UMARF, primarily represented by *Weinmannia* (10%) and *Myrsine* (6%). Most taxa of UMARF have their lowest values in this zone, however *Griselinia* and *Drimys* follow an opposite trend and are found at their highest densities in this zone, *c*. 1% each. In contrast to the UMARF group, the OARF pollen shows its highest values in this zone, averaging 8% and ranging from 4% to 13%, with Melastomataceae at *c*. 4% and Myrtaceae *c*. 2%. LMARF pollen are scarce in VAF-I and only average 3% of the pollen sum, primarily represented by Moraceae/Urticaceae (1.5%) and *Alchornea* (1%). Tree ferns occur only as a few single spores. Other fern spores show a roughly continuously percentage in the zone at about 12%.

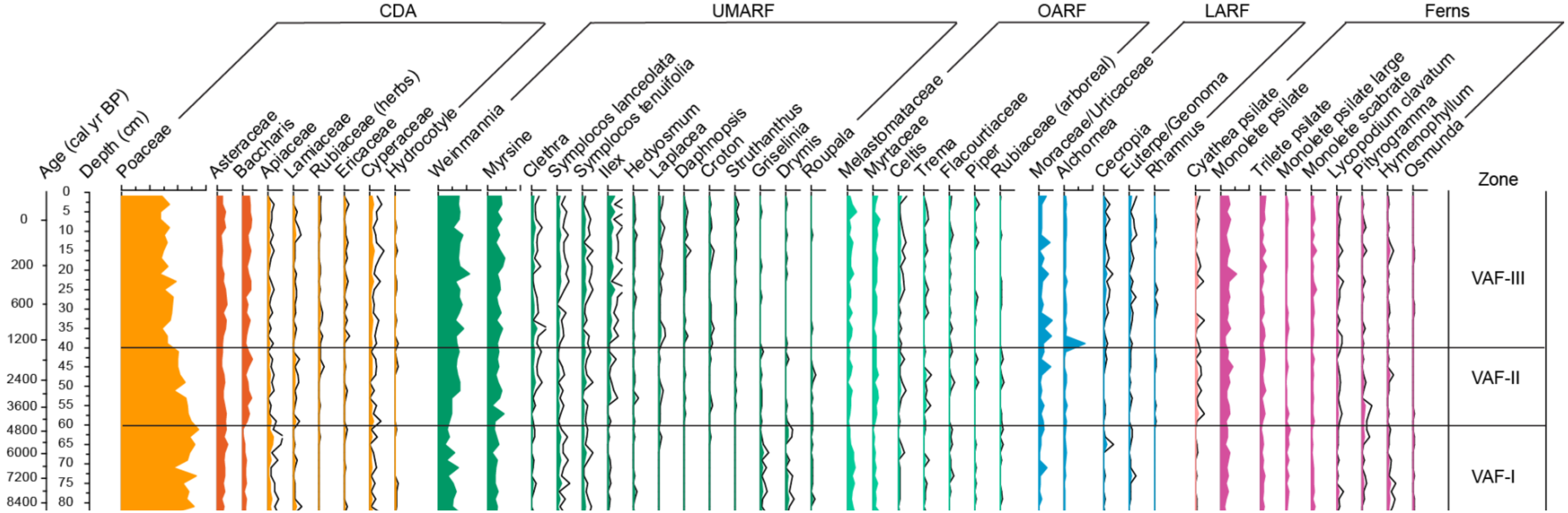

Fig 3a. Pollen percentage diagram of the most important and most frequent taxa of VAF core into each group.

4.2.2 VAF-II (60-40 cm; 4480-1350 cal yr BP) – 10 samples

The pollen CDA percentages slightly decrease to 59%, ranging from *c*. 70% at 50 cm to 54% at 41 cm core depth. Poaceae (43%) and Asteraceae types (*c*. 12%) continue as the main taxa, and *Baccharis* increases to *c*. 4%. The arboreal assemblage reaches *c*. 37% mostly due to the UMARF group (25%), characterized mainly by *Weinmannia* (12%) and *Myrsine* (*c*.7%). *Clethra*, *Symplocos lanceolata*, *S. tenuifolia* and *Ilex* represent *c*. 1% each. The OARF assemblage gradually decreases to 6.5%, with Melastomataceae pollen declining to less than 2% while Myrtaceae increases to 2.5%. LMARF increases slightly to 4.5% in VAF-II, driven primarily by Moraceae/Urticaceae which reaches almost 3%. Relatively speaking, tree fern pollen increases greatly in this zone, but only to *c*.1% while other fern spores are stable at 12%.

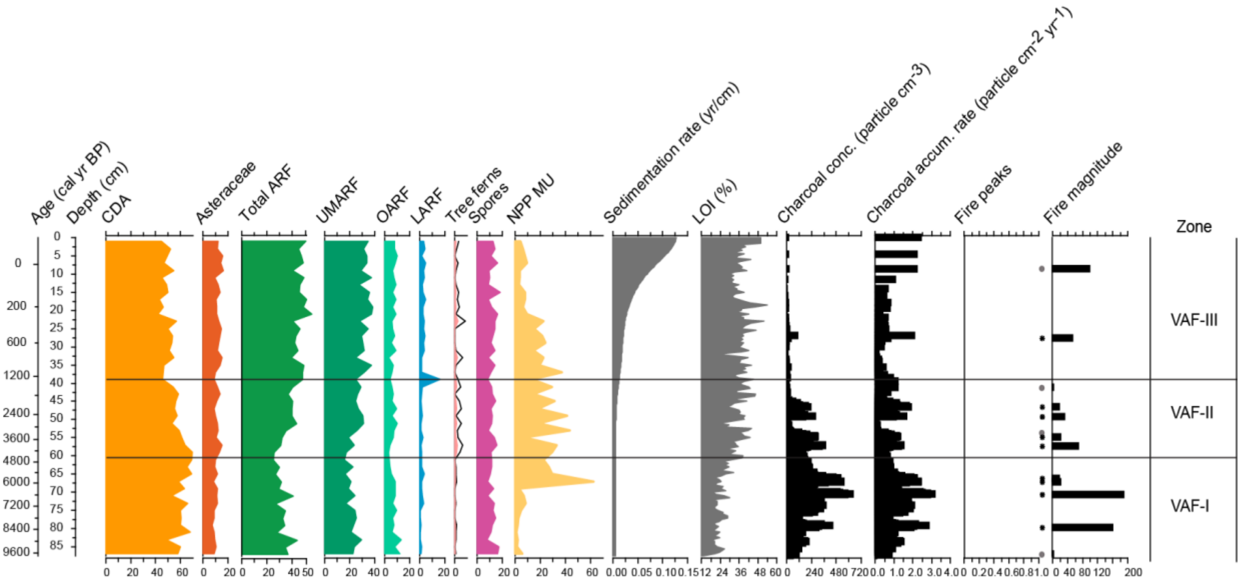

Fig. 3b. Summary diagram of the Vale das Antas Forest core, showing the ecological groups (%), sedimentation rate (yr/cm), loss of ignition (%), macro-charcoal concentration (particle cm-3) and accumulation rate (particle cm-2yr-1), fire peaks and fire magnitude.

4.2.3 VAF-III (40-0 cm; 1350 cal yr BP to present) – 20 samples

In this zone, CDA pollen show a noticeable decrease to 49% of the pollen sum. This is primarily driven by the decrease of Poaceae to 32%. Asteraceae oscillates but on average maintains the same sum as VAF-II (12%) while Cyperaceae reaches its maximum average value of 1.5%. Arboreal pollen increases to about 47%, led by UMARF pollen at 32% and LMARF pollen at 7.5%. Although *Weinmannia* and *Myrsine* remain the most important taxa in the UMARF group, increasing to 15% and *c*. 8% respectively, other taxa also contribute to the increase in VAF-III. *Clethra*, *S. lanceolata*, *S. tenuifolia* occur with *c*. 1% each and *Ilex* reaches about 2%. OARF continues with *c*. 7%, and its main taxa (Melastomataceae and Myrtaceae) remain constant. A stronger change is observed in LMARF, which reaches its maximum (mean = 7.5%, varying from 3% to 20%), due to the expansion of Moraceae/Urticaceae (3.7%), *Alchornea* (2%,) *Cecropia* (1%) and *Euterpe/Geonoma* (0.7%). As in the previously zones, non-tree fern spores are at 12%, while tree ferns show slightly reduced values.

4.3 Macro-charcoal and fire regime

The CharAnalysis of macro-charcoal characterize the fire history for the past 9840 years (Fig. 3b). Average concentration for the entire sediment is 190 particles cm$_{-3}$, decreasing from 250 particles cm$_{-3}$ in zone VAF-I, to 150 particles cm$_{-3}$ in VAF-II and only 30 particles cm$_{-3}$ in zone VAF-III. The local signal-to-noise exceeds 3.5, indicating a good separation between peak and non-peak values. From 13 fire peaks, 4 fire episodes failed to pass the Poisson minimum-count criterion, including the most recent peak at 9 cm depth (19 cal yr BP). The most recent significant peak is found at 28 cm depth, (565 cal yr BP). The mean fire return interval (FRI, 95% probability) calculated with a 1000-yr window and only using fires that met the minimum-count criterion is 998 yr (593-1449 yr). Using all 13 identified fire peaks and calculating the FRI across the entire record yields an FRI of 617 (446-827 yr). Under either measure, local fire events (fires within 500 m or so of the core site) were rare over the period of our sample, but the nearly continuous presence of charcoal through the core demonstrates fires were not regionally uncommon. Most fire peaks as well as the highest magnitude peaks occurred in zone VAF-I.

5 Interpretation and Discussion

Overall, the stratigraphy and the organic content of the VAF core in the Serra dos Órgãos National Park indicate that there was a change from drier to wetter climatic conditions in the region during the Holocene, demonstrated by the lower accumulation rate and lower organic matter in the bottom part of the core. From the beginning of the pollen record, the general study area was dominated by CDA, rich in grass and shrubs, mostly represented by species of Poaceae, Asteraceae, Apiaceae and Cyperaceae. The high elevation forest patch that currently occupies the study site is probably of relatively recent origin. Forest cover at high elevations (>1800 m) in the Serra dos Órgãos and other mountains in southeastern Brazil is extremely heterogeneous and controlled largely by climo-topographic and soils variables in combination with disturbance (Safford, 1999a,b; 2001). Climates during the Early Holocene were much drier than today and CDA vegetation was much more widespread than today. This and other studies of palaeovegetation in the southeastern Brazilian mountains (Behling, 1997b; Behling et al. 2007; Behling and Safford, 2010; Veríssimo et al., 2012; Behling et al., 2020) show a clear trend of increasing forest cover – and decreasing campos cover – at high elevations since the Early Holocene, with acceleration in this trend during the Late Holocene.

Our pollen data suggest that UMARF was not widely distributed at higher elevations (>1800 m) in the Serra dos Órgãos in Zone I (9840-4480 cal yr BP), and that the more continuous local forest may not have developed until after 1350 cal yr BP (Zone III). Before 4480 cal yr BP the study site was rich in genera of southern temperate-latitude ancestry such as *Weinmannia*, *Drimys* and *Griselinia*, implying a somewhat colder climate than today. UMARF taxa of tropical origin were also represented in the Early Holocene pollen, but their abundances were mostly low or very low before they began to rise substantially after 4480 yr cal BP. Examples of this pattern include *Clethra*, *Ilex*, *Laplacea*, *Daphnopsis*, *Croton*, and the tree ferns. Some UMARF genera were already relatively common before 4480 cal yr BP but saw their abundances rise further thereafter. Examples are *Weinmannia* (2x increase) and *Myrsine* (50% increase). *Symplocos*, Melastomataceae and Myrtaceae (the latter two very common in both UMARF and OARF) showed similar abundances throughout the Holocene. The modern UMARF is characterized by species of temperate, neotropical and tropical origin which occur in the majority of UMARF in southeastern and southern Brazil (e.g. Portes et al., 2001; Safford, 2007; Scheer and Mocochinski, 2009; Gomes, 2015; Moreira et al., 2018).

Modern pollen rain data from the Serra dos Órgãos (Portes et al., 2020) suggest that current areas of CDA are under-represented in pollen assemblage due to the low pollen production and low accumulation rate of CDA taxa and also the over-representation of some arboreal taxa, especially pioneer or secondary species of montane forest upwards wind-transported. They propose the use of a restricted group of typical upper montane forest, which should be more sensitive to detect the local trend of forest changes (within the mosaic landscape) than the full groups of ARF. Therefore, following Portes et al. (2020), we aggregated pollen sums from *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* to represent UMARF and aggregated the same taxa used by Behling and Safford (2010) to represent the CDA. Fig. 4 shows the temporal trends in forest and in CDA from our VAF core and the SDO core sampled by Behling and Safford (2010) (which stretched back into the Late Pleistocene [12380 cal yr BP]), and superimposes the macro-charcoal concentration (particles cm$_{-3}$) from VAF core and the δ$_{18}$O record from Bernal et al. (2016).

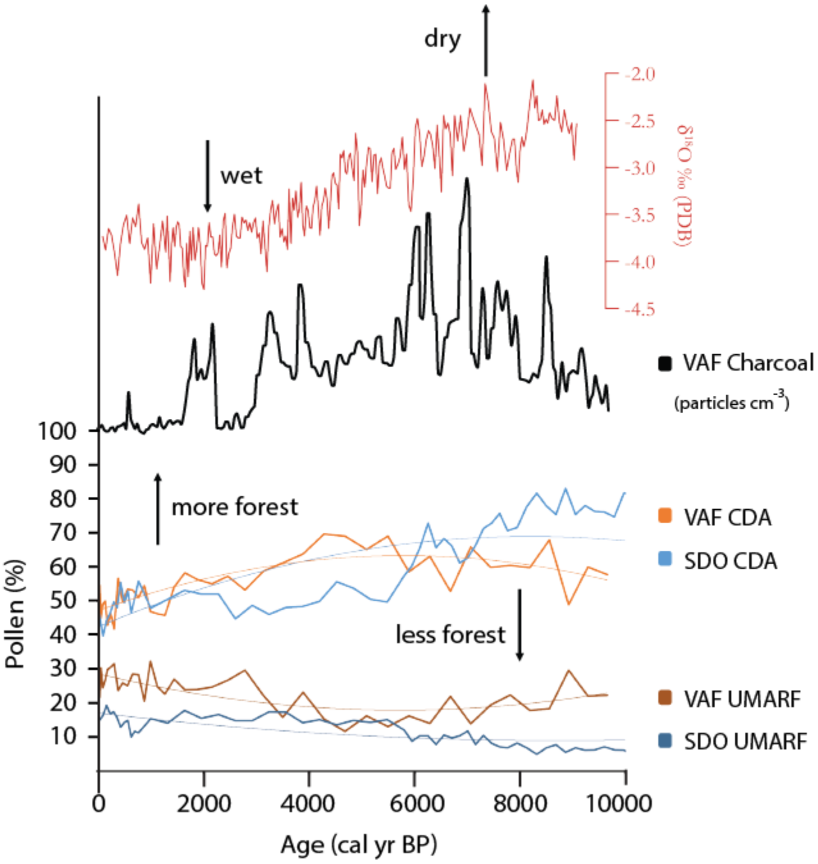

Fig. 4. Comparison of the sum (%) of *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* taxa representing UMARF from VAF core (VAF UMARF), the sum of *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* taxa representing UMARF from SDO core (SDO UMARF), the sum of CDA group from VAF core (VAF CDA) and the sum of CDA group from SDO core (SDO CDA), plotted with macro-charcoal concentration (particles cm$_{-3}$) from VAF core and δ$_{18}$O record from Botuverá Cave (Bernal et al., 2016) for the last 10,000 years. Trendline from 2$_{nd}$ order polynomial.

Our data suggest that the study site was dominated by CDA vegetation for most of the Holocene, with more or less uniform CDA vegetation in the Early Holocene and a notable contraction in the Late Holocene after about 4500 yr BP, corroborating the higher charcoal concentration as well as the drier climate at that period. As climate became wetter after around 1400 cal yr BP, charcoal concentration decreases, the CDA:forest ratio drops to 50:50 and the group of upper montane ARF increases to around 30%. The SDO core shows similar patterns, with an accentuated increase in forest pollen after about 5000 cal yr BP, and the balance of campos vs. forest pollen dropping below 50:50 after around 1500 cal yr BP (Fig. 4). While VAF core was collected in a currently UMARF patch surrounded by CDA vegetation, SDO core was cored from a more widespread CDA vegetation. We hypothesize therefore that the patch of forest that currently occupies the VAF site has only been extant since sometime in the Late Holocene, although the pollen data make clear that upper montane forest taxa have been in the broader region throughout the Holocene.

The VAF core also documents temporal floristic variation that points to important changes in climate over the course of the Holocene. We interpret the Early and Mid-Holocene as relatively cool and dry (but becoming gradually warmer and wetter over time), based on (1) the general lack of tree ferns; (2) low LOI values; (3) relatively high frequencies and magnitudes of fire; (4) relatively low pollen densities for *Baccharis*, which is a faithful campos indicator but under warmer temperatures; and (5) the elevated presence of cool climate indicators of southern temperate ancestry like *Drimys* and *Griselinia*. In addition, the nearby SDO core records *Araucaria* pollen until about 10,800 cal yr BP, further pointing to cooler Early Holocene temperatures. UMARF vegetation in the Early and Mid-Holocene seems to have been somewhat less species rich than today and composed of a more southern-temperate flora.

Zones VAF-II (4480-1350 cal yr BP) and III (1350 cal yr BP to present) represent the Late Holocene. After 4480 cal yr BP organic matter in the soil increased in coincidence with increases in a number of UMARF and OARF taxa. Taxa of tropical origin such as *Clethra, Symplocos, Celtis, Trema* and Flacourtiaceae expanded, as did the tree ferns. Associated with the rising elevation and expanse of forest, fire magnitude and frequency declined suggesting a shift to wetter conditions. A shift to even wetter conditions appears to have occurred at the beginning of VAF-III (around 1350 cal yr BP), demonstrated by a strong and abrupt intensification of sediment accumulation, a decrease in charcoal concentration, and a reduction of CDA pollen to *c.* 50% of the total. The sharp peak of *Alchornea* just after 1350 cal yr BP and the increase in other tropical LARF taxa (Moraceae/Urticaceae, *Cecropia* and *Euterpe*/*Geonoma* type) are indicative of a rapid change toward a warmer and wetter climate in the Late Holocene. Since about 1200 cal yr BP the CDA/UMARF relationship has remained in an approximate balance in the study area. During this period, the last significant fire peak at *c*. 600 cal yr BP occurred and may be related to the VAF-III peak in CDA pollen and concurrent drop in UMARF pollen that occurs shortly thereafter.

Other studies also suggest an intensification in Late Holocene precipitation. Moss spores in the nearby SDO core increased greatly in the Late Holocene sediment (Behling and Safford, 2010). Palaeoclimate data from the last 10,000 years at Botuverá Cave (27$_{o}$13’S, 49$_{o}$09’W, 230 m a.s.l.; Bernal et al., 2016) registered an increase in rainfall starting about 4000 years ago (see Fig. 4) which coincides with the spread of forest vegetation and declining occurrence and magnitude of fire in our core. Evidence for a relatively sudden increase in precipitation in VAF (see above) at around 1350 cal yr BP is also supported by studies of the SAMS (South American Monsoon System) over the last 2000 years, which show a strengthening monsoon during the Little Ice Age (LIA), resulting in a wetter period from *c*. 1400-1800 AD (Vuille et al., 2012).

