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**VEGETATION AND FIRE HISTORY IN
ARAUCARIA FOREST AND GRASSLANDS,
SOUTHERN BRAZIL**

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Si pudiera regalarte el mundo lo haría sin duda...

A mi Madre!

Sin tu sonrisa yo no sabría lo que es la alegría...

A mi Padre!

“We observed with astonishment..., how many things are connected with the existence of a single plant” Mauritia flexuosa “the tree of life”

Alexander von Humboldt

Notes during his expedition to the Llanos in: Personal Narrative of Travels to the Equinoctial Regions of America, During the Years 1799-1804

“The primal plant is going to be the strangest creature in the world, which Nature herself shall envy me. With this model and the key to it, it will be possible to go on forever inventing plants and know that their existence is logical; that is to say, if they do not actually exist, they could, for they are not the shadowy phantoms of a vain imagination, but possess an inner necessity and truth. The same law will be applicable to all other living organisms.”

Johann Wolfgang von Goethe

To Herder, 17 May 1787. Italian Journey (1816-17)

DECLARATION

This dissertation is the result of my own work and includes nothing, which is the outcome of work done in collaboration except where specifically indicated in the text. It has not been previously submitted, in part or whole, to any university or institution for any degree, diploma, or other qualification.

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SUMMARY

Southern Brazil offers a great opportunity to analyse woodland and grassland mosaics, their pollen-vegetation relationships and its long-term vegetation and fire history. This research was carried out in two stages; first an analysis of the relationship between pollen and vegetation percentages which provide insights into the general understanding of the landscape, the representativeness and the pollen productivity of selected taxa. Second, we study the long-term changes in the vegetation and fire from a sediment record recovered among this vegetation mosaic.

The relationships between pollen and vegetation indicated that the open vegetation taxon Poaceae, was the highest pollen producer in this forest-grassland mosaic. However, grasses were considered in here a poor reference taxon as they appeared in all vegetation types and obscured the results in shrublands and woodland scenarios. On the other hand, we documented the under-representation of *Araucaria angustifolia* despite the nature of its pollination mode (wind-pollinated). We believe that this result was perhaps hampered for its dioecious reproduction and for the mixed dispersion types involved in the mosaic of woodlands-grasslands which indirectly affect the dispersal models computed.

Long-term palaeoecological results from Lagoa Dourada, a Holocene sediment record from Vila Velha state park in Paraná state, showed that *Araucaria* forest, after its initial establishment at ~7000 cal yr BP, experienced a stepwise expansion first at ~5700 and second at ~3080 cal yr BP, thus periods were characterized by different climatic conditions, coming from a warm and dry Early Holocene, to a wet and cool Mid-Holocene and to a humid Late Holocene. We documented that fire activity also contributed to changes in the vegetation through the observation and analyses of pre and post-fire events in the region. Human activity has been detected in here during particularly some fire peaks episodes; at 1600 cal yr BP and at 1380 cal yr BP, which are concurrent with the agricultural practices of the Taquara/Itararé groups as already documented for southern Brazil. Another anthropogenic signal was detected in here for the last ~220 cal yr BP, this one related to the arrival of the Europeans between 1703 to 1800, we evidenced a complete reorganization of natural ecosystems in which particularly *Araucaria* was affected due to timber production and plantation of *Pinus* and *Eucalyptus* started.

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PREFACE

Araucaria forest and grassland mosaics in southern Brazil, are among the ecosystems that occur in the Atlantic Rainforest Biome. Due to its importance in this hotspot of biodiversity which has been highly affected and reduced in the last decades, they have become a target of research, protection and conservation. *Araucaria angustifolia* the main dominant tree in those forests is an endangered species with high socio-ecological value. Modern and fossil pollen studies have been carried out before in these vegetation types, however little is known about the relationships between pollen and vegetation and also about the long-term fire and vegetation history at a high-resolution level. The here presented results can help to better understand the dynamics of those ecosystems.

The overall aim of this research is to understand the relationships of pollen and vegetation, the natural fire dynamics and the vegetation changes in one of the world biodiversity hotspots, the Atlantic Rainforest biome.

Following research objectives will facilitate the achievement of this aim:

1. Analyse the pollen vegetation relationship in the *Araucaria* forest and grassland mosaics of southern Brazil to improve our ability to reconstruct changes in local forest cover.
2. Reconstruct the long-term past vegetation and fire history to improve our understanding of the causes and dynamics of past changes in the Atlantic Rainforest biome.

This thesis is structured as follows:

The Introduction presented in **Chapter 1** is a general overview of Brazil with a special focus on southern Brazil where this research was conducted. Geology, climate, and vegetation are described for the study regions included in here. **Chapter 2** gives an overview of the *Araucaria* forest and grasslands mosaics, its ecology and dynamics. **Chapter 3** describes briefly about palaeoecological topics. The results are highlighted in

Chapter 4, 5 and 6. Finally **Chapter 7** synthesises the main research outcomes, conclusion and future perspectives of this work.