Charcoal in the VAF and SDO cores suggests that fires have occurred in the Serra dos Órgãos since at least the Late Pleistocene, i.e., before the documented arrival of humans in southeastern Brazil. Longer records from other CDA sites in the southeastern Brazilian mountains show notably more fire even further back in time, such as the 35,000 years record from Morro do Itapeva in the southern Serra da Mantiqueira (Behling, 1997b), and the 18,600 years record from the Serra da Bocaina (Behling et al., 2007). However, fires in the immediate locality of the VAF core were infrequent during the Holocene. By using relatively large macro-charcoal (>150 μm) in our CharAnalysis, we restricted our assessment to fires that occurred within probably 500 m or so of the core site (Higuera et al., 2007). This permits a more site-specific understanding of fire history and suggests that the Holocene fire return interval in this wet but seasonally dry landscape was long, ranging from around 600 to 1000 years (depending on our assumptions). It is also clear however that fires were, and usually still are, relatively small, and our analysis thus under-represents the fire regime of the broader landscape. The Serra dos Órgãos landscape is topographically extremely abrupt and heterogeneous (the rise from Guapimirim to Pedra do Sino is 2210 m in less than 8 km and some of the tallest rock walls in all of Brazil are found here), and the high mountain summits and plateau that support CDA are small, ringed by cliffs and humid forest, and cut by deep gorges (see Fig. 1). As a result, lightning ignitions that occur on topographic eminences with combustible fuels (graminoids or dry woody fuels) have little chance to spread far. Most lightning strikes in southeastern Brazil occur during the wet season, but lightning at either the beginning or end of the wet season has the potential to cause fire. Today most ignitions are anthropogenic and occur during the dry season, when lightning ignitions are far more rare. Human ignitions that occur during very warm and especially windy conditions can spread from mountain to mountain and even burn appreciable areas of forest. Control of such fires is a major conservation issue in the Brazilian National Park system.

Another reason our charcoal analyses almost certainly under-represent palaeofire frequencies in the CDA is that macro-charcoal (>150 μm) is composed of charred woody fragments, but graminoids are the principal fuel for fire in the campos. Whitlock et al. (2004) note that the best correspondence between real fire frequency and charcoal records is where woody vegetation is dense and continuous, a condition that is rare at the highest elevations of the Serra do Mar. Behling et al. (2020) found a similar site-specific fire return interval for the AN core from the Serra do Itatiaia (mean = 630 years through the Mid- and Late Holocene) and noted similar issues with the dominance of graminoid vegetation in the surrounding landscape. Obvious directions for further research are to (1) conduct macro-charcoal analysis on already published cores that predated the development of the analytical techniques (such cores exist from a number of high montane sites in southeast Brazil); (2) obtain sediment core samples from more – and both elevationally and vegetationally more varied – locations in the southeastern Brazilian highlands; and (3) develop new techniques to better assess fire frequencies and magnitudes using charcoal from herbaceous sources.

6 Conclusion

The results of the VAF record indicate that the higher elevations of Serra dos Órgãos have been occupied by a mosaic of CDA and UMARF since the beginning of the record (9840 cal yr BP). Like other studies of palaeovegetation in the southeastern Brazilian mountains, VAF shows a clear trend from drier to wetter climatic conditions during the Holocene, and a clear trend of replacement of CDA vegetation by forest vegetation. Temporal trends in the CDA:forest pollen balance suggest that although forest taxa have been in the general region of the study site throughout the Holocene, the forest patch that occupies the VAF site has probably been extant only since about 1350 cal yr BP.

Both the VAF record (collected in a forest patch) and SDO record (cored in CDA vegetation) indicate that CDA was much more widespread in the Late Holocene than it is today, with major contraction occurring after about 5000 cal yr BP (5640 cal yr BP in the SDO core and 4480 cal yr BP in the VAF core). Both core sites also demonstrate a similar pattern of forest moving consistently upwards through much of the Holocene. This is especially the case for UMARF taxa but also for montane ARF. At around 1000 cal yr BP (1350 cal yr BP in VAF and 880 cal yr BP in SDO) the pollen data indicate a marked shift toward a warmer and wetter climate, further favouring the expansion of forest vegetation. The variability in timing of these climatic events between the two cores are likely related to differences in vegetation and relief as well as the error intrinsic to $_{14}$C dating.

The macro-charcoal record in the VAF core corroborates changes seen in climate and vegetation. Fires were more frequent and of greater magnitude in the Early Holocene, decreased after around 4000 cal yr BP, and have been very rare in the Late Holocene. The nearby SDO core (Behling and Safford 2010) showed similar patterns, with more frequent fire during the Early Holocene, especially from 10,800 to 7850 cal yr BP, and a decreasing trend until about 5640 cal yr BP, when charcoal concentrations and accumulation more or less levelled off.

Our results support the conclusions of previous studies (e.g., Behling, 1997b; Safford, 2001; Behling et al., 2007; Behling and Safford, 2010; Veríssimo et al., 2012) that fire has long been a natural disturbance factor in the campos de altitude. Most of these studies indicate fire frequencies were highest in the Late Pleistocene and Early Holocene, mostly well before humans settled southeastern Brazil. Before the arrival of humans at these mountain sites, fires were probably generally small and – based on the occurrence of lightning in the Serra do Mar – mostly occurred at the margins of the wet season. Today, anthropogenic ignitions occur primarily during the dry season in very warm and windy conditions and fire sizes can be enormous. Further research is needed to better define the natural fire regime in the Brazilian Highlands, especially since current methods are based on analysis of woody charcoal and likely miss the majority of paleo-fires. Another conservation concern is the long-term increase in precipitation and temperature that has been underway for centuries and is rapidly accelerating as greenhouse gas emissions rise. Forest expansion into previously grassland-dominated sites threatens the habitat heterogeneity than underlies the high biodiversity and endemism of these montane sites (Safford, 2001; Portes et al., 2018). We recommend that protected areas containing campos de altitude and upper montane rain forest develop management strategies that incorporate observation, measurement, experimentation, and active management techniques that help to retain landscape heterogeneity (see Portes et al., 2018). The standard “hands-off” protectionism that has characterized national park management for the last century may be particularly poorly suited to conservation in an age of rapid global change (Cole and Yung, 2010; Safford et al., 2012).

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9 Supplementary Material of Chapter 3

List of taxa identified in the VAF sediment.

Taxa	Subgroup	Group	Pollination
Asteraceae	Asteraceae	CDA	Entomophily
Ambrosia	Asteraceae	CDA	Entomophily
Baccharis	Asteraceae	CDA	Entomophily
Jungia	Asteraceae	CDA	Entomophily
Senecio	Asteraceae	CDA	Entomophily
Vernonia	Asteraceae	CDA	Entomophily
Alstromeria	Herbs & Shrubs	CDA	Entomophily
Amaranthaceae/Chenopodiaceae	Herbs & Shrubs	CDA	Entomophily
Apiaceae	Herbs & Shrubs	CDA	Entomophily
Borreria	Herbs & Shrubs	CDA	Entomophily
Ericaceae	Herbs & Shrubs	CDA	Entomophily
Eriocaulon	Herbs & Shrubs	CDA	Anemophily/Entomophily
Eryngium type 1	Herbs & Shrubs	CDA	Entomophily
Eryngium type2	Herbs & Shrubs	CDA	Entomophily
Fabaceae	Herbs & Shrubs	CDA	Entomophily/Aviphily
Hippeastrum	Herbs & Shrubs	CDA	Entomophily
Hypericum	Herbs & Shrubs	CDA	Entomophily
Hyptis	Herbs & Shrubs	CDA	Entomophily/Aviphily
Lamiaceae	Herbs & Shrubs	CDA	Entomophily/Aviphily
Malphigiaceae	Herbs & Shrubs	CDA	Entomophily
Malvaceae	Herbs & Shrubs	CDA	Entomophily
Poaceae	Herbs & Shrubs	CDA	Anemophily
Polygala	Herbs & Shrubs	CDA	Entomophily
Ranunculaceae	Herbs & Shrubs	CDA	Anemophily/Entomophily
Ripsalis	Herbs & Shrubs	CDA	Entomophily/Aviphily
Scrophulariaceae	Herbs & Shrubs	CDA	Entomophily
Spermacoce	Herbs & Shrubs	CDA	Entomophily
Valeriana	Herbs & Shrubs	CDA	Entomophily
Cyperaceae	Aquatics	CDA	Anemophily

Hydrocotyle	Aquatics	CDA	Entomophily
Liliaceae/Amaryllidaceae	Aquatics	CDA	Entomophily
Typha	Aquatics	CDA	Anemophily
Xyris	Aquatics	CDA	Anemophily
Allophylus	UMARF		Entomophily
Begonia	UMARF		Entomophily
Clethra	UMARF		Entomophily
Croton	UMARF		Entomophily
Daphnopsis	UMARF		Entomophily
Drimys	UMARF		Entomophily/Aviphily
Fuchsia	UMARF		Aviphily
Griselinia	UMARF		Entomophily
Hedyosmum	UMARF		Anemophily/Entomophily
Ilex	UMARF		Anemophily/Entomophily
Laplaceae	UMARF		Entomophily
Mimosa scabrella	UMARF		Entomophily/Aviphily
Myrsine	UMARF		Anemophily
Ouratea	UMARF		Entomophily
Podocarpus	UMARF		Entomophily
Roupala	UMARF		Entomophily/Aviphily
Struthanthus	UMARF		Entomophily
Styrax	UMARF		Entomophily
Symplocos lanceolata	UMARF		Entomophily
Symplocos tenuifolia	UMARF		Entomophily
Weinmannia	UMARF		Entomophily/Aviphily
Alseis floribunda	OARF		Entomophily
Araliaceae	OARF		Entomophily
Bignoniaceae	OARF		Entomophily/Aviphily
Celtis	OARF		Anemophily
Coccocypselum	OARF		Entomophily
Dodonea	OARF		Anemophily
Euphorbiaceae	OARF		Entomophily
Flacourtiaceae	OARF		Entomophily/Aviphily
Lamanonia	OARF		Entomophily
Matayba	OARF		Entomophily

Melastomataceae	OARF		Entomophily
Meliaceae	OARF		Entomophily
Meliosma	OARF		Entomophily
Menispermaceae	OARF		Entomophily
Mimosaceae	OARF		Anemophily/Entomophily/Aviphily
Myrtaceae	OARF		Entomophily/Aviphily
Oreopanax	OARF		Entomophily
Pera	OARF		Entomophily
Piper	OARF		Anemophily/Entomophily
Prockia	OARF		Entomophily/Aviphily
Prunus type	OARF		Entomophily
Rubiaceae	OARF		Entomophily
Sapindaceae	OARF		Entomophily
Schefflera	OARF		Entomophily
Sebastiana brasiliensis	OARF		Anemophily
Sebastiana commersoniana	OARF		Anemophily
Solanum	OARF		Entomophily
Trema	OARF		Anemophily
Urvillea	OARF		Entomophily
Vochysia	OARF		Aviphily/Entomophily/Monkeys
Alchornea	LARF		Anemophily/Entomophily
Cecropia	LARF		Anemophily/Entomophily
Euterpe/Geonoma	LARF		Entomophily
Hyeronima	LARF		Entomophily
Moraceae/Urticaceae	LARF		Anemophily
Rhamnus	LARF		Entomophily
Sapotaceae	LARF		Entomophily/Quiropterophily
Virola	LARF		Entomophily
Alsophila	Tree fern		Hydrophily
Cyathea psilate	Tree fern		Hydrophily
Cyathea reticulate	Tree fern		Hydrophily
Cyathea verrucate	Tree fern		Hydrophily
Dicksonia	Tree fern		Hydrophily
Lophosoria quadripinnata	Tree fern		Hydrophily
Nephalea	Tree fern		Hydrophily

Anemia phyllitides	Spore		Hydrophily
Hymenophyllum	Spore		Hydrophily
Lycopodium clavatum	Spore		Hydrophily
Lycopodium foveolate	Spore		Hydrophily
Monolete clavate	Spore		Hydrophily
Monolete echinate	Spore		Hydrophily
Monolete psilate	Spore		Hydrophily
Monolete psilate large	Spore		Hydrophily
Monolete scabrate	Spore		Hydrophily
Monolete striate	Spore		Hydrophily
Monolete with perispore	Spore		Hydrophily
Osmunda	Spore		Hydrophily
Phaeoceros	Spore		Hydrophily
Pityrogramma	Spore		Hydrophily
Polypodiaceae	Spore		Hydrophily
Pteridophyta type 4	Spore		Hydrophily
Pteridophyta type 7	Spore		Hydrophily
Pteris type	Spore		Hydrophily
Sellaginella excurrens	Spore		Hydrophily
Sphagnum	Spore		Hydrophily
Trilete clavate	Spore		Hydrophily
Trilete psilate	Spore		Hydrophily
Trilete scabrate	Spore		Hydrophily
Trilete striate	Spore		Hydrophily
Trilete verrucate	Spore		Hydrophily
Trilete with perispore	Spore		Hydrophily

CHAPTER 4

Humans and climate as designers of the landscape in Serra da Bocaina National Park, southeastern Brazil, over the last seven centuries

Maria Carolina Guarinello de Oliveira Portes [1,2,3], Hugh Safford [4,5], Hermann Behling[1]

[1] *Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Sciences, University of Göttingen, Germany*

[2] *Instituto Chico Mendes de Conservação de Biodiversidade (ICMBio), Brazil*

[3] *CNPq-Brazil Scholarship, Brazil*

[4] *USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA*

[5] *Department of Environmental Science and Policy, University of California, Davis, California, USA*

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Abstract

Campos de altitude and *Araucaria* forest are unique and highly diverse ecosystems and focus areas for conservation and restoration in southeastern Brazil. This paper reports a high-resolution paleoecological study of an approximately 700-year Late Holocene core, a period that includes the influence of two highly distinct civilizations and the transition between them: Amerindian/pre-Columbian and European/post-Columbian. Results highlight the interworkings of regional climate change and local human agency in “designing” the Late Holocene forest-grassland mosaic in the Serra da Bocaina. Amerindians maintained more open highland habitats probably through slash and burn agriculture. The depopulation of the study region after European arrival in the 1500s plus increasing precipitation led to a marked and rapid rebound in forest cover. After 1720 AD, establishment of permanent European communities and farming in the study area led to forest loss and a renewed expansion of grassland. Based on current knowledge about forest-grassland relationships, and in light of projections for warmer and wetter conditions in southeast Brazil, we provide suggestions for management strategies that might better maintain the mosaic of *Araucaria* forest and campos de altitude in the southeastern Brazilian highlands.

Key words: campos de altitude, *Araucaria* forest, Atlantic Forest, human impact, conservation, palaeoecology.

1 Introduction

The Atlantic Forest biome occupies 1,300,000 km^2 of coastal and eastern Brazil, stretching from 3° S latitude to almost 34° S. Due to centuries of exploitation, only 10-15% of the Atlantic Forest biome remains in a natural or semi-natural state (Fundação SOS Mata Atlântica/ INPE, 2017). The biome is one of the most diverse in the world, and is considered among the most important and most imperilled biodiversity hotspots on earth (Myers et al., 2000). It includes a mosaic of different ecosystems, including shoreline forests, lower, middle and upper montane rainforest, *Araucaria* forest, and campos de altitude (high elevation grass- and shrublands). Present at higher elevation, *Araucaria forest* has been reduced to <13% of its original distribution (Ribeiro et al., 2009), and campos de altitude is naturally restricted to small areas on the summits of the higher peaks and plateaux. One of the best preserved stretches of the Atlantic Forest is found between the highly populated metropolitan areas of São Paulo and Rio de Janeiro. Preservation here was promoted by mountainous topography and establishment of the firsts national park in South America (Itatiaia 1937, Serra dos Órgãos 1939). In 1972, the Serra da Bocaina National Park (SBNP) was added to the system to protect 100,000 ha of highly threatened forest on the south flank of the Serra do Mar.

Amerindians probably arrived in southeastern Brazil about 10,000 years ago (Figuti et al., 2004). They settled originally along the coast, but migrations and cultural transitions led a greatly increased human footprint in inland forests by 1800 yr BP (Noelli, 2008). By the time Portuguese settlers arrived in Brazil beginning in 1500 AD, centuries of swidden agriculture had altered much of the lowland forest, but the low population densities and primitive technologies of the Amerindians left some forest areas untouched and most cultivated areas were in some stage of recovery at any given time (Dean, 1995; Drummond, 1997). The first permanent Portuguese coastal settlements were built in SBNP beginning in the late 16th century, however inland colonization in the Paraíba do Sul valley dates from the early to mid-17th century (Nehren et al., 2013). The region experienced a number of economic cycles after Portuguese settlement, including coffee plantations which were the main cause of forest loss inland of SBNP (Dean, 1995; Drummond, 1997).

Since the Last Glacial Maximum (LGM), there has been high temporal variability in the structure and distribution of ecosystems in southeastern Brazil. Behling et al. (2007) studied Late Pleistocene and Holocene vegetation development in the SBNP spanning the period 18,570 cal yr BP to 1280 cal yr BP. The climate was cold and dry in the Late Pleistocene, with frequent frost during winter months, and the landscape was dominated by campos de altitude with forests in lower elevation, protected locations, for example along streams. Arboreal pollen became much more common in the Holocene, comprised mainly of species from *Araucaria* forest, but it is clear that large areas of grassland persisted at upper elevations (Behling et al., 2007). Charcoal is found throughout the 17,000 yr record, demonstrating that the highland flora was subjected to periodic fire and that the extent of fire adaptations in the flora cannot be attributed to recent anthropogenic fire alone (Behling et al., 2007; Safford, 2001). The greatest expansion of forest occurred during the Late Holocene (~ 4200 BP to present, Walker et al., 2012) when wetter conditions were established, resulting in a mosaic of campos de altitude, *Araucaria* forest and Atlantic Forest (Behling et al., 2007; Behling and Pillar, 2008). Many studies document the maximum expansion of *Araucaria* forest in southeastern and southern Brazil after 1500 AD, supporting the hypothesis of increasing effective moisture in the Late Holocene (Behling, 1995, 1997, 2007; Behling et al., 2004; Behling and Safford, 2010; Jeske-Pieruschka et al., 2010, 2012). At the same time, continued expansion of *Araucaria* in southern Brazil after 500-1000 AD during a period of slightly drier climate suggests an important role for human dispersal as well (*Araucaria* was a major staple of the indigenous diet) (Bitencourt and Krauspenhar, 2006; Robinson et al., 2018).

A major question is the relative extent to which climate and humans have influenced ecosystem conditions in the Americas since human arrival at the beginning of the Holocene. It was long presumed that pre-Columbian human influence on ecosystem status and distribution in the Atlantic Forest was minimal (Drummond, 1997; Guidon, 1992). However, science continues to uncover more and more evidence of extensive and sometimes intensive influence of pre-Columbian cultures on ecological conditions in southern and southeastern Brazil (Noelli, 2000; Robinson et al., 2018). Here we focus on the spatial and temporal relationships between *Araucaria* forest and campos de altitude on the Bocaina Plateau over the last seven centuries, a period that includes the influences of two highly distinct civilizations and the transition between them: Amerindian and post-Columbian. Late Holocene, current, and future trends of atmospheric warming and increasing effective moisture favour continued forest expansion. We use high-resolution paleoecological data to discern the conditions under which campos de altitude have been maintained in the Serra do Mar highlands, in the face of forest expansion and at altitudes that are lower than the climatic “treeline”. Campos de altitude and *Araucaria* forest are both unique, diverse ecosystems and focus-areas for conservation and restoration in southeastern Brazil. In this contribution, we seek (1) to disentangle the influences of climate and humans on the changing status of the forest-grassland mosaic in the Serra da Bocaina during the Late Holocene; and (2) to provide a foundation for better understanding how the grassland component of the mosaic might be conserved under a future climate that will greatly favour forest expansion.

2 Environmental Setting

2.1 Geomorphology

Our study area is located on the Bocaina Plateau in the SBNP (22°44'02.0” S, 44°38’39.4” W, 1539 m a.s.l.) at the border of São Paulo and Rio de Janeiro states in southeastern Brazil (Fig. 1). Topographic relief is related to tectonic events resulting from the western Gondwana breakup and the opening of the South Atlantic Ocean throughout the Cretaceous, followed by reactivation of Proterozoic shear zones and uplift during the Late Cenozoic (Hiruma et al., 2010; Siqueira Ribeiro et al., 2011). The Bocaina Plateau, the highest part of this section of the Serra do Mar, is a remnant erosional surface, mostly underlain by decomposed Proterozoic gneisses and granites (Ab´Saber, 2003; Hiruma et al., 2010). Colluvium are common at the bases of slopes on the Bocaina Plateau and are normally characterized by a sandy or clayey matrix (Hiruma et al., 2012). Carbonate bearing rocks are absent in the region. Overall the landscape is characterized by rounded mountaintops interrupted with valleys, interspersed with scattered inselberg formations, probably caused by repeated cycles of tropical/wet morphoclimatic processes punctuated by drier periods over the last few million years (Ab´Saber, 2003; Safford and Martinelli 2000). The study area also constitutes the headwaters for two important rivers, the Paraitinga and Mambucaba, which flow north and south, respectively.

2.2 Climate

The climate is categorized as tropical humid with seasonal precipitation (IBAMA, 2002). Annual average precipitation is 1670 mm, with ca. 40 mm in the driest month (July) and 265 mm in the wettest (January) (D1-022-Areias pluviometry station, http://www.hidrologia.daee.sp.gov.br, accessed 15 January 2018). Orographic precipitation from the Atlantic Ocean plays an important role as the Serra do Mar forms a barrier to easterly moisture. On the plateau, the temperature ranges from 29 to -4 $_{o}$C and the annual average temperature is 17 $_{o}$C, with mild, wet summers and cool, dry to moist winters (IBAMA, 2002; Nimer, 1977).

The software NewlocClim (http://www.fao.org/nr/climpag/locclim/locclim_en.asp) estimates the mean maximum of the warmest month of 29.7 $_{o}$C and the mean minimum of the coolest month of 7.6 $_{o}$C. At the highest elevations, frost is common in the winter months, especially in high elevation basins. Increasing precipitation in southeastern Brazil since the Early Holocene is thought to be connected to gradual intensification of the South American Monsoon System (SAMS), which has resulted in higher austral summer insolation and a more southerly position of the Intertropical Convergence Zone in summer (Bernal et al., 2016).

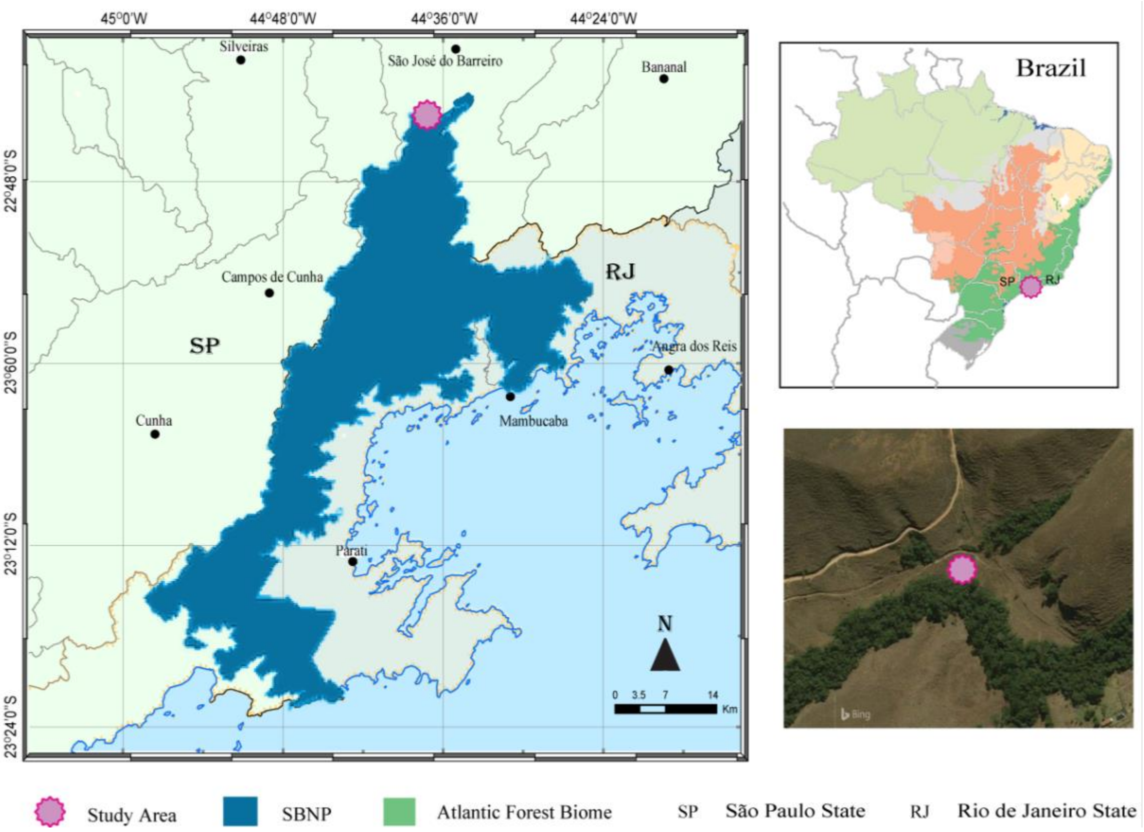

Fig 1: Location of SBNP and the study site.

2.3 Vegetation

IBAMA (2002) classifies the vegetation of the SBNP to three main ecosystems: campos de altitude, *Araucaria* forest and “Atlantic Forest” (referring to the various subzones and associated ecosystems that comprise the lowland and montane rainforest). The Bocaina Plateau itself is characterized by a mosaic of campos de altitude and *Araucaria* forest. The campos de altitude, which have clear modern human impacts, occupy the summits and the upper mountain slopes above 1500 m a.s.l. (Hiruma et al., 2010; IBAMA, 2002). The campos de altitude is rich in endemic species, predominantly characterized by non-arboreal species in the families Poaceae, Cyperaceae, Melastomataceae, Asteraceae, Ericaceae and Eriocaulaceae (Martinelli and Bandeira, 1989). Shrubby species of Asteraceae and Melastomataceae are dominant where the forest meets the grassland. *Araucaria* forest occurs as riparian forests as well as in small patches of forest surround by grassland between 1400 and 1800 m a.s.l. (IBGE, 2012). Important species of the *Araucaria* forest are *Araucaria angustifolia*, *Podocarpus lamberttii* and *Drimys brasiliensis*. The families Myrtaceae, Lauraceae, Fabaceae, Melastomataceae are common together with the tree ferns *Dicksonia sellowiana* (Dicksoniaceae) and *Alsophila capensis* (Cyatheaceae) (IBAMA, 2002; IBGE, 2012). Apiaceae, Piperaceae and Rubiaceae characterize the forest shrub layer (IBAMA, 2002).

In the IBAMA classification, the Montane Atlantic Forest subzone is distributed between 700-1500 m a.s.l., on the mountain slopes, characterized by species of Lauraceae, Arecaceae, Fabaceae, *Cedrela fissilis*, *Luhea* sp., epiphytes and lianas. The Upper Montane subzone occurs in general above 1500 m a.s.l. in small fragments close to the mountain summits (IBAMA, 2002) characterized by the presence of fog, high humidity, low temperatures, strong winds and shallow soils (Portes, 2000). *Miconia*, *Weinmannia*, *Myrsine*, *Drimys*, *Clethra* and *Roupala* as well as the families Aquifoliaceae and Myrtaceae are common (IBAMA, 2000; Portes, 2000).

The swampy area from which the sediment was recovered is located near a small river and is covered by species of Poaceae and Cyperaceae. Surrounding the study site, the vegetation is a mixture of riparian forest with *Araucaria angustifolia* and *Podocarpus lambertii* and human influenced grassland, mostly used as a livestock pasture. The studied swamp is well preserved, without signs of disturbance and compaction as cattle access the pasture via paths that do not intersect the wetland.

2.4 Local history of human occupation

Several Amerindian groups inhabited the coast, mountains and inland territory around the Paraíba do Sul River valley over the last 8000 years (Bueno and Dias, 2015; Guidon, 1992). These were originally hunter-gatherers, but slash and burn agriculture began at least 1500 years before the arrival of Europeans (Corrêa, 2006; Noelli, 2008). Larger, more permanent settlements were mostly at lower elevations, but the nutritional value of *Araucaria* – and its high importance to Amerindians (Robinson et al., 2018) – suggests the possibility that there may have been some level of cultivation of this species on the Bocaina Plateau as well. Dean (1995) similarly suggests that the “islands” of *Araucaria* forest found in the southeastern highlands may not be totally natural, as they could have been planted in groups and protected from fire. Outside of major villages, native populations tended to be nomadic, typically moving every four years or so after exhausting the local land (Miller, 2000; Pádua, 2004). As a result, much of the landscape was comprised of secondary forest when the Europeans arrived. After European arrival, it is thought that up to 90% of the indigenous population died in the first hundred years of contact, which permitted some recovery of the forest during the early colonial period (Dean, 1995; Pádua, 2004).

The SBNP region was occupied by European settlers beginning in the middle of the 16th century, when small settlements were established along major indigenous pathways that crossed the forest. From these settlements, towns arose by the middle of the 17th century. Among these transportation routes, the “Caminho Novo da Piedade” was opened between 1725 to 1778 AD (André Bazzela, per. comm.). Today this route is highway SP-068, and connects the SBNP to the series of small towns and cities located along the inland escarpment of the Serra da Bocaina. Along the route, land was distributed to workers, who carried out subsistence agriculture and built extensions from the main road, further intensifying conflict with the native peoples (Antonio Filho, 2011).

During the coffee economic cycle (1800-1930 AD) several farmhouses were built on the Bocaina Plateau, among them the “Stone House” beside the study site, built in 1910 (Antonio Filho, 2011; IBAMA, 2002). The areas originally used for agriculture were burned and converted to coffee plantations (Almeida and Nötzold, 2008); after the decrease of coffee production in the region, most plantations were abandoned and converted to livestock pastures (IBAMA, 2002). Today, slash and burn is still a common practice to promote the renewal of pasture and agricultural areas. Soils on the Bocaina Plateau are not highly fertile, and this practice tends to result in exhausted lands dominated by weeds after 2-3 years (Pádua, 2004) and a perpetuation of the expansion of secondary vegetation.

3 Material and Methods

3.1 Sediment core and dating

In 2015, a 228 cm-long core was collected in an undisturbed swampy area in the SBNP using a Russian Corer. The core is called Serra da Bocaina Fazenda da Entrada (SBE). The stratigraphic description of the core was done using the Troels-Smith lithological symbols (Troels-Smith, 1955) and Munsell Colours System and the diagram was constructed in Psimpoll (Bennet, 1992).

Three samples were collected along the core for radiocarbon dating. Two samples (wood material) were sent to the AMS Laboratory at National Taiwan University (NTUAMS) and one sample (bulk) to the AMS Poznan Radiocarbon Laboratory (LAMS) (Table 1). A possible carbon reservoir effect can be excluded, as the test by HCl was negative. The age-depth model was performed with R script Clam version 2.2 (Blaauw, 2010) in R Studio (R Core Team, 2016) using the South Hemisphere calibration curve SHCal13.14C and postbomb curve SH 1-2.

Table 1: AMS radiocarbon dates from SBE core, calibrated age ranges at 95% confidence intervals.

Lab-code	Depth (cm)	Material dated	Date (^{14}C age BP)	Calendar Age (cal yr BP)	Median probability (cal yr BP)
Poz-89783	38	bulk sediment	130±30	-1 – 145 (77.5%) 222 – 260 (17.5%)	91
NTUAMS-2308	69	wood	355±8	360 – 446 (82.5%) 319 – 334 (12.3%)	393
NTUAMS-2017	204	wood	607±2	541 – 559 (93.3%) 619 – 621 (1.4%)	550

3.2 *Palynological analysis*

A total of 39 samples of 0.5 cm^3 were taken along the core. Considering the sedimentation rate and lithological characteristics, in the lower core part (228–76 cm) samples were taken at 8 cm intervals and in the upper part (76-0 cm) in 4 cm intervals. Standard pollen preparation techniques were used to prepare the samples applying 40% hydrofluoric acid (HF) and acetolysis (Faegri and Iversen, 1989). One tablet with exotic *Lycopodium clavatum* spores as marker was added to each subsample prior to pollen extraction for the calculation of pollen concentration (grains/cm^3) and accumulation rate (grains/cm^2/yr) (Stockmarr, 1971). Slides were prepared with glycerol jelly for pollen taxa identification and counting under a light microscope up to a minimum of 300 pollen grains per sample. Identification is based on the reference collection of pollen and spores of the Department of Palynology and Climate Dynamics of University of Goettingen and literature (Behling, 1993, Melhem et al., 2003, Neotropical Fossil Pollen Search Tool developed by Dr. Hermann Behling and Dr. Chengyu Weng (unpublished)). Nomenclature follows the Flora do Brasil, 2018 (http://floradobrasil.jbjr.gov.br).

The pollen taxa exhibit in the diagram were classified in six ecological groups according to the habit and ecology of the taxa: Aquatics, campos de altitude (CDA), *Araucaria* forest (*A*F), Atlantic Forest (ARF) (Montane and Upper Montane), others (species that occur in all ecosystems) and ferns (ferns and tree ferns). Indeterminate, unknown, mosses and other Pteridophyta are excluded from the diagram as they were present at low percentages. The separation of the groups follows Behling et al. (2007) and modern vegetation surveys in southeastern Brazil (Freitas, 2010; Meireles et al., 2014; Ribeiro et al., 2013; Spolidoro, 2001). The pollen sum did not include aquatic pollen taxa and spores. The pollen percentage diagram and summary diagram were developed with C2 (Juggins, 2007). Pollen assemblage zones were determined using stratigraphic constrained cluster analysis of the taxa forming the pollen sum by CONISS (Grimm, 1987).

A Principal Component Analysis (PCA) was performed with R Core Team (2015) using the package Vegan (Oksanen et al., 2017) to analyse the relationship among vegetation community composition. The PCA was carried out with pollen taxa with a relative abundance greater than 2% to maximize the signal to noise ratio. Data were centred and square root transformed prior to the ordination to minimize the effect of over-represented taxa in the record due to the difference in pollen productivity and dispersal rate among taxa (Prentice, 1980).

3.3 Macro-charcoal analysis

For analysing the past fire regime and its influence on vegetation, 1 cm^3 subsamples were extracted from the core at 1-cm resolution from 0-69 cm and 4-cm resolution from 69-228 cm. Lower sampling resolution was employed from 69 cm to the bottom of the core due to the higher sedimentation rate. Each sample was prepared following the method of Stevenson and Haberle (2005) adapted from Rhodes (1998). Weak hydrogen peroxide (6% H_2O_2) was added to remove organic material in the sediment. Samples were gently wet-sieved. All macro-charcoal particles >150 μm were counted under a binocular dissecting microscope. Concentrations were determined as particles/cm^3. The software CharAnalysis (Higuera, 2009) was applied to reconstruct the past fire regime characteristics. The charcoal raw data were interpolated according to the median temporal resolution (5 years) and converted into charcoal accumulation rates (CHAR particles/cm^2/yr). To separate background ($C_{background}$) and peak components (C_{peaks}), a 200-year window weighted regression robust to outliers was defined (Higuera et al., 2010). A Gaussian mixture model was used to identify the noise distribution (C_{noise}). Peaks greater than the 99th percentile threshold were identified as fire peaks. The

Poisson minimum-count criterion was also used to eliminate the peaks from statistically insignificant counts. “Fire episode” frequencies over time were calculated based on the frequency of fire peaks per 200 years. Peak magnitude as an estimation of total charcoal deposition per fire event was used to reflect fuel consumption per fire and/or fire size (Biagioni et al., 2015; Higuera et al., 2010)

4 Results

4.1 Stratigraphy and chronology

The 228 cm-long sedimentological sequence shows 12 distinct deposits and can be grouped in three major sections. The largest part of the core, from 228 to 76 cm consists of clayish-sandy material, mainly olive brownish in colour with poor pollen preservation. Within this section, at 205-200 cm, there is a layer of wood fragments with clay. The following section from 76 to 46 cm consists of brown clay/silt. An important change in the sediment occurs from 53 to 46 cm, within an interval from 50 to 47 cm in which siltier material is incorporated. The boundary with the uppermost section consists of a yellowish brown fine clay material. From 46 cm to the core top the sediment is comprised of brown organic somewhat clayey material, with the presence of roots, rootlets and plant remains. A complete detailed description of the stratigraphy can be found in the supplementary material.

The three Accelerator Mass Spectrometry (AMS) radiocarbon dates show that the SBE core reflects continuous sedimentation (Fig. 2). The smoothing spline age-depth model which provides better results for the data, indicates the core spans the last 600 cal yr BP (Fig. 2). The sedimentation rate decreases from the bottom to the top of the core (0.81-0.18 cm/yr). The lower section (228-70 cm) has a mean of 0.58 cm/yr, the middle section (69-38 cm) 0.22 cm/yr, whilst the uppermost section (37-0 cm) the rate is 0.19 cm/yr.

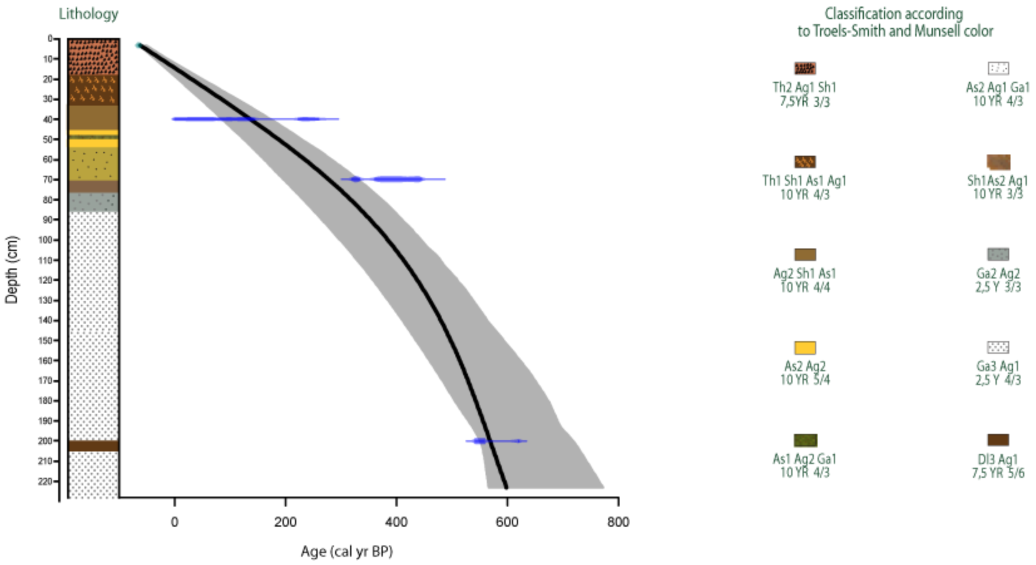

Fig. 2: Stratigraphy, characteristics of the sediment according to Troels-Smith (1955) and Munsell colour.

4.2 Palynological results

A total of 85 pollen and 36 spore taxa were identified in the 39 samples. The pollen diagram (Fig. 3) shows the dominant and most important taxa. The complete list of taxonomic groups can be found in the supplementary material.

The cluster analysis by CONISS resulted in four palynological zones: SBE-I, SBE-II, SBE-III and SBE-IV. The PCA ordination demonstrates that PC1 explains 36% of the variance and PC2 17%, after standardization of pollen data (Fig. 4). *Podocarpus* shows a strong correlation to PC1, whereas Poaceae is correlated with PC1 and PC2, although closer to PC1. Several taxa load more strongly on PC2, such as Moraceae/Urticaceae, *Mimosa scabrella*, Amaranthaceae and Mimosaceae. *Araucaria*, *Myrsine*, *Ilex* and Melastomataceae are placed very close to the origin, and their variance is not well explained by the first two PCA axes. The ordination separates four zones in accordance with the pollen diagram. Grass, herbs and some *AF* taxa are closely related to zone SBE-I. Following this zone, SBE-II is dominated by *Podocarpus*, with some connection to other *AF* taxa. In SBE-III, the dominance of *AF* taxa continues within species that represent both *AF* and Upper Montane ARF, and in SBE-IV Moraceae/Urticaceae is highlighted.