The following chapters (4 to 6) are the compilation of the manuscripts submitted or to be submitted in peer-reviewed journals. Those were written based on the three themes related to the main topic of this research:

Chapter 4

Towards quantifying changes in forest cover in the *Araucaria* forest Grassland mosaic in southern Brazil - (Published in Vegetation History and Archaeobotany Journal) DOI: <https://doi.org/10.1007/s00334-021-00841-2>

Chapter 5

Late Quaternary palaeoecological changes in southern Brazil: a multi-proxy and high-resolution record

Chapter 6

High-resolution Mid-Holocene fire history in the *Araucaria* forest Grassland (Campos) mosaics in southern Brazil

Chapter 7

The main findings of the research are summarized and synthesised, conclusions are presented as well as recommendations for future investigations.

1. INTRODUCTION

Brazil, with an area of 8'515.767 km², is the fifth country in territorial extension on the planet occupying almost half of the South American continent. Extends from the Northern Hemisphere-Northern Amazon- to the Prata Estuary, between Uruguay and Argentina and from the Atlantic Ocean to Peru. Due to its location, Brazil contains a vast mosaic of ecosystems, product of the wide climatic and topographic diversity. In consequence, is a source of natural resources, represented by high biodiversity, the relative abundance of water and minerals (Instituto Brasileiro de Geografia e Estatística & Adma Hamman de, 2016; Rodrigues Salgado et al., 2019).

Politically Brazil is divided into five principal regions: North, Northeast, Southeast, South and Central-West, wherein total 26 states and one Federal District are part of them (Lima et al., 2002):

- North: Rondônia, Acre, Amazonas, Roraima, Pará, Amapá and Tocantins.
- Northeast: Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia.
- Southeast: Minas Gerais, Espírito Santo, Rio de Janeiro and São Paulo.
- South*: Paraná, Santa Catarina and Rio Grande do Sul.

** Study area of the present research*

- Central-West: Mato Grosso do Sul, Mato Grosso, Goiás and Distrito Federal.

1.1 Climate of Southern Brazil

Southern Brazil is characterized by subtropical climate as it lies below the Tropic of Capricorn (**Fig. 1**). In Paraná, Santa Catarina and Rio Grande do Sul, oceanic climate without dry season; with hot summer and with temperate summer is dominant, where the

altitude (<700 m.a.s.l.) or the temperature ($T < 22^{\circ}\text{C}$) limits them. In general rainfall, seasonality is not usually marked and is consider well distributed throughout the year. Rainfall levels vary depending on the topography and range from 1300 mm to 2200 mm (Alvares et al., 2013).

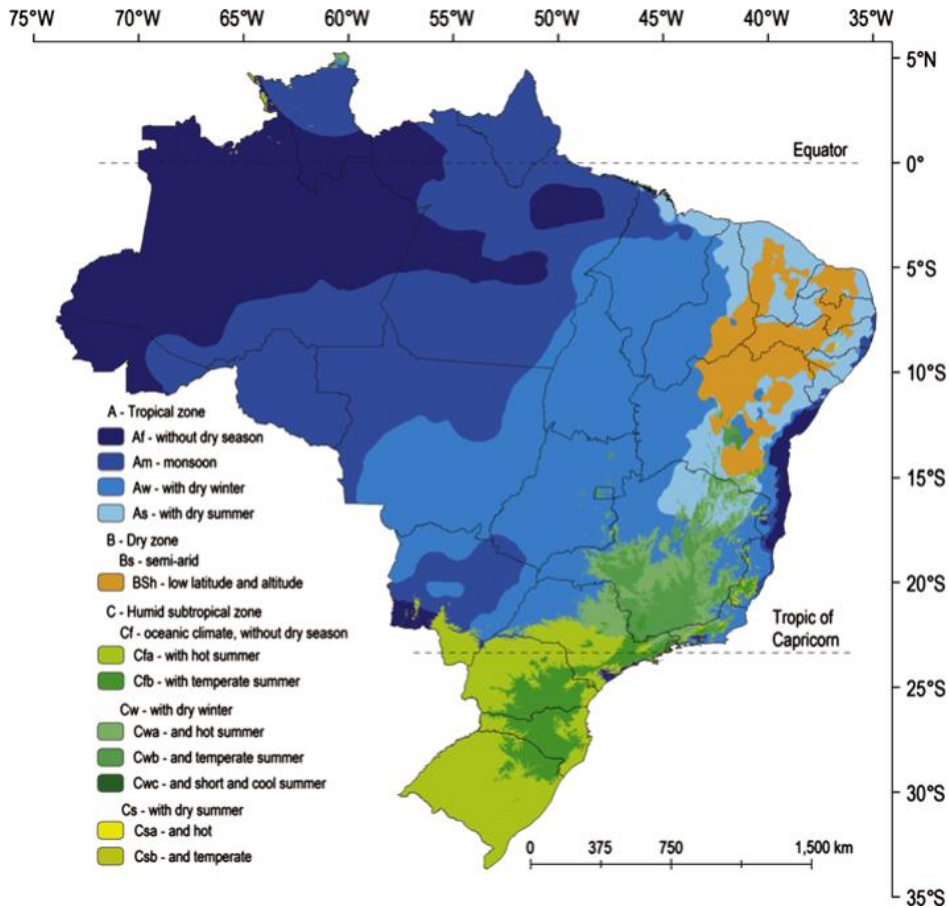


Fig. 1 General climate classification for Brazil, according to the Köppen (1936) criteria. Retrieved from Alvares et al. (2013).