Pollen concentration varies from ca. 19,000 to 320,000 grains/cm$_3$ along the sediment core. Average values are 86,000 in zone SBE-I, 260,000 in SBE-II, 178,000 in SBE-III and 160,000 grains/cm$_3$ in zone SBE-IV (Fig. 3,5). Influx values range from 8,000 to 160,000 per cm$_2$/yr. Average values are 56,000 in zone SBE-I, 670,000 in SBE-II, 37,000 in SBE-III and 30,000 per cm$_2$/yr in zone SBE-IV (Fig. 3,5). In the next section we describe each of the zones (all pollen percentages are averages).

4.2.1 SBE-I (228-88 cm; 600-350 cal yr BP; 1350-1600 AD) - 18 samples:

The pollen assemblages are characterized by the highest values of CDA pollen in the core (44%, ranging from 35% to 55%), primarily represented by Poaceae (32%) and Asteraceae (9%). Pollen of Forest (48%, ranging from 35% to 60%) is slightly more abundant than CDA. *A*F (27%) is represented mainly by *Podocarpus* (10%) and *Weinmannia* (11%) while the ARF (8%) is represented mainly by Moraceae/Urticaceae (5%) and *Alchornea* (1.4%). *Araucaria angustifolia* pollen grains are found only in two samples. Other taxa (13%) are represented by Melastomataceae (6%) and Myrtaceae (5%). Cyperaceae shows the lowest values in this zone (<5%). Tree fern spores present their highest values in the core (3%), represented mainly by *Cyathea* (psilate form), as do fern spores (12%).

4.2.2 SBE-II (88-62 cm; 415-330 cal yr BP; 1540-1615 AD) - 5 samples:

In this zone both Poaceae (16%) and Asteraceae (4%) are at core minima, contributing to the low value of CDA pollen (24%). The pollen assemblages are dominated by forest pollen (>70%), with the increase almost completely driven by an enormous increase in *Podocarpus* (38%). As a consequence, *A*F represents up to 52% of the pollen assemblages even with the decrease of *Weinmannia* (6%). *Symplocos tenuifolia* type (2%) and *Myrsine* (2%) are also important *Araucaria* forest taxa. Single grains of *A. angustifolia* occur in two samples. ARF (8%) is characterized by Moraceae/Urticaceae (4%) and *Alchornea* (3%). The group of Others (11%) is mostly composed by pollen of Melastomataceae (5%) and Myrtaceae (5%). Cyperaceae shows a slight increase (6%) as do tree fern spores (2%).

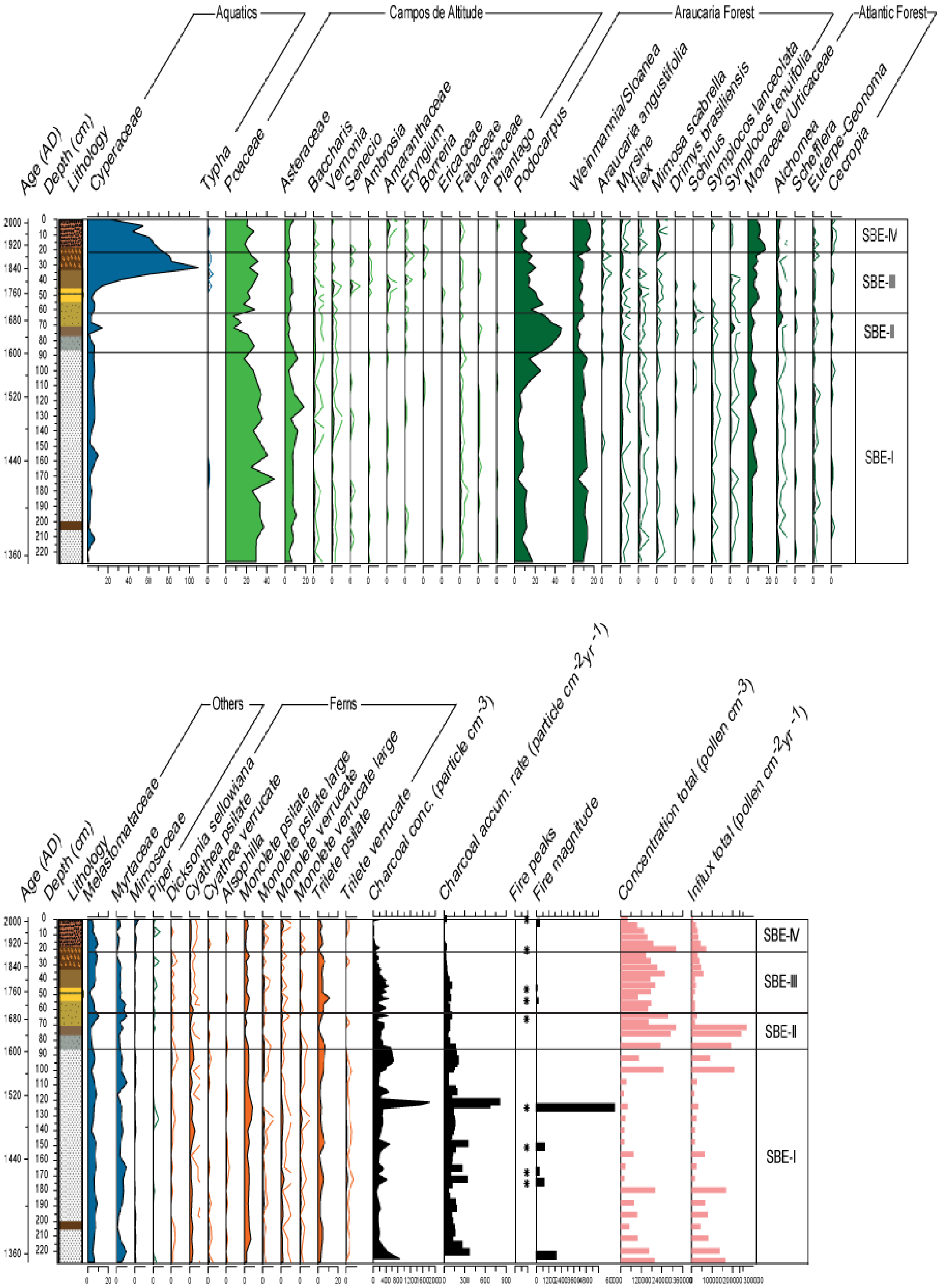

Fig. 3: Pollen percentage and charcoal diagram of SBE. A 5x exaggeration scale line is shown for low percentage values.

4.2.3 SBE-III (62-22 cm; 330-35 cal yr BP; 1615-1920 AD) - 10 samples:

Values of CDA pollen (36%), characterized largely by Poaceae (26%) and Asteraceae (6%), are higher than *A*F (32%), although Forest taxa still represent the main portion of the pollen assemblage (55%). Decrease in the *A*F assemblages is primarily due to the reduction of *Podocarpus* pollen (18%), though other *A*F taxa also decline such as *S. tenuifolia* type (0.6%) and *S. lanceolata* type (0.1%). Despite the low values of *A*F pollen, *A. angustifolia* shows the highest value in this zone (0.7%), as well as *Myrsine* (2%). The ARF assemblage increases continuously (11%), marked by Moraceae/Urticaceae (7%) and *Alchornea* (3%). Melastomataceae (6%) and Myrtaceae (4%) are the most abundant taxa in the group of Others (13%). There is a marked increase of Cyperaceae pollen (40%) after 1800 AD. Fern spores increase (10%), while there is a slight decrease of tree fern spores (1.7%).

4.2.4 SBE-IV (22-0 cm; 35 - -65 cal yr BP; 1920-2015 AD) - 6 samples:

CDA pollen (31%) decreases slightly in this zone mainly as a result of lower Poaceae (22%) and Asteraceae (5%) values. Forest taxa represent the main pollen group (57%). *A*F pollen maintains almost the same abundance as in the previous zone (30%). *Mimosa scabrella* (3%) and *Weinmannia* (15%), have the highest values, while *Podocarpus* decreases (9%). *A. angustifolia* also decreases and occurs only in three samples. ARF reaches its maximum value (17%) as Moraceae/Urticaceae achieves its highest average (12%) and pollen of the pioneer taxon *Cecropia* is more frequent (0.6%). The group of Others (11%) decreases slightly, characterized by Melastomataceae (6%), Myrtaceae (2%) and Mimosaceae pollen (1%). Cyperaceae pollen achieves maximum values (53%). There is a minor decrease of tree fern spores (1.5%) and a marked decrease of Ferns (7%).

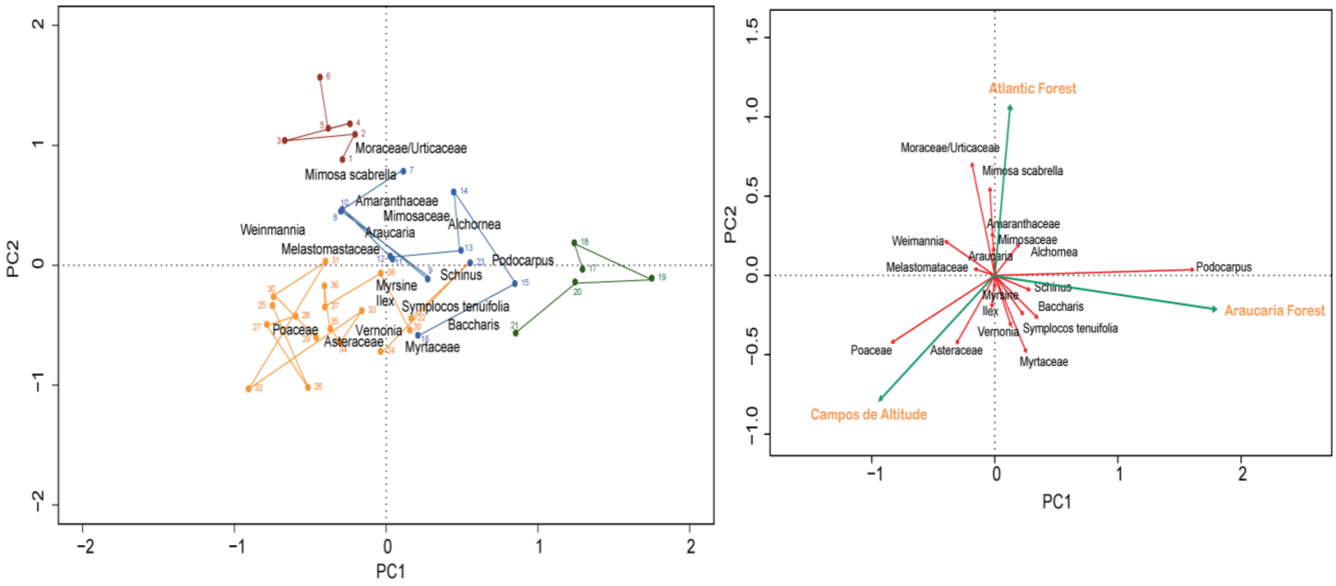

Fig 4: Principal Components Analysis of the 18 most abundant species present at SBE.

4.3 Macro-charcoal and fire regime

The CharAnalysis of macro-charcoal shows an average concentration of 270 particles/cm$_3$ for the entire record, decreasing from zone SBE-I to SBE-IV (averages 370, 325, 260 and 50 particles/cm$_3$) (Fig. 3,5). Simultaneously, average charcoal accumulation rates also decrease from SBE-I to SBE-IV (Fig. 3,5). The local signal-to-noise is 5.1351, indicating a good separation between peak and non-peak values. The mean fire return interval (FRI, 95% probability) was 74 yr (38-114 yr). One fire episode failed to pass the Poisson minimum-count criteria (at 221 cm). Two of the three fire episodes occurred when the CDA summed pollen percentage was ≥40% and/or the forest sum pollen percentage was ≤50%. The highest concentration of particles is found at 121 cm of zone SBE-I (440 cal yr BP, 1510 AD); in this zone the highest magnitude fire peaks (> 100 particles per peak) are all found (Fig. 3,5). Zone SBE-I also supported the shortest mean FRI: including the fire episode at 221 cm, the mean FRI was about 40 years. Since 1720 the mean FRI has been about 71 years. The most recent peak fire event was detected at the uppermost 1 cm (2015-2007 AD).

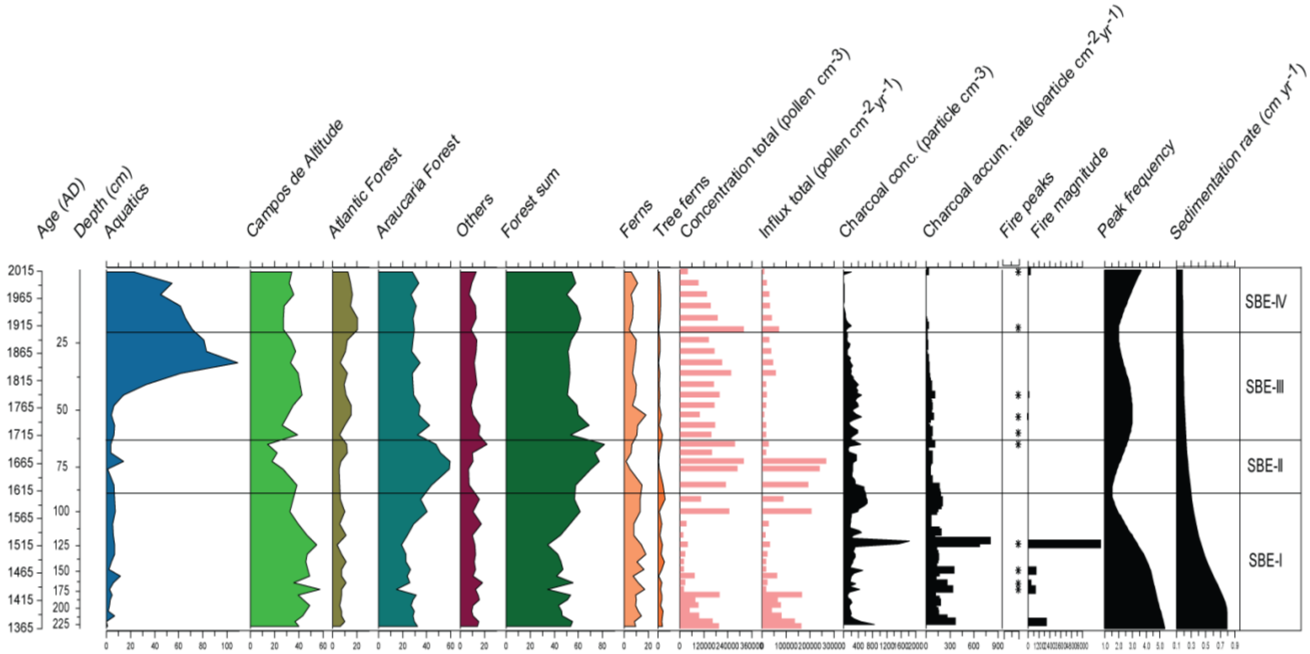

Fig. 5: Summary diagram of types of vegetation and macro-charcoal by age (AD).

5 Interpretation and Discussion

5.1 Late Holocene vegetation dynamics

The results from the studied environmental archive span the period from 1350 AD (150 years before the European arrival in Brazil) to 2015 AD. This record provides an opportunity to analyse human effects on vegetation composition and the differences between pre- and post-Columbian anthropogenic impacts and possible climatic influences.

Speleothem studies from Cristal Cave and Botuverá Cave, located 450 km and 700 km south from the study area respectively, show an increase in precipitation from the Early to Late Holocene in southern and southeastern Brazil (Bernal et al., 2016; Vuille et al., 2012). According to Vuille et al. (2012) the wettest period at Cristal Cave was between ~1600 to ~1820 AD. The sand and silty sediment from the bottom of the core until 76 cm (1350 to 1640 AD) suggests that colluvial and/or alluvial deposits formed this section of the soil. The shift to a more organic soil at 45 cm (1775 AD) may indicate a higher water table, which could be related to increasing precipitation as registered by Vuille et al. (2012), and/or to changes in local hydrology.

The general expansion of forest recorded in our core, as indicated by higher proportions of forest pollen like *Podocarpus, Weinmannia, Ilex, Myrsine,* and Melastomataceae relative to grassland vegetation, implies a trend toward wetter climate during the Late Holocene (Fig. 5). The increase in Atlantic Forest around 1900 AD (especially in Moraceae/Urticaceae and *Alchornea*) suggests the onset of warmer conditions in the last century coinciding with the Current Warm Period (CWP) (Vuille et al., 2012). The general rarity of *Araucaria angustifolia* in the core is also suggestive of warmer conditions characteristic of the Late Holocene. As background however, it is important to note that data from Behling et al. (2007) show that *Araucaria* has not been an abundant member of the high elevation forests in the Serra da Bocaina since at least 18,570 cal yr BP (beginning of the record). This is likely due to the lower and warmer environment in this tropical-marginal mountain site compared to much larger *Araucaria* populations in the higher and colder Serra da Mantiquiera and sites to the south.

After about 1520 AD and continuing to about 1670 AD, there is a marked and rapid increase in *Podocarpus* pollen, rising from near 10% to over 40%, followed by a similarly marked decrease to about 1720 AD. The coincidence of the first date with the period of European arrival in Brazil and rapid destruction of the Amerindian cultures and populations (Pádua, 2004), and the second date with the European settlement of the Paraíba do Sul Valley and the introduction of farming and livestock, suggest that forest expansion into grassland during this period may have been a result of a reduction in human activities. *P. lambertii* is a species of late secondary and climax forest, and typically found in dense, highly shaded and moist stands; it is rarely present in highly disturbed forest stands (Carvalho, 2004; Longhi et al., 2010). The lack of a positive response in fern pollen or ARF pollen during this time period argues against an increase in precipitation, further supporting the anthropogenic hypothesis. We interpret the reduction in Poaceae from 1600-1700 AD as a response to the expansion of forest. The expansion of forest after the arrival of the European settlers and the presence of more fire peaks and higher fire magnitude before 1520 AD further support the idea that pre-Columbian populations had important influence on the vegetation at the study site. Albeit lightning-ignited fires certainly occur in the Brazilian highlands (charcoal is found throughout pollen cores from campos habitat from well before Amerindian settlement of the region, e.g. Behling, 1996; Behling et al., 2007), it seems likely that the pre-1500 extent of highland grassland-type vegetation at this relatively low site was influenced to some extent by human cutting and burning.

After 1680 AD, fire peaks begin to appear again, likely marking a new cycle of human influence on the local vegetation. Given the timing, we interpret the (slight) increase of grassland at this time as a result of renewed forest clearing and the introduction of cattle to the region. The sediment deposits also indicate a strong change (47-53 cm) overlapping the period when the Caminho Novo da Piedade was built between 1725-1778 AD. During this period, several minor roads/paths linking farms were established on the Bocaina Plateau, one of which passed close to the study site (it is still extant). We believe the construction of this path probably influenced the local water table and/or stream hydrology. The increase in Cyperaceae pollen after 1780 AD is due to a local rise in soil moisture and probably related to this change in hydrology, as is the increase in organic matter and plant remains in the core above 46 cm.

The increase in *Podocarpus* reversed by the late 18th century, and pollen percentages returned to a plateau (albeit a higher one than before 1520 AD). CDA pollen rebounded in return, but to a level fluctuating between 30% and 40%, rather than 40-50% as before 1520 AD. As noted above, the nature of the local depositional environment also rapidly changed at this time. Although local fires at the SBE site have not been very frequent in the last seven centuries (FRI = 74 yr, ranging from 38-114 yr), until the 20th century charcoal was constantly deposited at the site and background charcoal was present throughout the core, indicating that biomass was burning regionally. The near absence of charcoal from about 1910 AD (1887-1936 AD) to present, with only one peak fire event at 1 cm (2015-2007 AD) (Fig. 5), suggests that the 20th century expansion of forest in the study area may have to do both with increasing precipitation and a reduction in forest disturbance. There are late 20th century increases in a number of taxa indicative of early forest succession (e.g., both *Mimosa* pollen groups, *Cecropia*, Melastomataceae), providing further indication of a changed campos-forest dynamic.

5.2 The future of the campos-forest mosaic

The campos de altitude and similar mountain grasslands are highly species diverse and support many endemic and unique taxa (Rambo, 1953; Martinelli and Bandeira, 1989; Overbeck et al., 2006; Safford, 1999, 2007). It is clear from the paleoecological data that campos de altitude covered extensive areas of the southeastern Brazilian mountains during the LGM, and that cooling was sufficient to permit biogeographic connections with cold, temperate grassland habitats far to the south and southeast (Rambo, 1953; Behling, 1996; Behling et al., 2007; Safford, 2007; Behling and Safford, 2010). Today, after thousands of years of gradual warming and increasing precipitation, forest has "recovered" much of this area. Species diversity at the landscape scale is maximized by habitat heterogeneity – in this case, a forest-grassland "mosaic" (Overbeck et al., 2006; Bond and Parr, 2010) – and in the face of continued forest expansion, the maintenance of a forest-grassland balance is an important conservation goal in much of southern and southeastern Brazil (Behling and Pillar, 2007; Overbeck et al., 2015).

The balance between grasslands and forests in humid, tropical and subtropical environments is dependent on local or regional conditions that negatively influence the growth and/or competitive ability of woody plants. Such circumstances can include soil conditions (e.g. saturated soils or very thin or very nutrient-poor soils), cold and/or frost, and disturbance (Eiten, 1972; Smith, 1975; Van Langevelde et al., 2003). The campos de altitude sustains a flora dominated by species adapted to cold and to periodic fire (Safford, 1999, 2001). Fire occurred in the campos de altitude long before human settlement of Brazil (Behling, 1996; Behling et al., 2007; Veríssimo et al., 2012), but it is also clear that anthropogenic disturbances – livestock grazing and logging as well as fire (Pillar and Quadros, 1997; Oliveira and Pillar, 2004) – have played a role in driving grassland-forest relationships in the southern and southeastern Brazilian highlands. Various studies have documented or postulated human agency in Late Holocene vegetation dynamics in the southern and southeast Brazilian mountains (e.g. Behling, 1996; Behling and Pillar, 2007; Bitencourt and Krauspenhar, 2006; Dean, 1995; Hueck, 1966; Robinson et al., 2018; Veríssimo et al., 2012; this study). The broad expanse of campos de altitude during glacial periods was largely driven by much colder and somewhat drier climates, with help from periodic lightning-ignited fire. Today, the extent of campos de altitude is much reduced, but its current area is certainly larger than climate alone would dictate, especially in warmer, lower elevation sites like the Serra da Bocaina. Safford (2001) noted that frequent burning in what was originally upper montane forest leads to the presence of ruderal C_4 grasses like *Andropogon*, *Aristida*, *Axonopus*, and *Paspalum* in lower elevation campos de altitude. Members of these genera are widespread in the Serra da Bocaina.

Annual mean temperatures in southeastern South America have risen about 1 ºC over the last century, and projections suggest further increases of 2-3 ºC by 2050 AD and 3-5 ºC by 2080 AD, with greater seasonality in precipitation (which could lead to more dry season fire) and greater potential for heavy precipitation in the wet season (Marengo, 2009; Marengo et al., 2012; Nuñez et al., 2009). Blanco et al. (2014) used a Dynamic Global Vegetation Model (DGVM) to predict a slight increase in the rate of forest expansion for the next decades, based on relative advantages for C_3 trees compared to C_4 grasses. Similarly, Behling and Safford (2010) suggested that future global warming was likely to intensify the upward movement of the Atlantic Forest at the expense of open ecosystems like the campos de altitude. Based on what we know about forest-grassland relationships in southeastern Brazil and what we know about current and projected climate trends, only two future scenarios seem reasonably plausible: eventual forest dominance in the absence of management, or forest-grassland coexistence in the presence of management (Blanco et al., 2014). Ensuring coexistence will require active management based on reference conditions and what we have learned about forest-grassland dynamics from both paleo- and modern ecological studies (Behling and Pillar, 2007).

Therefore, maintenance of much if not most campos de altitude habitat into the future will require (1) a change in conservation focus from forest to non-forest habitats, which runs counter to current policy emphasis in Brazil (Overbeck et al., 2015) and (2) serious consideration of active disturbance *management*, rather than disturbance *avoidance*, which is the current Brazilian National Park policy. In the SNBP and other conservation units protecting campos de altitude, we recommend the following steps (among others) be taken:

1. Carry out further studies to better elucidate the relative roles of anthropogenic and “natural” factors in driving the extent of campos de altitude and their relationship to neighbouring forested ecosystems. These include studies of both current and past conditions, and can range from high-resolution paleoecological studies, to comparisons of aerial photo-based time series, to empirical field studies (see next).
2. Carry out field research to better understand the effects of fire and grazing on successional processes, the forest-grassland balance, and key sensitive species in both grassland and forest habitats. Such research may be observational and

opportunistic, but we especially recommend research and monitoring tied to the planned use of fire and grazing in controlled, experimental fashion, and the installation of areas that are protected from grazing (fenced exclosures), fire, and both grazing and fire. Experimental prescribed fire in campos de altitude has been recently implemented in Itatiaia National Park and we hope that this sort of "learning from managing" is soon extended to other conservation units.

3. Deploy remote data loggers to measure temperature and relative humidity patterns across the forest-grassland mosaic. After two to three years of data collection, use these data in combination with digital elevation models to map potential climate refugia for cold-adapted taxa. Such work is already underway in the Serra dos Órgãos National Park.
4. Develop a conservation assessment and conservation strategy for campos de altitude in southeastern Brazil. The conservation assessment would summarize information about the campos de altitude and key species and ecological processes across multiple spatial and temporal scales, with a focus on current and potential future threats. The assessment would serve as the foundation for a conservation strategy, which would provide science-based guidance for reducing threats to the campos de altitude and improving campos de altitude habitat quality and resilience.

Although Brazilian law directs that ecosystems protected by the national system of conservation units (SNUC) be managed "free of alterations caused by human interference" (Federal Law 9.985/2000), the same law also directs that management in the SNUC (1) contribute to the preservation and restoration of the diversity of natural ecosystems, and (2) recuperate or restore degraded ecosystems. Most Brazilian national parks are managed under the aegis of a management plan. In the case of SBNP, the use of fire is prohibited under any circumstances and livestock is considered an "interference" (IBAMA, 2002). At the same time, the main goal of the SBNP management plan is the protection of "natural vegetation", with a particular focus on ecosystems above 1500 m elevation (IBAMA, 2002), i.e. the campos de altitude-forest mosaic.

Major changes are underway in Brazilian national fire management policy, and the New Forest Code (Federal Law 12.651/2012) permits fire use in vegetation in the following cases:

1. Areas where local or regional peculiarities justify use of fire in agropastoral or forest settings (requires previous approval by applicable environmental agency)
2. Use of controlled fire in conservation units, conforming to a management plan and previously approved by conservation unit management agency
3. Scientific research activities carried out by recognized research institution and previously approved by applicable environmental agency

In addition, the New Forest Code also mandates (Article 40) that the Brazilian Federal government should establish a National Policy for Fire Management, Prevention, and Combat, including, among other things, fire management policy for protected natural areas. At this point in time, a draft policy document that effects a change from total fire suppression to a more nuanced, science-based approach of fire management has been written by IBAMA and partner agencies and is under consideration by the Brazilian Congress. Overall, it appears that there is already sufficient legal flexibility to experiment with fire in campos de altitude management, and such flexibility is likely to increase.

6 Summary and Conclusion

We carried out a high-resolution paleoecological study of an almost 700-year core (1350-2015 AD) from the mosaic of *Araucaria* forest and campos de altitude in the Serra da Bocaina National Park, southeastern Brazil. We sought principally to elucidate interactions between the vegetation, climate and human activities before, during, and after arrival of Europeans in Brazil in the early 16th century. Our results demonstrate important changes in these interactions across this period of major cultural change. Amerindians had important impacts on the mountain vegetation, maintaining a more open habitat probably through slash and burn agriculture. After European arrival, the rapid depopulation of the study region plus increasing precipitation led to a strong rebound in forest cover, indicated principally by a four-fold increase in the pollen contribution of *Podocarpus*. After 1750, the establishment of permanent Portuguese communities and farming in the study area let to a renewed expansion of grassland, driven by land clearing, grazing, and anthropogenic fire.

Our results highlight the interworkings of regional climate change and local human agency in “designing” the Late Holocene forest-grassland mosaic in the Serra da Bocaina. Such forest-grassland mosaics are important contributors to landscape heterogeneity and biodiversity in southern and southeastern Brazil. Given projections of continued warming into the future and the strong momentum such warming will lend to forest expansion, we recommend that Brazilian ecosystem managers consider transitioning from the current emphasis on passive management to a more active and experimental management agenda. We believe such an agenda is much more likely to answer the critical questions we have about how these important ecosystems might be sustained through the coming climate crisis.

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9 Supplementary Material of Chapter 4

Stratigraphy of the SBE core. Classification by Troels-Smith (1955) and Munsell Colour.

Depth (cm)	Classification	Description
0-18	Th2Ag1Sh1 7,5YR 3/3	Dark brown peat with great amount of roots and rootlets, some plant remains, decomposed organic material and somewhat fine clay.
18-33	Th1Sh1As1Ag1 10YR 4/3	Brown decomposed organic material with some roots and rootlets, plant remains, clay and silt.
33-46	Ag2Sh1As1 10YR 4/4	Dark yellowish brown organic material strongly decomposed with silt and some clay.
46-47/ 50-53	As2Ag2 10YR 5/4	Yellowish brown fine clay and silt material.
47-50	As1Ag2Ga1 10YR 4/3	Brown silt material, somewhat fine clay and sandy.
53-71	As2Ag1Ga1 10YR 4/3	Brown clay material, with some fine clay and fine sand (wood fragment within this layer).
71-76	Sh1As2Ag1 10YR 3/3	Dark brown organic material strongly decomposed, mixed with fine clay and somewhat silty.
76-86	Ga2Ag2 2,5Y 3/3	Dark olive brown material composed of sand and clay in equal parts.
86-200/ 205-228	Ga3Ag1 2,5Y 4/3	Olive brown sand material somewhat clayey.
200-205	Dl3Ag1 7,5YR 5/6	Dark brown wood fragment.

List of taxa found in the SBE core. All taxa shown in the pollen diagram of Fig. 3 are in bold.

AQUATICS	***Podocarpus***	*Solanum* type
Cyperaceae	*Roupala* type	*Trema* type
Hydrocotyle type	***Schinus* type**	
Typha dominguensis	Solanaceae	FERNS
	Struthanthus	*Anemia phyllitidis*
CAMPOS DE ALTITUDE	***Symplocos lanceolata* type**	*Hymenophyllum*
Amaranthaceae	***Symplocos tenuifolia* type**	Monolete echinate
Amaryllidaceae	***Weinmannia* type**	**Monolete psilate**
***Ambrosia* type**	*Xylosma* type	**Monolete psilate large**
Apiaceae	*Zanthoxylum* type	Monolete reticulate
Asteraceae		Monolete scabrate
***Baccharis* type**	ATLANTIC FOREST	Monolete scabrate large
***Borreria* type**	*Acalypha* type	**Monolete verrucate**
Brassicaceae	***Alchornea***	**Monolete verrucate large**
Convolvulaceae	***Cecropia***	*Osmunda*
Cuphia type	*Clusia*	*Pityrogramma*
Dalechampia	*Chrysophyllum marginatum*	Pteridophyta type 6
Epidendrum	*Croton* type	*Pteris* type
Ericaceae	***Euterpe-Geonoma* type**	*Schizaea*
Eriocaulon type	*Hedyosmum*	**Trilete psilate**
***Eryngium* type**	Menispermaceae	Trilete psilate large
Fabaceae	**Moraceae/Urticaceae**	Trilete scabrate
Jungia type	*Oreopanax* type	Trilete scabrate large
Iridaceae	*Psychotria* type	**Trilete verrucate**
Lamiaceae	***Piper***	
Liliaceae	***Schefflera***	TREE FERNS
Moritzia dasiantha		***Alsophila***
Onagraceae type 1	OTHERS	***Cyathea* psilate**
***Plantago australis* type**	Anacardiaceae	*Cyathea schanschin*
Poaceae	Araceae	***Cyathea* verrucate**
***Senecio* type**	Bromeliaceae	***Dicksonia sellowiana***
Spermacoce	*Celtis*	*Lophosoria*
***Vernonia* type**	*Esenbeckia*	*Nephalea*
Xyris	Euphorbiaceae	
	Flacourtiaceae type	MOSS
ARAUCARIA FOREST	*Laplacea* type	*Phaeroceros laevis*
Allophylus edulis type	Malphigiaceae	*Sphagnum*
Araucaria angustifolia	**Melastomataceae**	
Clethra type	Meliaceae	PTERIDOPHYTA
Drimys brasiliensis	*Meliosma* type	Isöetes
Ilex	**Mimosaceae**	*Lycopodium alopecuroides*
Luhea type	**Myrtaceae**	*Lycopodium clavatum*
Matayba	*Pera* type	*Lycopodium* foveolate type
***Mimosa scabrella* type**	Rubiaceae	*Selaginella excurrens*
Myrsine	Rutaceae	
Ocotea	Sapindaceae	

CHAPTER 5

Synthesis

This chapter synthesizes the main outcomes of the research carried out in the Atlantic forest on the Brazilian coastal highlands in southeastern Brazil. The integrated analyses of the three studies provide important information for a more comprehensive view on large-scale vegetation changes resulted of either human actions or climate changes. According to the main findings of the research, this section is divided into the present vegetation of campos de altitude and forest distribution, the climate drivers among the Holocene and the human disturbances observed in the records.

1 Present Distribution of Vegetation

The chapter 2 explores the representation of each vegetation type into the pollen assemblage, aiming to identify the patterns of plants distribution and pollen deposition in order to improve interpretation of past vegetation and environmental data (e.g. Markgraf et al., 2002; Tonello et al., 2009; Niemann et al., 2010; Bartlein et al., 2011; Schäbitz et al., 2013; Schüler et al., 2014; Mauri et al., 2015; Rodrigues et al., 2016; Peyron et al., 2017; Zanon et al., 2018).

The results of the pollen traps indicated that the assemblages in campos de altitude and in forest vegetation are compounded in different ways. In campos de altitude, the pollen assemblage of each trap represents a wider area than in the traps installed in the forest. Excluding Poaceae, the majority of the species occurring in campos de altitude is insect pollinated and presents low accumulation rate. In addition, it seems that wind direction is predominantly upwards, resulting in an upslope transport of pollen from lowland. Therefore, there is an overlap of distribution ranges between open and close vegetation in the campos de altitude assemblage. Meanwhile mostly of the vegetation surrounding the campos traps is campos de altitude, its assemblage is composed of taxa from its vegetation mixed with taxa from forest. Its assemblage is predominantly composed by Poaceae, which is the main characteristic family of campos de altitude (Rodrigues et al., 2016; Montade et al., 2019), *Baccharis* (which is a faithful campos indicator under warmer temperatures) and Asteraceae, another emblematic family of campos de altitude, as well as by the widely pollen producers from upper montane forest and lowland forests. Specially *Weinmannia* and *Myrsine* from upper montane forest together with Moraceae/Urticaceae, *Cecropia* and *Celtis* from lower montane forest are abundant in the campos de altitude assemblage.

On the other hand, albeit the pollen traps located in upper montane vegetation are surrounded by significant percentage of campos de altitude vegetation, they mainly show quite higher percentage of arboreal pollen, indicating a more local assemblage under closed canopy. Typically, *Weinmannia*, *Myrsine*, Melastomataceae, *Clethra*, *Symplocos*, *Drimys*, *Croton*, Myrtaceae and *Ilex* compound the upper montane forest assemblage. Nevertheless, still the pioneers and anemophilous taxa from lowland forest Moraceae/Urticaceae, *Celtis, Trema, Cecropia, Alchornea* have a strong influence in its assemblage as registered by Niemann et al. (2010) and Montade et al. (2016). In addition, probably due to the high air humidity, a high percentage of pteridophyta is observed. The pollen assemblage in montane vegetation is barely influenced by campos de altitude pollen taxa with completely dominance of arboreal taxa whereas campos de altitude vegetation appears in the circumferences of the pollen trap.

Aiming to better distinguish between forest habitats and campos, a suite of taxa typical of upper montane forest was proposed for tracking local fluctuations. Using this group composed of *Weinmannia*, *Myrsine*, *Clethra* and Myrtaceae, over-representation taxa from lowland are excluded from forest assemblage. It may be applied to fossil pollen data to support the interpretation of palaeorecords, as long as in mosaic in similar environmental conditions.

2 Climate Drivers During Holocene

Overall, this research suggests a trend of colder and drier conditions from Early Holocene to warmer and moister Late Holocene in southeastern Brazil, corroborating other palynological analyses in southeastern Brazilian mountains (e.g. Behling, 1997; Behling et al. 2007; Behling and Safford, 2010; Veríssimo et al. 2012). This tendency is also demonstrated by palaeoclimatic data (Vuille et al., 2012; Bernal et al., 2016).

The interpretation of a colder and drier Early and Mid-Holocene is based on the general lack of tree ferns; the low LOI values; relatively high frequencies and magnitudes of fire; relatively low pollen densities for *Baccharis* (which is a faithful campos indicator but under warmer temperatures); and the elevated presence of cool climate indicators of southern temperate ancestry like *Drimys* and *Griselinia* in the section of the core that represents 9840-4480 cal yr BP in Serra dos Órgãos record.

Continuing with the record from Serra dos Órgãos, a shift to warmer and wetter conditions occurred in the beginning of Late Holocene, demonstrated by the expansion of upper montane forest at higher elevations before about 4480 cal yr BP and the accelerated contraction of campos de altitude vegetation after about 4500 cal yr BP. Moreover, the increase of organic matter in the soil coincidences with the increase in the number of upper montane and montane Atlantic rain forest taxa. Likewise, fire magnitude and frequency declined suggesting a shift to wetter conditions. At around 1350 cal yr BP a shift to even wetter conditions occurred, showed by a strong and abrupt intensification of sediment accumulation, a decrease in charcoal concentration, and a reduction of campos de altitude pollen to around 50% of all pollen.

Other studies also suggest an intensification in Late Holocene precipitation. According to Behling (1995) the last around 1000 yr are the wettest period of the Holocene. Vuille et al. (2012) study of the South American Monsoon System (SAMS) over the last 2000 yr shows a strengthening monsoon during the Little Ice Age (LIA), resulting in a wetter period from c. 1400-1800 AD.

The record of Serra da Bocaina also implies a trend toward wetter climate during the Late Holocene indicated by a general expansion of forest from around 600 cal yr BP, presented by higher proportions of forest pollen like *Podocarpus*, *Weinmannia*, *Ilex*, *Myrsine*, and Melastomataceae relative to grassland vegetation. At around 50 cal yr BP the increase in Atlantic rainforest species such as Moraceae/Urticaceae and *Alchornea*, suggests the onset of warmer conditions in the last century coinciding with the Current Warm Period (CWP) (Vuille et al., 2012). The general rarity of *Araucaria angustifolia* in the core is also suggestive of warmer conditions characteristic of the Late Holocene. As background however, it is important to note that data from Behling et al. (2007) show that *Araucaria* has not been an abundant member of the high elevation forests in the Serra da Bocaina since at least 18,570 cal yr BP (beginning of the record). This is likely due to the lower and warmer environment in this tropical-marginal mountain site compared to much larger *Araucaria* populations in the higher and colder Serra do Mantiqueira and sites to the south.