1.2 Vegetation of Southern Brazil

Southern Brazil forms part of the Atlantic Forest Biome (**Fig. 2**), this harbour a high species richness and endemism, hence is considered one of the most important hotspots of biodiversity in the world (Myers et al., 2000). It is also a target of conservation because it has been strongly threatened, with over 70% of its original cover destroyed, by anthropogenic action, fragmentation, introduction of exotic species, trafficking and extraction of native species, among others (Myers et al., 2000; Rodrigues Salgado et al., 2019). Nonetheless its loss of extension, today still host more than 60 percent of all

terrestrial species on the planet (Galindo-Leal & Camara, 2003).

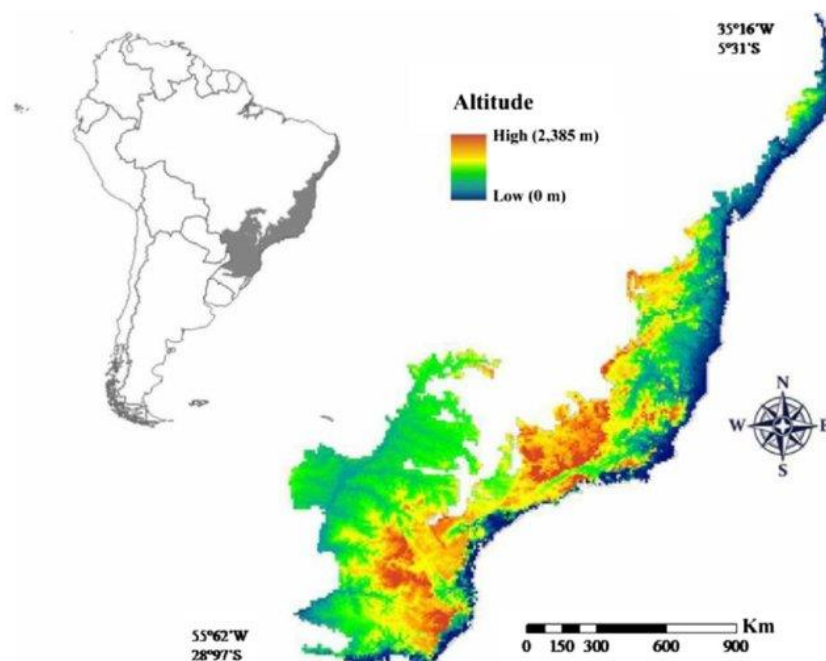


Fig. 2. Map of distribution of the Atlantic Forest Biome. Colors indicate change in elevation. Retrieved from Lourenço-de-Moraes et al. (2019) – original source.

The south of Brazil hosts several types of ecosystems of the Atlantic Rainforest Biome, such as Mixed Ombrophilous Forest (*Araucaria* forest), Dense Ombrophilous Forest, Semi-Deciduous and Deciduous Forest, Savanna (Cerrado), Grassland (Campos), and it is therefore ideal for our research aims. For this research the mosaics of *Araucaria* forest and Grassland (Campos) were selected in two different locations, Vila Velha State Park (Paraná) and National Park of Aparados da Serra (Rio Grande do Sul).

Mixed Ombrophilous Forest (*Araucaria* forest)

High rates of endemism (~40%) characterize the mixed ombrophilous forest, here more than 350 species of tree flora occur. This type of vegetation can be defined as a phytogeographic unit, whose characteristic element is *Araucaria angustifolia* (Bertol.) Kuntze, a long-lived and heliophilous (adult phase) conifer that reach a mean width of 3 m and height of 50 m. In general, its occurrence is registered from 200 m to 1500 m in altitude (Kersten et al., 2015) and its limited by a temperate climate, high amount of

rainfall and periods of frost. In all of its distribution area, it rarely registers less than 1400 mm of rain per year, reaching up to 2450 mm in the west of Serra do Mar. Mean annual temperature of maximum 18°C, with a monthly one oscillating between 10°C (coldest months) to >20°C (warmest months) (Fritzsos & Wrege, 2017; Rodrigues Salgado et al., 2019).

Dense Ombrophilous Forest

Characterized by a great plant richness and endemism with all year green leaf tree species reaching up to 50 m of height, together with abundant species of epiphytes and lianas (woody ones), this type of vegetation occurs between 800 and 1500 – 1700 m in altitude. Some of the most important plant families are Asteraceae, Bromeliaceae, Lauraceae, Melastomataceae, Myrtaceae, Orchidaceae and Rubiaceae (Boeger et al., 2005; Reginato & Goldenberg, 2007). Ecologically, highlights its ombrophilous environments, which are associated with the tropical climate factors with high temperatures and high amount of rainfall, this well distributed along the year and without periods of drought (Galindo-Leal & Camara, 2003).

Semi-deciduous forest

This forest type is ecologically established according to the occurrence of a seasonal climate that determines the semi-deciduous nature of the forest cover foliage. In the tropical zone, it is associated with the region marked by severe winter drought and intense summer rains; in the subtropical zone, refers to a climate without a dry period, but with a cold winter (average monthly temperatures <15°C), thus determines physiological dormancy and partial fall of foliage. The percentage of deciduous trees in the forest, rather than the species that lose their leaves individually, is usually between 20% and 50% (IBGE, 2012).