3 Human Disturbances

The record from Serra dos Órgãos suggested that fire occurred in the area before the documented arrival of humans in southeastern Brazil, decreasing in Late Holocene. The fire regime behaviour coincides with the increasing in precipitation starting about 4000 years ago (Bernal et al, 2016) and spreading of forest vegetation. The last about 1000 years were the wettest period during the whole Holocene (Behling and Safford, 2010) and the last fire significant peak in this record occurred about 600 cal yr BP (1350 AD), suggesting that fire in Serra dos Órgãos were from natural origins. In this part of Serra do Mar the relief is extremely abrupt and the high mountain summits and plateau that support campos de altitude are small (Ab´Saber, 2003), which may be the reason for lightning ignitions that occur on topographic eminences with combustible fuels have little chance to spread far.

On the other hand, in Serra da Bocaina, where the relief is mostly characterized by rounded mountaintops interrupted with valleys (Ab´Saber, 2003; Safford and Martinelli 2000), fire peaks and higher fire magnitude were registered before the arrival of European, indicating that probably pre-Columbian populations had important influence on the vegetation. In addition, forest expanded after the arrival of the European and rapid destruction of the Amerindian cultures and populations (Pádua, 2004), suggesting that pre-1500 AD extent of grassland vegetation was influenced to some extent by human cutting and burning. After the European settlements, at around 1680 AD (270 cal yr BP) fire peaks begin to occur again, likely marking a new cycle of human influence on the vegetation.

The vegetation composition also registered human disturbances in the more accessible site of Serra da Bocaina. From about 1520 AD (430 cal yr BP) to about 1670 AD (280 cal yr BP) there is a marked and rapid increase in *Podocarpus* pollen, rising from about 10% to over 40%, followed by a similarly marked decrease to about 1720 AD (230 cal yr BP). The coincidence of the first date with the period of European arrival in Brazil and the second date with the establishment of European settlement and the introduction of farming and livestock in the region, suggest that forest expansion into grassland may have been a result of a reduction in human activities. The lack of a positive response in fern pollen or Atlantic rainforest pollen during this time period argues against an increase in precipitation, further supporting the anthropogenic hypothesis. After 1680 AD (270 cal yr BP) a slight spread of grassland appears to be caused by a renewed forest clearing and the introduction of cattle to the region. A sharp expansion of aquatics species (mainly Cyperaceae) after 1780 AD (170 cal yr BP) seems to be due to local interference in the water table and/or stream hydrology. Moreover, the increase in the number of taxa indicative of early forest succession in late 20th century (e.g., both *Mimosa* pollen groups, *Cecropia*, Melastomataceae) provides further indication of a changed campos-forest dynamic resulted from human disturbances.

4 Outlook and Future Perspective

The results of this research together with other palaeoecological data demonstrate that campos de altitude covered extensive areas of the southeastern Brazilian mountains during the LGM (Last Glacial Maximum), and that cooling was sufficient to permit biogeographic connections with cold, temperate grassland habitats far to the south and southeast (e.g. Rambo, 1953; Behling, 1997; Behling et al., 2007; Behling and Safford, 2010; Safford, 2007). After gradual warming and increasing precipitation especially in Late Holocene, forests expanded, reducing the habitat heterogeneity – and species diversity - of the forest-grassland mosaic (Bond and Parr, 2010; Overbeck et al., 2006).

It has been shown that the balance between grasslands and forests depends on local or regional conditions and the increase of primarily wetter, but also warmer, conditions favour the growth and/or competitive ability of woody plants. The results also suggested that fire occurred in the campos de altitude long before human settlement of Brazil (e.g. Behling, 1997; Behling et al., 2007; Veríssimo et al., 2012; this work) and adaptations to fire were widespread in the campos de altitude flora (Safford, 2001). Albeit the currently extent of campos de altitude is much reduced, it is certainly larger than climate alone would dictate, especially in warmer, lower elevation sites. Hence, it is clear that anthropogenic disturbances such as fire, livestock grazing and logging have played a role in driving grassland-forest relationships in southeastern Brazilian highlands. Nevertheless, lighting ignitions normally occur during wet season, having little change to spread far. Otherwise, today most of ignitions are anthropogenic and occur during the dry season in very warm and windy conditions, when fire can spread from mountain to mountain and even burn appreciable areas of forest.

Climate investigations indicate that annual mean temperatures in southeastern South America have risen about 1º C over the last century, and climate changes predictions suggest further increases of 2-3º C by 2050 AD and 3-5º C by 2080 AD, with greater seasonality in precipitation (which could lead to more dry season fire) and greater potential for heavy precipitation in the wet season (Marengo et al., 2009; Marengo et al., 2012; Nuñez et al., 2009). A Dynamic Global Vegetation Model (DGVM) simulated for Morro do Santana, southern Brazil, predicted a slight increase in the rate of forest expansion for the next decades, based on relative advantages for C_3 trees compared to C_4 grasses (Blanco et al., 2014). Similarly, Behling and Safford (2010) suggested that future global warming was likely to intensify the upward movement of the Atlantic Forest at the expense of open ecosystems like the campos de altitude.

The conservation of the complexity, beauty and highly biodiverse forest-grassland mosaic is a major goal in much of southern and southeastern Brazil (Behling and Pillar, 2007; Overbeck et al., 2015). Based on the knowledge from both paleo- and modern ecological studies of why and how ecosystems changed, it seems that the maintenance of the forest-grassland coexistence in the current and projected climate trends depends on an active disturbance management and a changed in conservation focus from forest to non-forest habitats (Behling and Pillar, 2007; Blanco et al., 2014; Overbeck et al., 2015).

Nowadays, it is already accepted that fire plays an important role in some ecosystems and experiments of fire management are being applying in protected areas in Brazil, changing conservation focus from no-action for active disturbance management. In savanna, for example, prescribed fires have a positive effect on richness of graminoids and grassland, and prevention of shrub encroachment (Lohmann et al, 2014; Durigan et al, 2020). Nevertheless, ecological conditions must be considering when discussing fire management, specially resilience of the species. In campos de altitude in Itatiaia National Park, Aximoff et al. (2016) registered that, although richness has restored after fire, some endemic species have disappeared.

Therefore, as a result of this research some management strategies and further investigations are suggested:

- Develop a conservation assessment and conservation strategy for campos de altitude in southeastern Brazil with a focus on current and potential future threats.
- Map potential climate refugia for cold-adapted taxa.
- Control anthropogenic fires which occur during very warm and especially wind conditions during the dry season by reducing available burning biomass.
- Develop new techniques to better assess fire frequencies and magnitudes using charcoal from herbaceous sources.
- Carry out further studies to better elucidate the relative roles of anthropogenic and “natural” factors in driving the extent of campos de altitude and their relationship to neighbouring forested ecosystems.
- Carry out field research to better understand the effects of fire and grazing on successional processes by comparison of experimental use of fire and grazing in controlled and the installation of areas that are protected from grazing (fenced exclosures), fire, and both grazing and fire.

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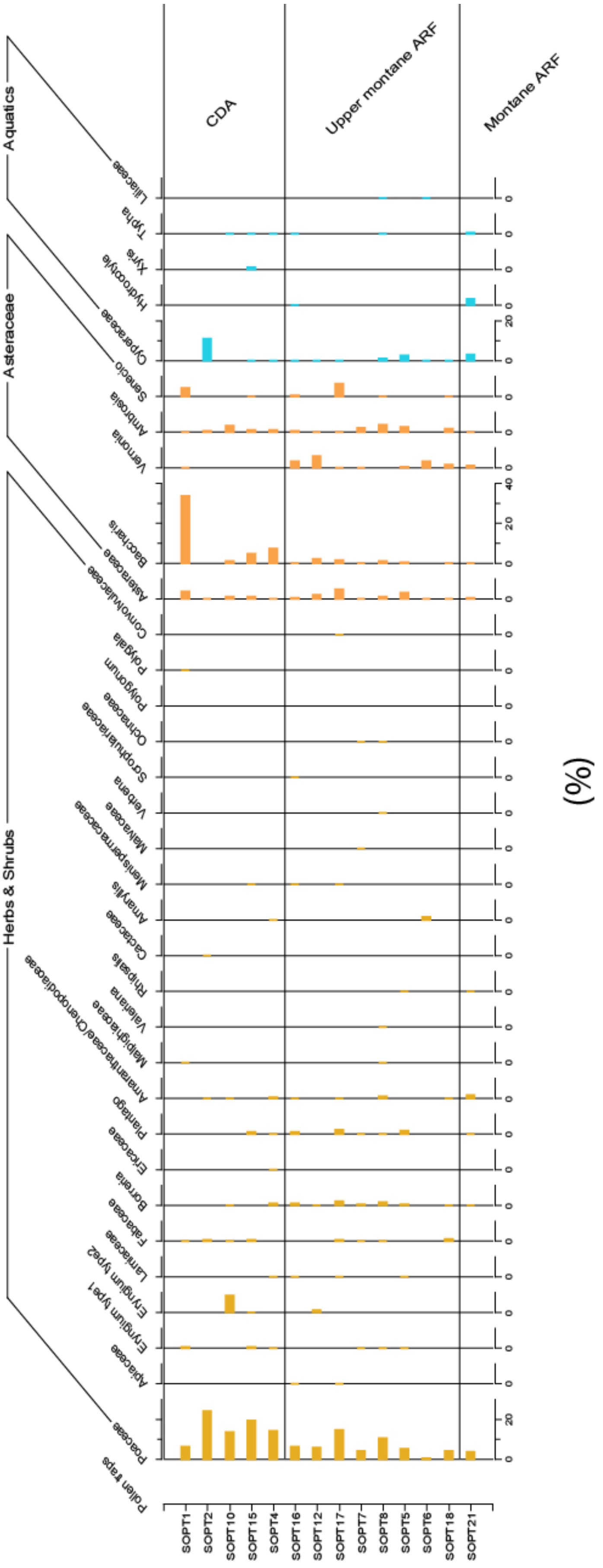
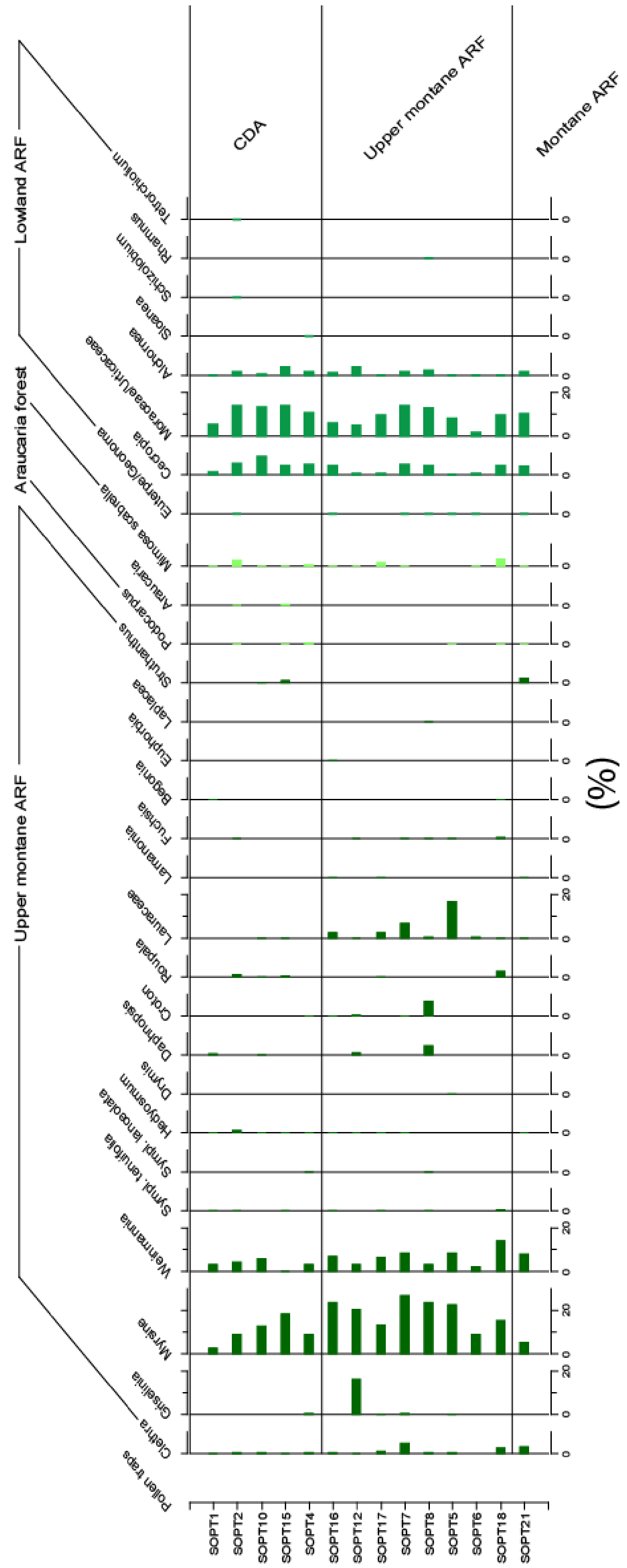
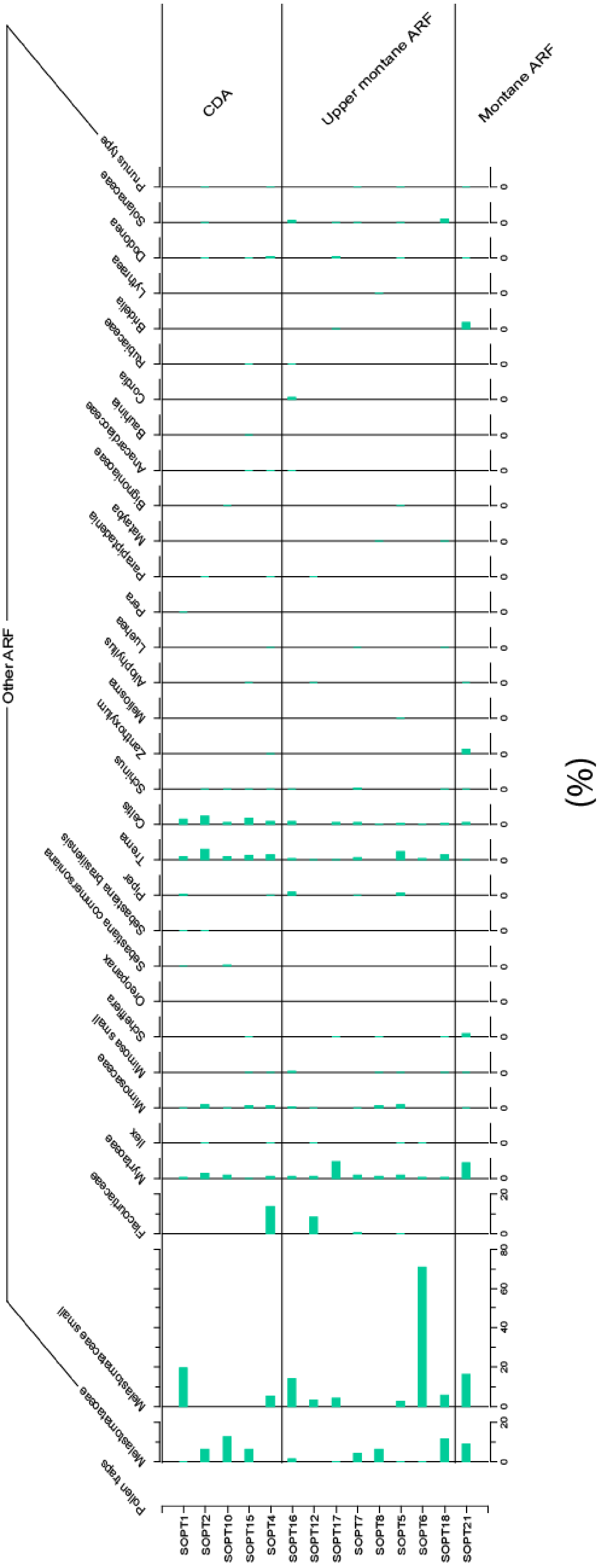
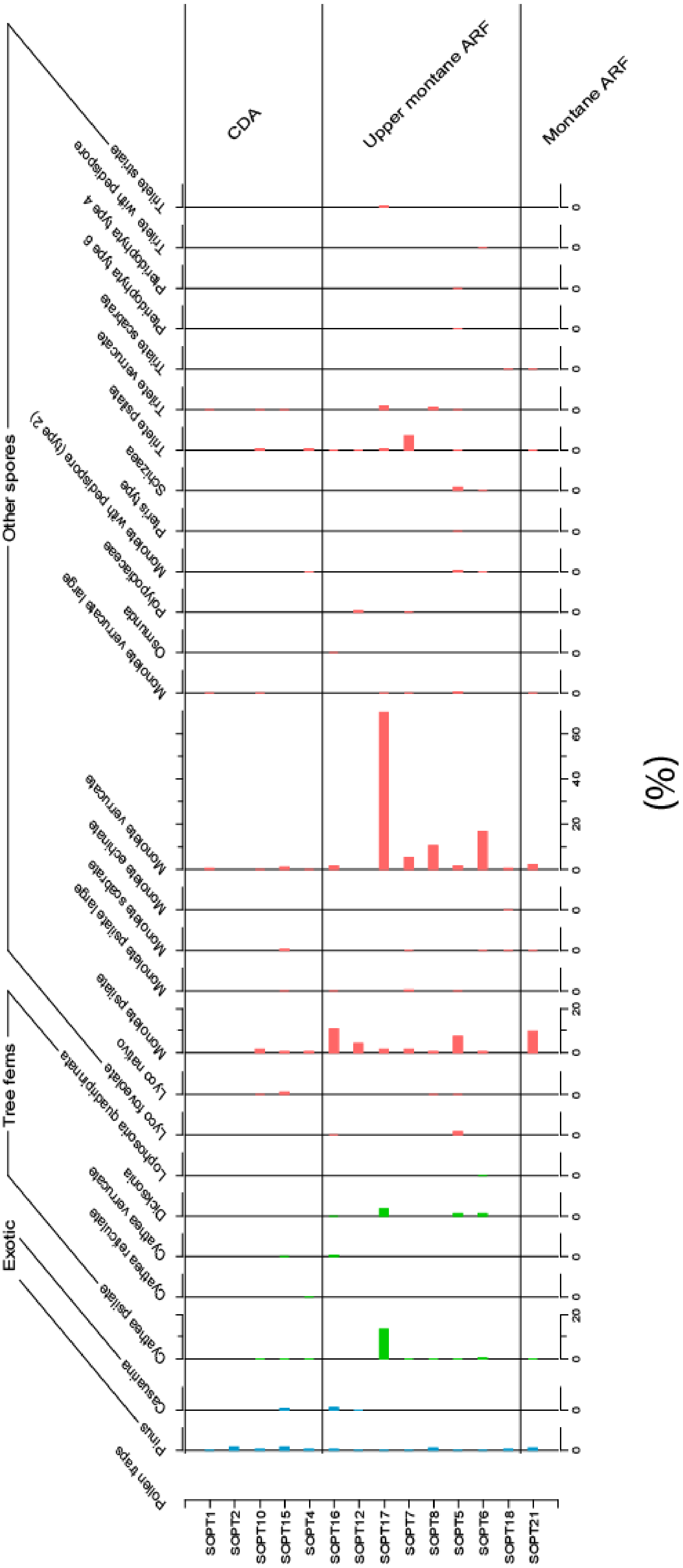
Appendix I

Complete pollen diagram of modern pollen rain


Pollen traps
Poaceae
Apiaceae
Eryngium type1
Eryngium type2
Lamiaceae
Fabaceae
Borreria
Ericaceae
Plantago
Amaranthaceae/Chenopodiaceae
Malpighiaceae
Valeriana
Rhipsalis
Cactaceae
Amaryllis
Menispermaceae
Malvaceae
Verbena
Scrophulariaceae
Ochnaceae
Polygonum
Polygala
Convolvulaceae
Asteraceae
Baccharis
Vernonia
Ambrosia
Senecio
Cyperaceae
Hydrocotyle
Xyris
Typha
Liliaceae
Herbs & Shrubs
Asteraceae
Aquatics
SOPT1
SOPT2
SOPT10
SOPT15
SOPT4
SOPT16
SOPT12
SOPT17
SOPT7
SOPT8
SOPT5
SOPT6
SOPT18
SOPT21
CDA
Upper montane ARF
Montane ARF
0
20
40
(%)

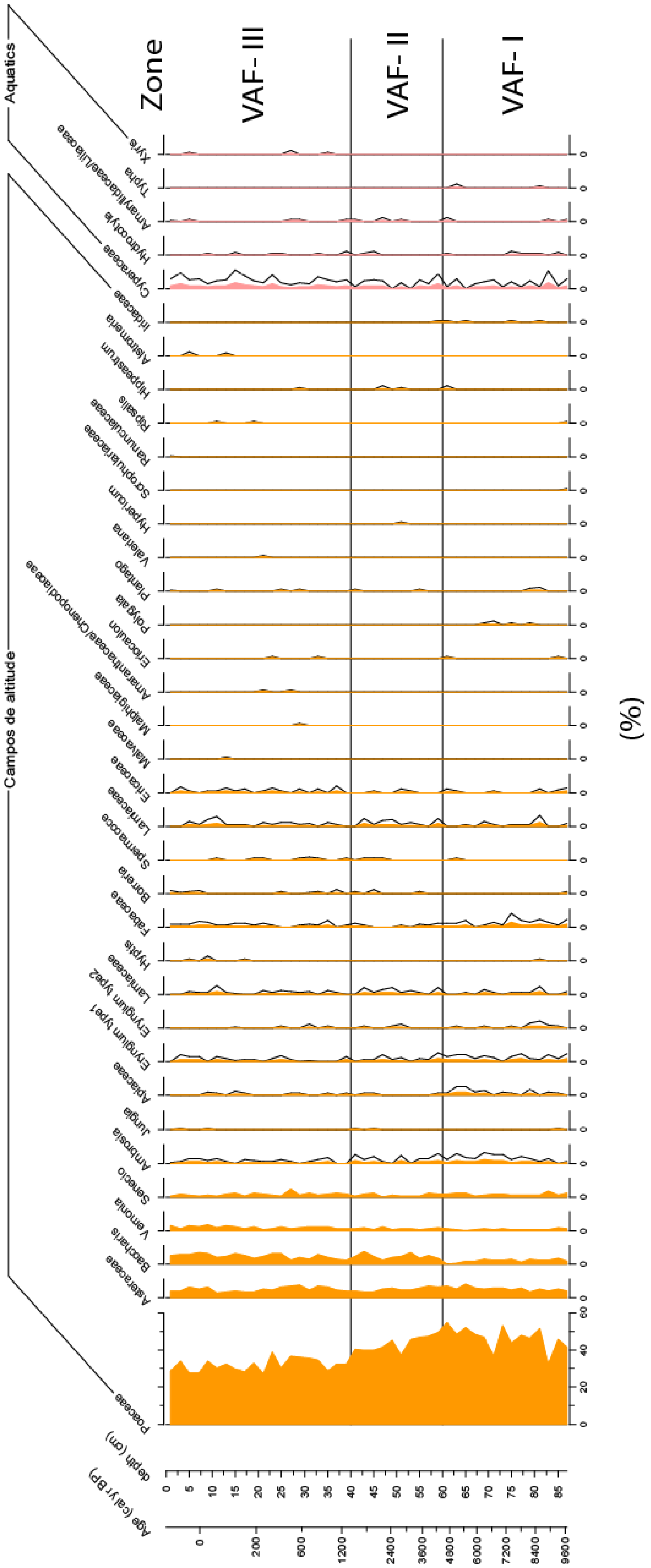

Lowland ARF
Araucaria forest
Upper montane ARF
Tetrorchidium
Rhamnus
Schizolobium
Sloanea
Alchornea
Moraceae/Urticaceae
Cecropia
Euterpe/Geonoma
Mimosa scabrella
Araucaria
Podocarpus
Struthanthus
Lamiaceae
Euphorbia
Begonia
Fuchsia
Lamanonia
Lauraceae
Roupala
Croton
Daphnopsis
Drymis
Hedyosmum
Sympl. lanceolata
Sympl. tenuifolia
Weinmannia
Myrsine
Griselinia
Clethra
Pollen traps
CDA
Upper montane ARF
Montane ARF
SOPT1
SOPT2
SOPT10
SOPT15
SOPT4
SOPT16
SOPT12
SOPT17
SOPT7
SOPT8
SOPT5
SOPT6
SOPT18
SOPT21
0
20
(%)

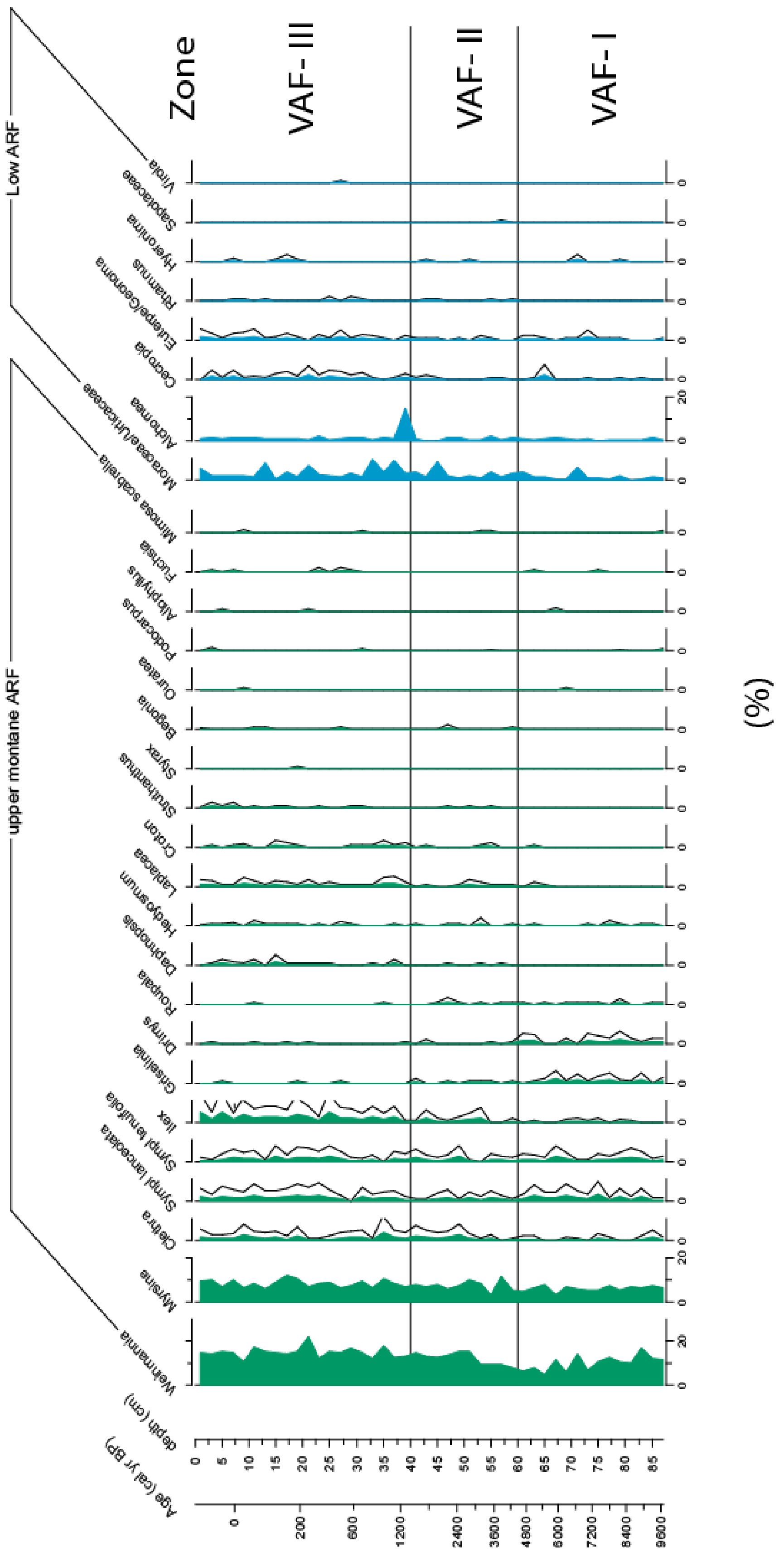

Pollen traps
SOPT1
SOPT2
SOPT10
SOPT15
SOPT4
SOPT16
SOPT12
SOPT17
SOPT7
SOPT8
SOPT5
SOPT6
SOPT18
SOPT21
CDA
Upper montane ARF
Montane ARF
Melastomataceae
Melastomataceae small
Other ARF
Flacourtiaceae
Myrtaceae
Ilex
Mimosaceae
Mimosa small
Schefflera
Oreopanax
Sebastiana commersoniana
Sebastiana brasiliensis
Piper
Trema
Celtis
Schinus
Zanthoxylum
Meliosma
Allophylus
Luehea
Pera
Parapiptadenia
Matayba
Bignoniaceae
Anacardiaceae
Bauhinia
Cordia
Rubiaceae
Bridelia
Lythraea
Dodonea
Solanaceae
Prunus type
0
20
40
60
80
(%)

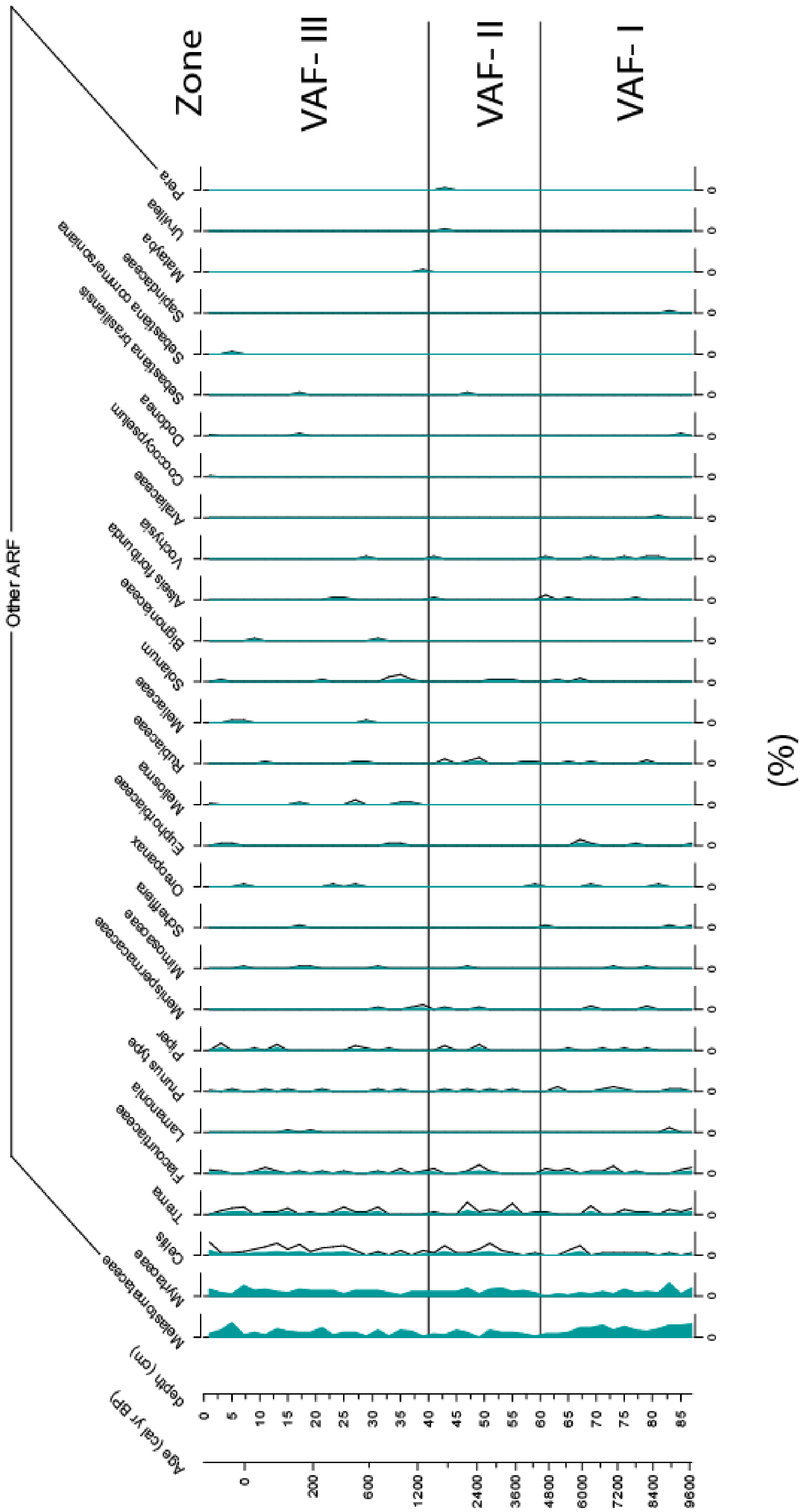

Pollen traps
Pinus
Casuarina
Cyathea psilate
Cyathea reticulate
Cyathea verrucate
Dicksonia
Lophosoria quadripinnata
Lyco foveolate
Lyco nativo
Monolete psilate
Monolete psilate large
Monolete scabrate
Monolete echinate
Monolete verrucate
Monolete verrucate large
Osmunda
Polypodiaceae
Monolete with pedispore (type 2)
Pteris type
Schizaea
Trilete psilate
Trilete verrucate
Trilete scabrate
Pteridophyta type 6
Pteridophyta type 4
Trilete with pedispore
Trilete striate
Exotic
Tree ferns
Other spores
CDA
Upper montane ARF
Montane ARF
SOPT1
SOPT2
SOPT10
SOPT15
SOPT4
SOPT16
SOPT12
SOPT17
SOPT7
SOPT8
SOPT5
SOPT6
SOPT18
SOPT21
0
20
40
60
(%)

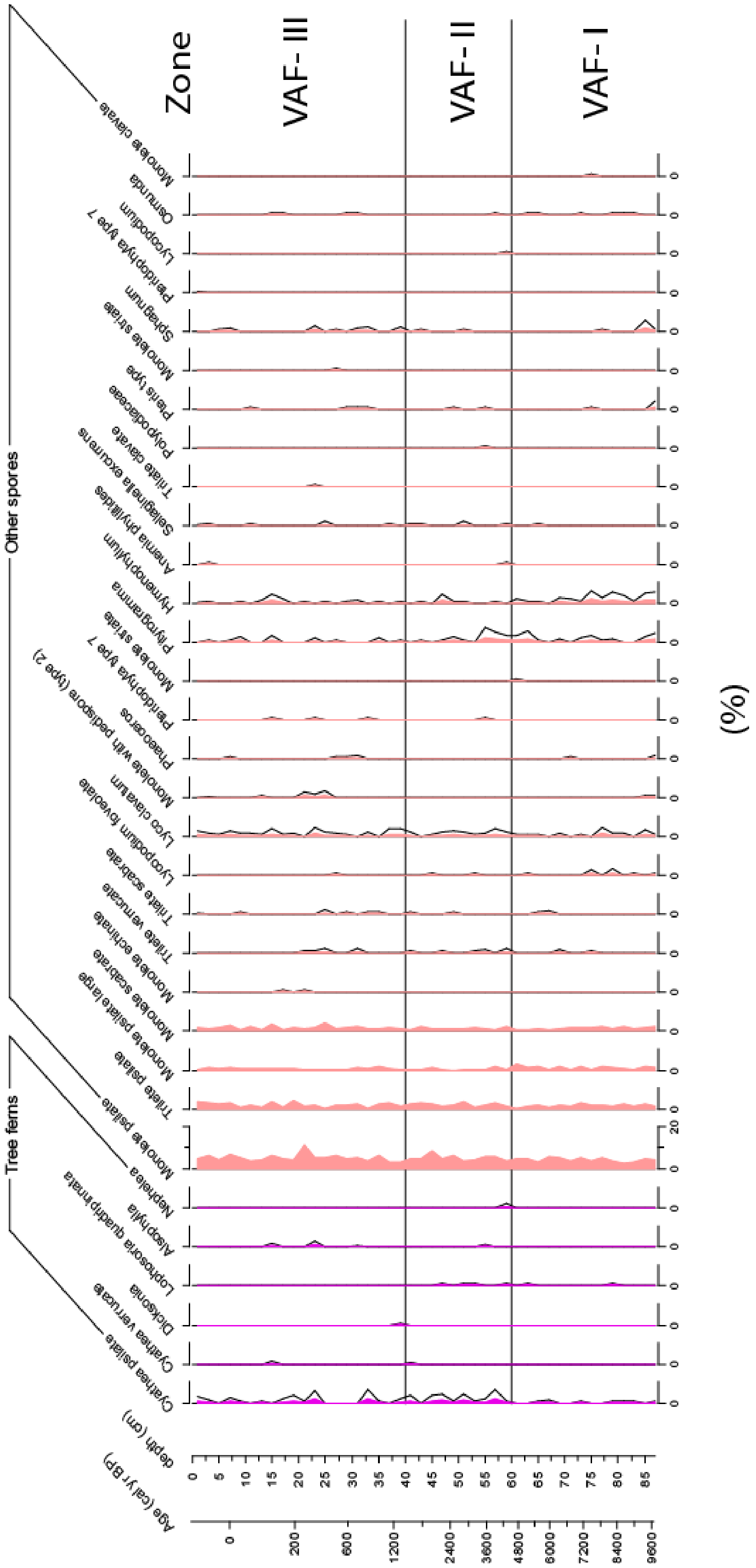
Appendix II

Complete pollen diagram of Serra dos Órgãos


Aquatics
Campos de altitude
Zone
VAF- III
VAF- II
VAF- I
Xyris
Typha
Amaryllidaceae/Liliaceae
Hydrocotyle
Cyperaceae
Iridaceae
Alstromeria
Hippeastrum
Ripsalis
Ranunculaceae
Scrophulariaceae
Hypericum
Valeriana
Plantago
Polygala
Eriocaulon
Amaranthaceae/Chenopodiaceae
Malpighiaceae
Malvaceae
Ericaceae
Lamiaceae
Spermacoce
Borreria
Fabaceae
Hyptis
Lamiaceae
Eryngium type2
Eryngium type1
Apiaceae
Jungia
Ambrosia
Senecio
Vernonia
Baccharis
Asteraceae
Poaceae
depth (cm)
Age (cal yr BP)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
0
200
600
1200
2400
3600
4800
6000
7200
8400
9600
0
20
40
60
(%)