Deciduous forest

In here, dual climate seasonality conditions the forest. This seasonality is determined by a rainy season, this can last even more than seven months in the tropical region, and followed by a long dry season, in which prolonged cold weather can last five months or more in the subtropical region, with average temperatures below 15°C. About 50% of the trees that form part of this type of forest are deciduous, meaning that they lose their leaves seasonally (IBGE, 2012; Rodrigues Salgado et al., 2019).

Savanna (Cerrado)

Savanna is the principal used term and Cerrado belongs to a regionalist synonym. Savanna was chosen as the vegetation type presents an ecological phytophysiology similar to that of Africa and Asia. Is conceptualized as xeromorphic vegetation and its flora present peculiar adaptations to fire, it occurs under different types of climate with two contrasting seasons, dry winter and a moist summer. The Cerrado is the tropical savanna with the largest number of plant species on Earth (~12,000), with one-third considered endemic (Forzza et al., 2012; Haridasan, 2008; Henriques, 2005).

Grassland (Campos)

Defined as territorial extensions devoid of arboreal or uncultivated vegetation, that is, regions that are deserted in terms of use and not necessarily in the geobotanical sense, although it also includes it (IBGE, 2012). Campos vegetation is characterized by high species richness, with more than 4000 species identified just in Rio Grande do Sul state. The most species-rich plant families are Asteraceae, Poaceae, Leguminosae and Cyperaceae and the two main factors that shape this vegetation type are grazing and fire (Overbeck et al., 2007, 2018).

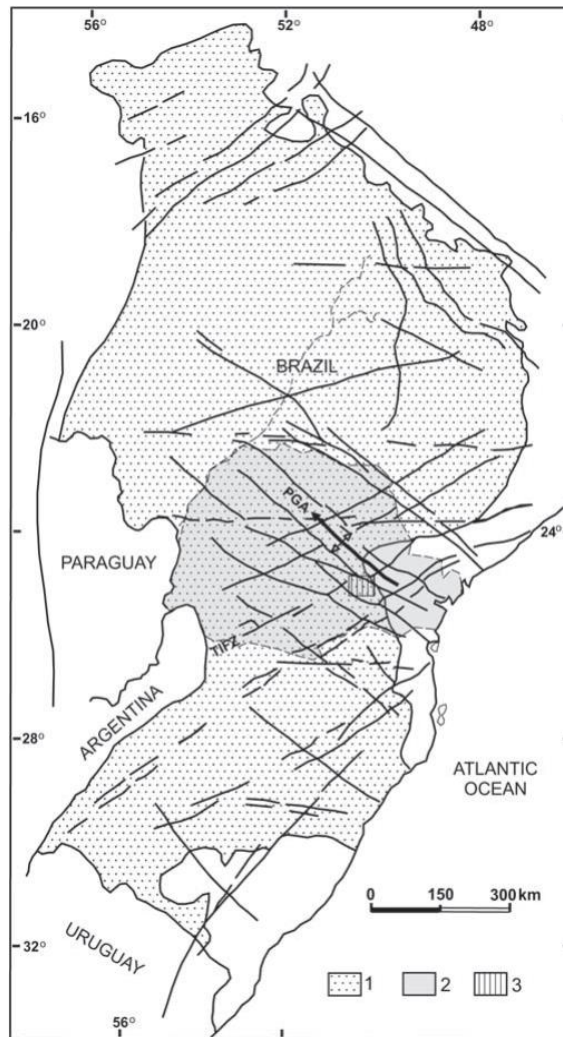
1.3 Study sites: Paraná and Rio Grande Do Sul

1.3.1 Vila Velha State Park and Lagoa Dourada (Paraná)

The park lies between the coordinates 25°08' - 25°15'S and 49°53' - 50°03'W and it has an area of approximately 3122.11 ha. It is part of the Municipality of Ponta Grossa, about 25 km southeast from Ponta Grossa city and 120 km northeast from the capital of the State of Paraná, Curitiba city. The park was created as a consequence of its ecological and geological history, so-called a rich natural heritage, with its particularly rock outcrops, its flora and fauna (Governo do Estado de Paraná, 2004). To the southwest of the park is found Lagoa Dourada at an altitude ca. 850 m a.s.l., it is a small round lake (100 m diameter) that contain Late Pleistocene - Holocene sediments (Moro et al., 2004).

1.3.1.1 Geology and Geomorphology

The study area is located geologically on the eastern border of the Paraná Basin, a vast depression on the lithosphere, that spread across Brazil, Uruguay, Argentina and Paraguay. The Basin is affected by the up warping of the Ponta Grossa Arch, moving to the Northwest and Southeast (**Fig. 3**). During the Mesozoic, the lower sedimentary rocks of the Paraná Basin were exposed, as a consequence of erosional processes, fractures and



up warping. Among the exposed elements are the sandstones of the Furnas Formation (Devonian), they constitute the main basal unit of the Paraná Basin in the study region. Here Carboniferous (Itararé Group) and Mesozoic (diabase dykes) formations also occur (**Fig. 4**) (Assine, 1996; Melo et al., 2003; Melo & Fonseca, 2007). Geomorphologically the study area is located on the Second Paraná Plateau, this plateau is one of the compartments of the stepped relief of the State of Paraná, occurring at elevations between 1100 and 800 m and having a gentle westerly slope (Melo & Fonseca, 2007; Moro et al., 2004). Besides, the study area corresponds to the hydrographic basin of the Guabiroba River (**Fig. 4**), which watershed is the source area of Lagoa Dourada sediments.