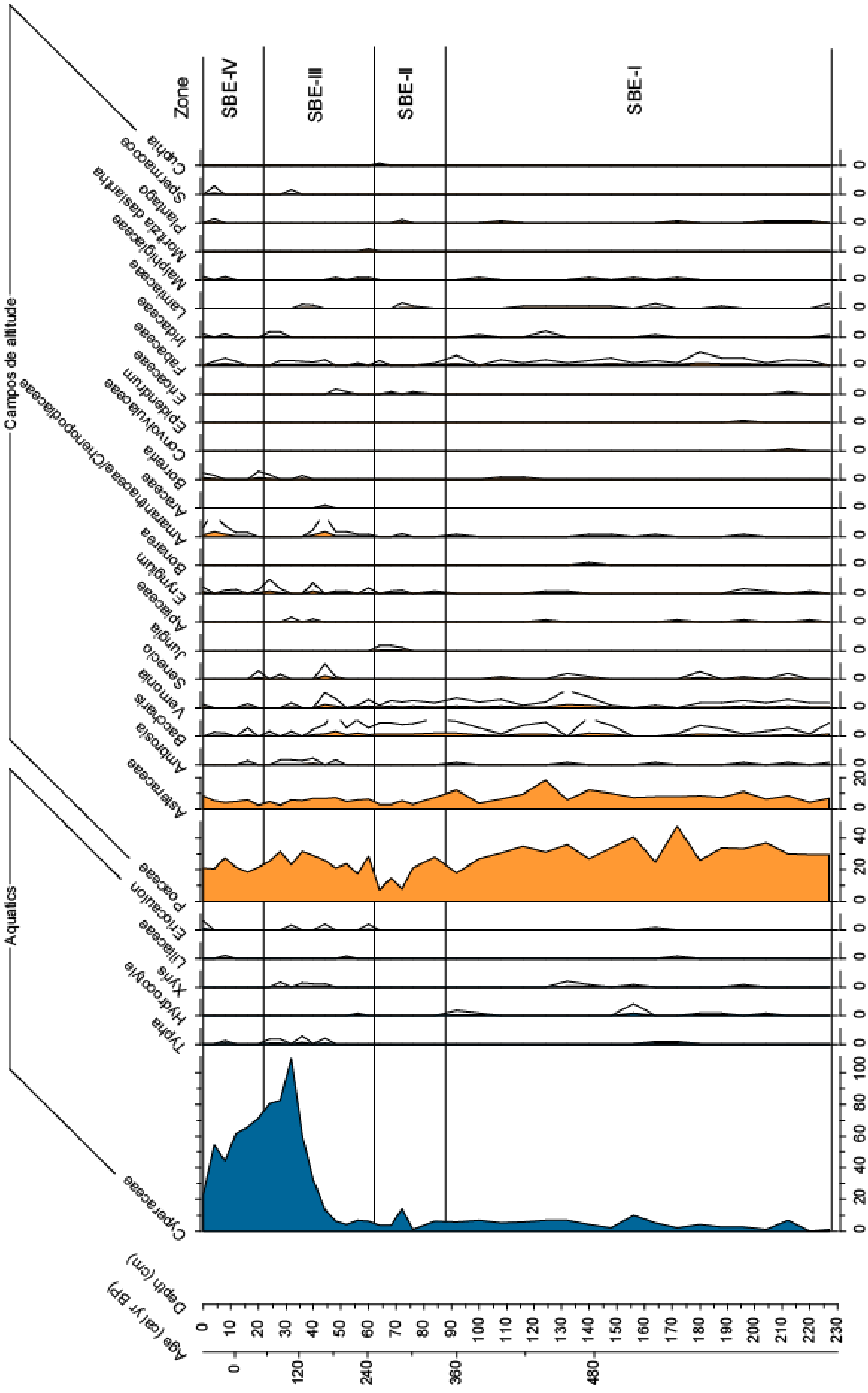

Low ARF
upper montane ARF
Zone
VAF- III
VAF- II
VAF- I
Virola
Sapotaceae
Hyeronima
Rhamnus
Euterpe/Geonoma
Cecropia
Alchornea
Moraceae/Urticaceae
Mimosa scabrella
Fuchsia
Allophyllus
Podocarpus
Ouratea
Begonia
Styrax
Struthanthus
Croton
Lapiaceae
Hedyosmum
Daphnopsis
Roupala
Drimys
Griselinia
Ilex
Sympl tenuifolia
Sympl lanceolata
Clethra
Myrsine
Weinmannia
depth (cm)
Age (cal yr BP)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
0
200
600
1200
2400
3600
4800
6000
7200
8400
9600
0
20
(%)

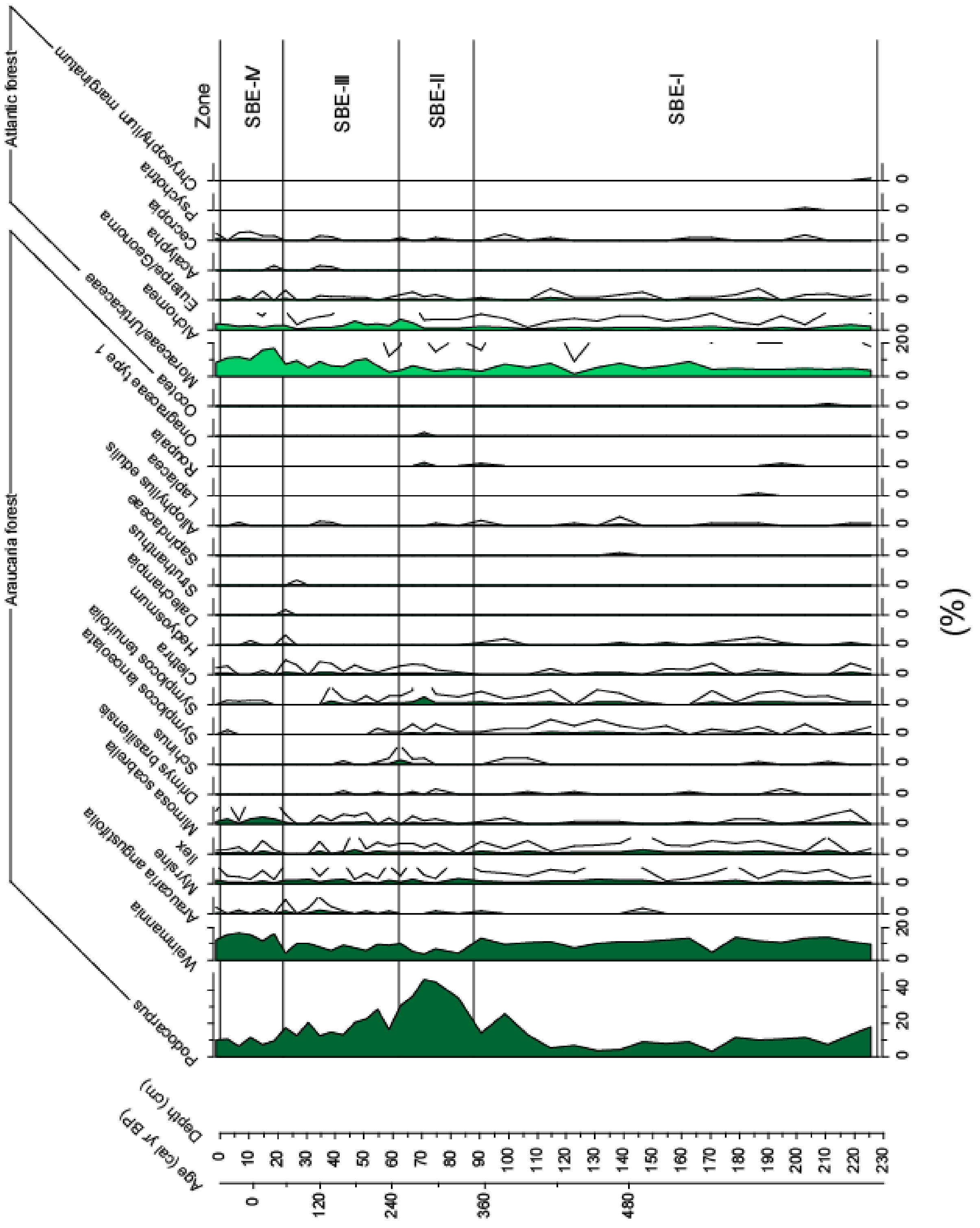

Other ARF
Pera
Urvillea
Matayba
Sapindaceae
Sebastiana commersoniana
Sebastiana brasiliensis
Dodonea
Coccocypselum
Araliaceae
Vochysia
Alseis floribunda
Bignoniaceae
Solanum
Meliaceae
Rubiaceae
Meliosma
Euphorbiaceae
Oreopanax
Schefflera
Mimosaceae
Menispermaceae
Piper
Prunus type
Lamanonia
Flacourtiaceae
Trema
Celtis
Myrtaceae
Melastomataceae
depth (cm)
Age (cal yr BP)
Zone
VAF- III
VAF- II
VAF- I
(%)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
0
200
600
1200
2400
3600
4800
6000
7200
8400
9600

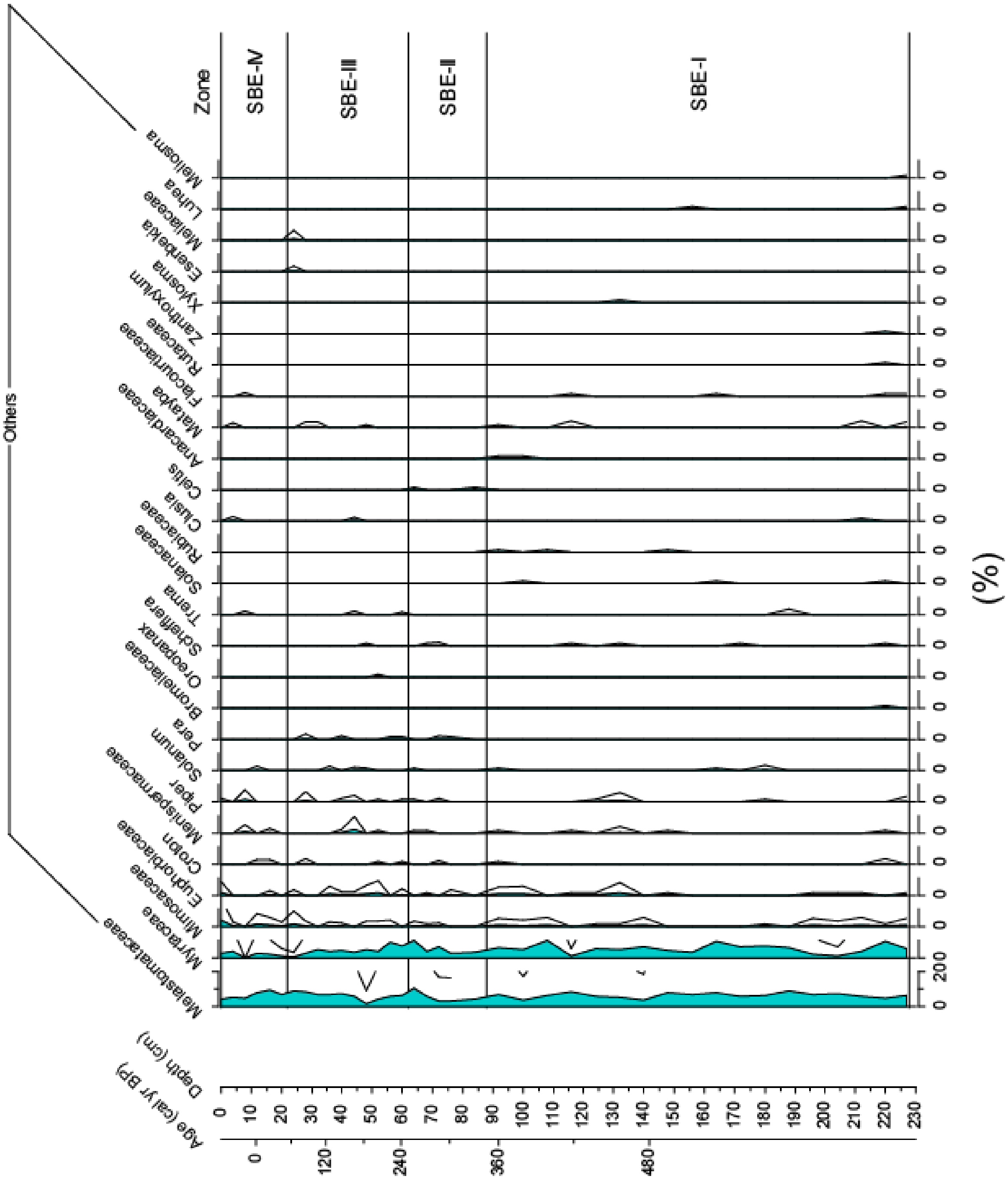

Zone
VAF- III
VAF- II
VAF- I
Other spores
Tree ferns
Monolete clavate
Osmunda
Lycopodium
Pteridophyta type 7
Sphagnum
Monolete striate
Pteris type
Polypodiaceae
Trilete clavate
Selaginella excurrens
Anemia phyllitides
Hymenophyllum
Pityrogramma
Monolete striate
Pteridophyta type 7
Phaeoceros
Monolete with perispore (type 2)
Lyco clavatum
Lycopodium foveolate
Trilete scabrate
Trilete verrucate
Monolete echinate
Monolete scabrate
Monolete psilate large
Trilete psilate
Monolete psilate
Nephelea
Alsophila
Lophosoria quadripinnata
Dicksonia
Cyathea verrucate
Cyathea psilate
depth (cm)
Age (cal yr BP)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
0
200
600
1200
2400
3600
4800
6000
7200
8400
9600
20
(%)

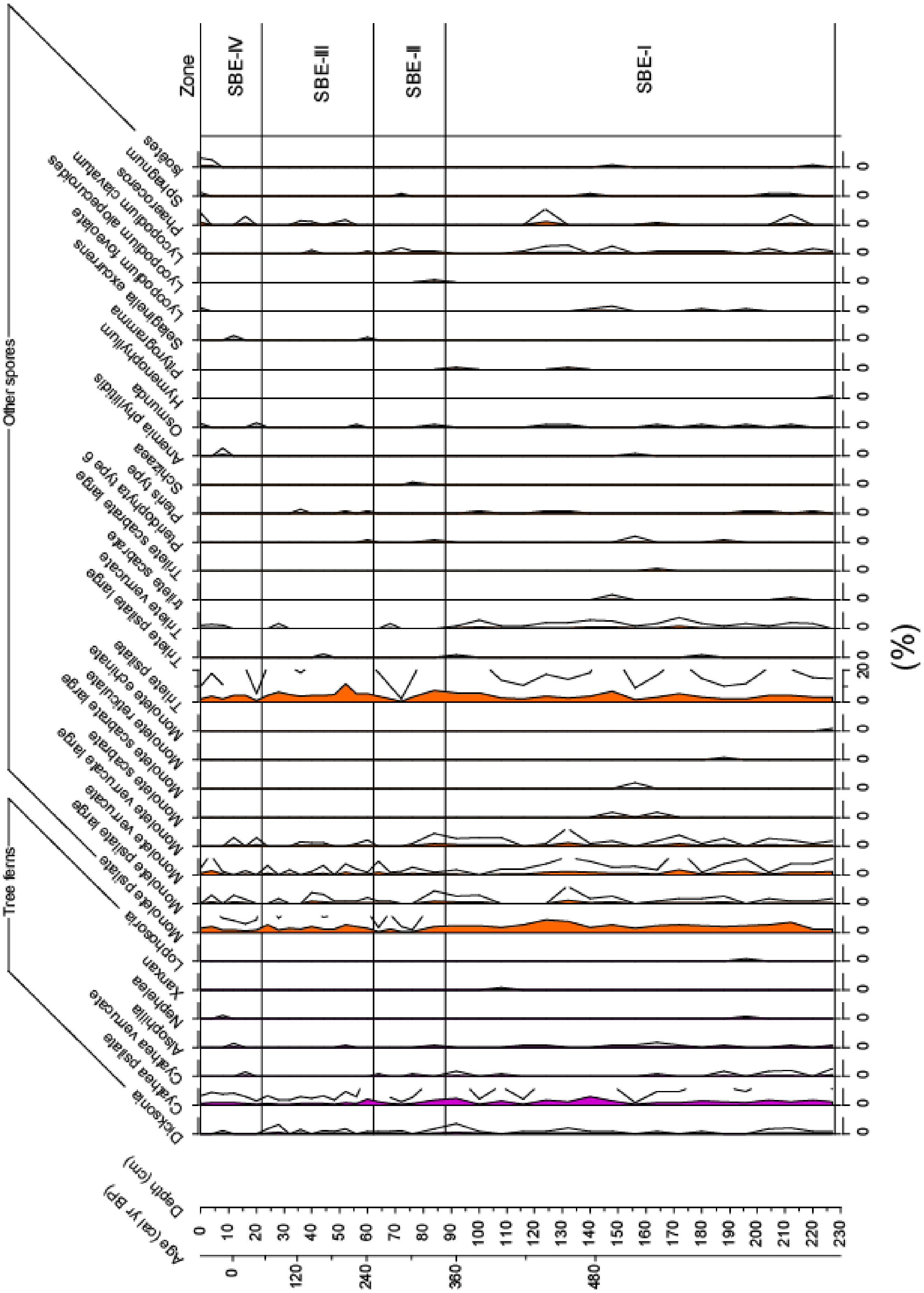
Appendix III

Complete pollen diagram of Serra da Bocaina


Zone
SBE-IV
SBE-III
SBE-II
SBE-I
Campos de altitude
Aquatics
Cuphea
Spermacoce
Plantago
Moritzia dasiantha
Malpighiaceae
Lamiaceae
Iridaceae
Fabaceae
Ericaceae
Epidendrum
Convolvulaceae
Borreria
Araceae
Amaranthaceae/Chenopodiaceae
Bonarea
Eryngium
Apiaceae
Jungia
Senecio
Vernonia
Baccharis
Ambrosia
Asteraceae
Poaceae
Eriocaulon
Liliaceae
Xyris
Hydrocotyle
Typha
Cyperaceae
Depth (cm)
Age (cal yr BP)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
0
120
240
360
480
20
40
60
80
100
(%)


Atlantic forest
Araucaria forest
Chrysophyllum marginatum
Psychotria
Cecropia
Acalypha
Euterpe/Geonoma
Alchornea
Moraceae/Urticaceae
Ocotea
Onagraceae type 1
Roupala
Lamiaceae
Allophylus edulis
Sapindaceae
Struthanthus
Dalechampia
Hedyosmum
Clethra
Symplocos tenuifolia
Symplocos lanceolata
Schinus
Drimys brasiliensis
Mimosa scabrella
Ilex
Myrsine
Araucaria angustifolia
Weinmannia
Podocarpus
Depth (cm)
Age (cal yr BP)
Zone
SBE-V
SBE-III
SBE-II
SBE-I
(%)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
0
120
240
360
480
0
20
40
200


Others
Melastomataceae
Myrtaceae
Mimosaceae
Euphorbiaceae
Croton
Menispermaceae
Piper
Solanum
Pera
Bromeliaceae
Oreopanax
Schefflera
Trema
Solanaceae
Rubiaceae
Clusia
Celtis
Anacardiaceae
Matayba
Flacourtiaceae
Rutaceae
Zanthoxylum
Xylosma
Esenbeckia
Meliaceae
Luhea
Meliosma
Zone
SBE-IV
SBE-III
SBE-II
SBE-I
0
200
(%)
Depth (cm)
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230
Age (cal yr BP)
0 120 240 360 480


Other spores
Tree ferns
Zone
SBE-IV
SBE-III
SBE-II
SBE-I
Isoetes
Sphagnum
Phaeroceros
Lycopodium clavatum
Lycopodium alopecuroides
Lycopodium foveolate
Selaginella excurrens
Pityrogramma
Hymenophyllum
Osmunda
Anemia phyllitidis
Schizaea
Pteris type
Pteridophyta (type 6
Trilete scabrate large
Trilete scabrate
Trilete verrucate
Trilete psilate large
Trilete psilate
Monolete echinate
Monolete reticulate large
Monolete scabrate large
Monolete scabrate
Monolete verrucate large
Monolete verrucate
Monolete psilate large
Monolete psilate
Lophosoria
Xanxan
Nephelea
Alsophila
Cyathea verrucate
Cyathea psilate
Dicksonia
Depth (cm)
Age (cal yr BP)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
0
120
240
360
480
200
(%)