Fig. 3. Geological characteristics and main structures of the Paraná Basin, southern Brazil. 1: Paraná Basin rocks in Brazil; 2: State of Paraná; 3: Study area; PGA: Ponta Grossa Arch. Retrieved from Melo & Fonseca (2007)

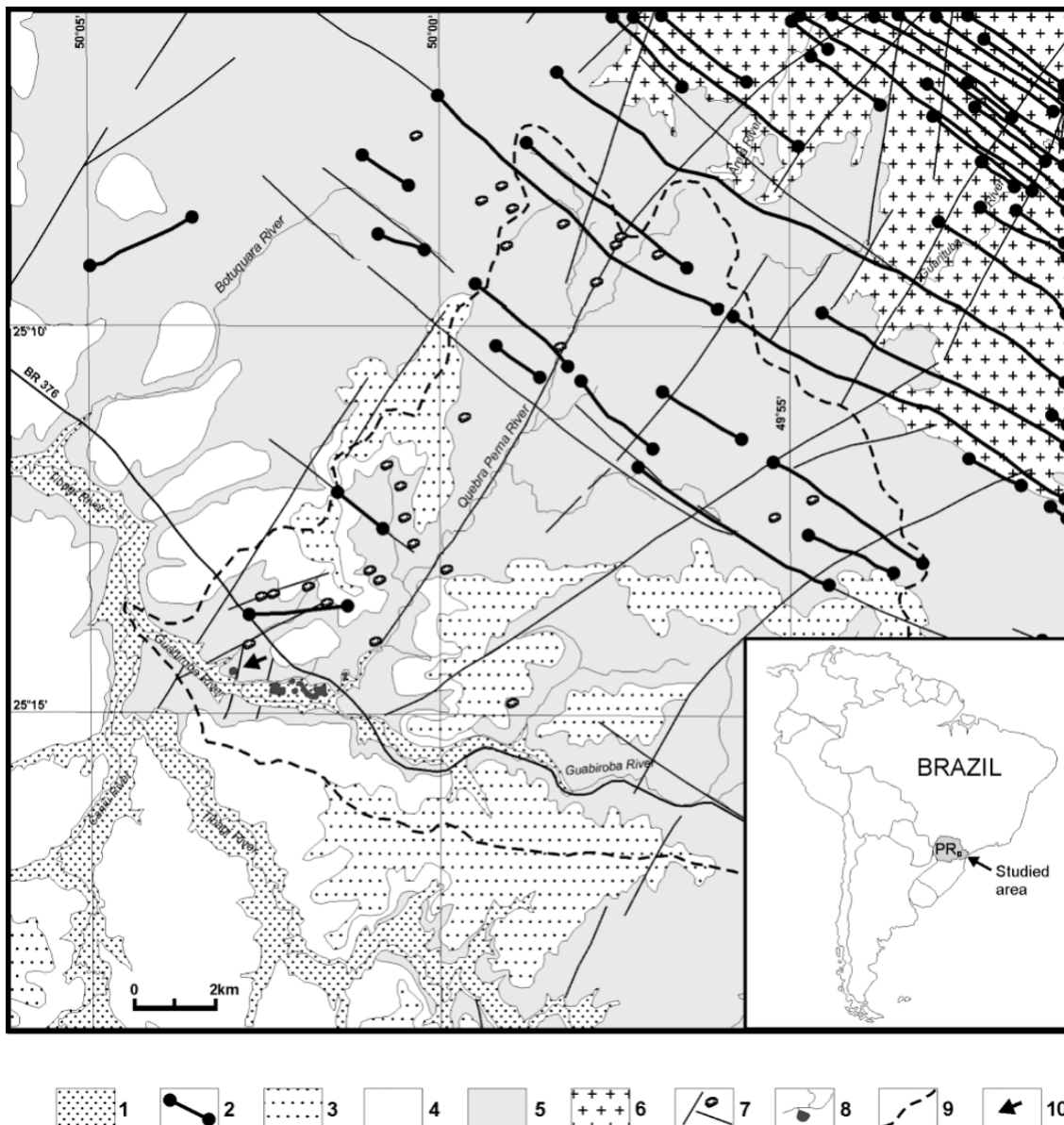


Fig. 4 Geography and geology of the study area; 1: Quaternary alluvium; 3: Itararé Group; 4: Ponta Grossa Formation; 5: Furnas Formation; 6: Proterozoic basement; 7: main geological structures (faults, fractures and furnas); 8: rivers and ponds; 9: limits of hydrographic basin of the Guabiroba River; 10: Lagoa Dourada. Retrieved from Melo et al. (2003)

1.3.1.2 Climate and Vegetation

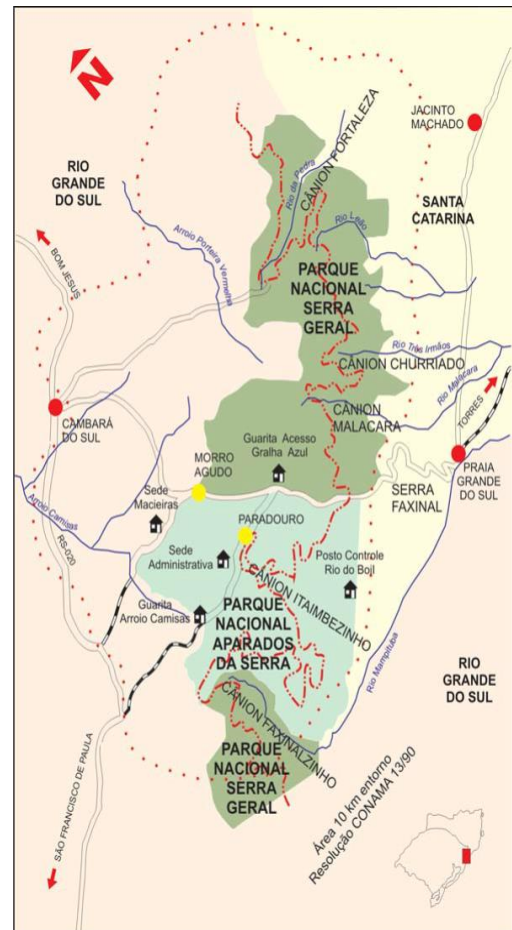
The climate in Vila Velha is characterized by a mean annual temperature of 17,4°C and annual precipitation of 1554 mm with more moisture availability during January and February and a small decline in April to August (Alvares et al., 2013; Melo et al., 2003).

Located in the Atlantic Forest Biome (IBGE, 2004) Vila Velha contains several ecosystems like; the Mixed Ombrophilous Forest (*Araucaria* forest), Alluvial Mixed Ombrophilous Forest (Gallery forest), Grasslands (Campos), open Savanna (Campo limpo/sujo) and Fluvial Influence Pioneer formations (wetlands, marshlands or várzea) (Cervi et al., 2007).

1.3.2 Aparados da Serra National Park (Rio Grande do Sul)

Located between the coordinates 29°07' - 29°15' S and 50°01' - 50°10' W, about 197 km away from the city Porto Alegre, the capital city of Rio Grande do Sul state. Aparados da Serra National Park has an extension of 59505 ha that extends also to the state of Santa Catarina, however, this investigation was carried out on the portion of the park located in Rio Grande do Sul state (**Fig. 5**). The park was created in 1957 as a measure to protect the natural beauties of the region, such as its particular canyon formation Itaimbézinho and the *Araucaria* forests (MMA & IBAMA, 2007).

Fig. 5. Location map showing the limits of the Aparados da Serra National Park and Serra Geral National Park. Retrieved from IBAMA.



1.3.2.1 Geology and Geomorphology

The study area geologically is located in the Paraná Basin on the Serra Geral and Botucatú formations. Lithologically Serra Geral formation is a sequence of basic rocks to intermediaries of the Serra Geral Formation, composed of rocks belonging to 3 large groups: basalt, andesite and basalt with glass, those formed from the rapid cooling of lava rich in magnesium and iron (MMA & IBAMA, 2007).

1.3.2.2 Climate and Vegetation

Located at the edge of the high-land the park receives a strong influence from the Atlantic. Climate is characterized by a mean annual temperature of 14,8°C and annual precipitation of 1807 mm with September and October as the wettest months (Alvares et al., 2013).

The vegetation in the park and surroundings is an extremely heterogeneous vegetation complex, conditioned mainly by geological, geomorphological, pedological, climatic and hydrographic factors. In the study area and surroundings, there are few remnants of the Dense Ombrophylous Forest with great richness and diversity, also encountered are *Araucaria* forest, Cloud Forest and Grassland (Campos, seco, rupestre and turfoso) (MMA & IBAMA, 2007).

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2. *ARAUCARIA* FOREST GRASSLAND MOSAICS, ECOLOGY AND PRIOR RESEARCH

2.1 Morphology and phenology of *Araucaria angustifolia*

Araucaria angustifolia taxonomically belongs to the Araucariaceae, a family of conifers from the southern hemisphere originated in the Triassic period. The shade-intolerant conifer dominates the canopy strata of the mixed ombrophilous forest in South America (Hueck, 1972). It occurs in a range of climatic scenarios and different plant associations (Wrege et al., 2009) and is characterized for being a dioecious wind-pollinated tree, that generally present high-density populations (>20 reproductive trees/ha) in which the proportion of females and males goes from 52% to 48%, respectively (Bittencourt and Sebbenn 2008).

Flowers are developed in the second-order branches, the male cones are robust, dense and cylindrical, they extend shortly beyond the axil of the leaves. Female cones are globular growing at the youngest ends of lateral branches (Hueck, 1972). In natural stands, cone production usually starts in trees older than 20 years, while seed dispersal occurs generally only by autochory near to seed-tree due the size and weight of the seeds (Bittencourt & Sebbenn, 2007). Seeds are highly nutritious in which about 23% of its dry weight is amylose, which is similar to the amylose content of corn and potato, in consequence, they are of value and interest for several birds and mammals (Conforti & Lupano, 2007).

Flowering occurs between April and June, fecundation between September and October, seed production from April to July, and germination time take place between 60 to 120 days, those ranges can slightly vary depending on factors such as climatic conditions (Bittencourt & Sebbenn, 2007; Wanderley et al., 2002). Palynologically *A. angustifolia* is characterized by relatively large pollen grains (60 µm), non-saccate, with a reduced ability to float and a high pollen producer (Cárdenas et al., 2019; Sousa & Hattemer, 2003).

2.2 Dynamics of the *Araucaria* forest Grassland mosaic: a general overview

Nowadays, the southern highland region of Brazil is covered by a dominated mosaic of grasslands (Campos) and *Araucaria* forest vegetation. This natural vegetation and its boundaries are believed to be determined by grazing and fire regimes (Overbeck et al., 2007). Regarding the distribution of *A. angustifolia*, the tree originally, *Araucaria* forests occupied 175000 km² in Brazil and 2100 km² in Argentina in a wide range of elevations, from 200 to 1800 m (Carvalho, 1994; Giraudo et al., 2003; Mesquita & Filho, 1990). Today is natural distribution (**Fig. 6**) is reduced about 1–3% of its original area and it remains as isolated patches still mixed with Campos, this reduction is mainly attributed to changes in land use, grazing, agriculture, plantations, the lack of protective policies and natural reproduction difficulties, which may be related to climate change (Cattaneo et al., 2013).

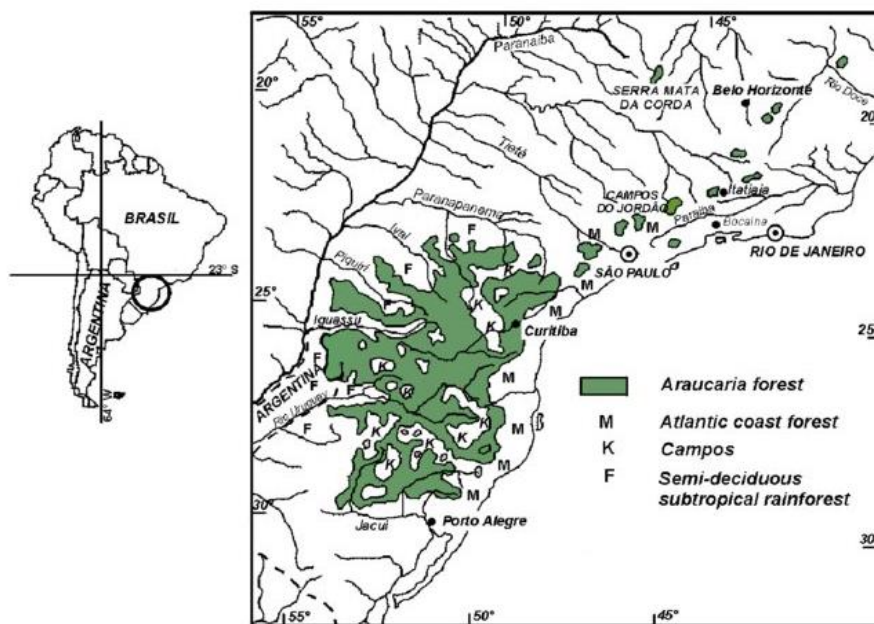


Fig. 6 Map with the distribution of *Araucaria* forest and Campos in South Brazil (according to Hueck 1966). Taken and modified from Rau (2005).

In southern Brazil palynological studies from the states of Paraná (Behling, 1997; Jeske-Pieruschka et al., 2013), Santa Catarina (Behling, 1995) and Rio Grande do Sul (Behling et al., 2001, 2004) proved that Campos covered extensive areas on the highlands during glacial times, and early until Mid-Holocene times. This dominance of Campos is attributed to the climatic conditions in which during glacial times was cold and dry, while Early Holocene is characterized by a warm and dry climate. *Araucaria* forests are also registered during late Pleistocene times since ~42000 cal yr BP (Behling et al., 2004). Nonetheless, it is to believe that those occurrences of the *Araucaria* pollen were most likely due to wind transport from possible forest refugia in deep and protected valleys in the highlands, the slopes of Serra Geral mountains or even from the lowland vegetation of the coastal region. The expansion of *Araucaria* is hypothesized to start due to the migration from gallery forest and wetlands along the rivers about 3210 cal yr BP, indicating a change to somewhat wetter climatic conditions. The strongest expansion occurred later and at different times, first in Paraná state about 1400 cal yr BP (Behling, 1997, 2007) and later in Santa Catarina at about 1000 cal yr BP (Behling, 1995), both areas characterized by humid climate without a marked dry period.

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3. PALAEOECOLOGY

3.1 The multi-proxy approach and high-resolution analysis

A complex network of countless interactions throughout an ecosystem among biotic and abiotic parameters is hard to estimate, understand and interpreted. Many changes can occur in different directions and times before observation is possible. The study of fossil records allows us to look at the past in different time scales (resolution). High-resolution analyses refer to those in which temporal scales of observation are as small as they can be, giving us detailed information of an ecosystem and therefore allowing us to better understand biotic processes and species responses to climate change and disturbances like fire and human impact (Finsinger et al., 2017; Tinner et al., 2013)

The data obtained from different proxies permit us to reconstruct the past history of the ecosystems and its response to different process as mentioned, climate change and disturbances. The main advantage while analysing different proxies, both biotic and physical is that allows to reduce misinterpretation that can derive when just one proxy is been used in the reconstruction. Besides, it allows generating hypotheses on causalities on changes and them to be tested (Birks & Birks, 2006).

In the present research coring of lake sediments was done in Lagoa Dourada in the state of Paraná. The investigations follow a high-resolution multi-proxy approach in collaboration with other researchers. However, the body of my research (the one presented in here) is based on pollen and charcoal analyses.

3.2 Pollen-vegetation relationships and Quantitative Reconstructions

Estimating several vegetation parameters makes vegetation history more accurate and interesting, by giving a better picture of the past plant diversity and the way this has changed through time (Broström et al., 2004). The analysis of pollen is one of the most

useful and effective proxies to reconstruct past vegetation history and it is applied globally, during years these reconstructions have been done presenting data as pollen percentages of taxa (Davis, 2000). However, reconstructing past vegetation, quantitatively, from fossil pollen samples has been a goal of palaeoecologist since the beginning of pollen analysis (von Post, 1916).

The production and dispersion of the pollen spectrum vary between species; therefore, the pollen percentages are not assumed to be equal to relative abundances of the species in the vegetation (Cassino et al. 2015). This theoretical approach is known as the Fargerlind effect and using the appropriate factors for correct pollen percentages this effect can be made to disappear (I. C. Prentice & Webb, 2009).

To estimate past vegetation abundances, it is necessary to understand modern pollen-vegetation relationships. Establishing the relationship of surface sediment pollen spectrum of different ecosystems with the actual vegetation cover has been proven essential for correctly interpret fossil pollen assemblages and the palaeoecological reconstructions, as well as to estimate past vegetation abundances and quantitative reconstruct vegetation cover (Medeanic et al. 2016). Nonetheless, different factors can affect this relationship such as pollen productivity, dispersion and deposition, spatial patterns of the plants, structure, distance from pollen sample point and basin size, among others (Broström et al., 2004; Bunting & Middleton, 2009; Sugita, 2007).

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4. TOWARDS QUANTIFYING CHANGES IN FOREST COVER IN THE *ARAUCARIA* FOREST GRASSLAND MOSAIC IN SOUTHERN BRAZIL

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Abstract

Quantitative estimates of past vegetation cover are needed regionally, so human-landscape interactions can be better understood and globally to evaluate the effects of changing vegetation cover on the climate system. Models reducing the bias in the pollen representation of vegetation cover have been developed in the temperate regions of the northern hemisphere, while experience applying them in other parts of the world is limited. The *Araucaria* forest-grassland mosaic of southern Brazil is an area where open and forested plant communities exist naturally and have changed their cover over time due to changing climate and human activities. Therefore, this area is of particular interest for such studies. Modern pollen and vegetation comparisons were carried out in two protected areas: Vila Velha State Park in Paraná state and Aparados da Serra National Park in Rio Grande do Sul. Vegetation mapping and analysis focused on *Araucaria angustifolia* as the characteristic tree of this vegetation type.

In the *Araucaria* forest-grassland mosaic open vegetation and woodland change on the scale of hundreds of meters. These changes are difficult to capture based on pollen proportions in surface samples. While the abundance of Poaceae pollen is not a good indicator of locally open conditions, several pollen taxa can be used as indicators of the local vegetation cover. Pollen vegetation ratios (R-values) compare well between the two study regions indicating that pollen production of individual species within the large plant families of Poaceae and Asteraceae are similar within the overall region. *Araucaria angustifolia* pollen is underrepresented with regards to its vegetation cover, while Poaceae are among the highest pollen producers in the region. Diverse woodland species other than *Araucaria angustifolia* were grouped as one forest taxon and as the species composition of woodlands differed between the two study areas, so did the estimated pollen productivity of this group. It would be rewarding in future investigations to estimate pollen productivity for groups of trees with the same pollen dispersal syndrome. The application of pollen dispersal models designed for closed canopy in the protected areas was challenging. Further model development is required to deal with pollen released at different levels in semi-open vegetation types.

4.1 Introduction

One of the main goals of pollen analysis is to reconstruct the vegetation cover of past landscapes. Pollen provides a biased representation of the vegetation resulting in the need to study the relationship between pollen and modern vegetation to reduce that bias. A simple but effective approach is to collect modern samples from different landscapes as modern analogues to interpret the fossil record, which can be matched statistically (e.g. Zanon et al., 2018). While this method is utilized since the development of pollen analysis (e.g. Auer, 1927), it still provides valuable insights where a numerical description of environmental parameters associated to surface samples is available (e.g. Davis et al. 2013). In Europe and North America, pollen vegetation comparisons were developed with the final goal to correct the values in pollen diagrams directly. Davis (1963) introduced the R-value as the ratio of pollen to vegetation in the same vegetation plot. However, pollen coming from beyond the vegetation plot require more sophisticated analytical approaches to the problem (Parsons and Prentice 1981). Andersen (1970) used absolute pollen deposition data obtained from pollen traps and compared it to the basal area of the trees in the vicinity of the traps producing correction factors for the production of common European trees. In this case of pollen traps situated under the canopy, differential pollen transport is not important. However, the physical properties of different pollen types result in some pollen types staying airborne for longer, which will influence the pollen signal in most situations.

Mechanistic models of pollen transport can describe this differential dispersal of pollen types. Applied within the Extended R-value Model (ERV), the differential pollen production relative to a reference taxon can be evaluated (Prentice 1985; Sugita 1993). Motivated by the desire to reconstruct the deforestation of European landscapes with the introduction and intensification of agriculture (Roberts et al. 2018), these models and approaches were refined mainly in Europe (Gaillard et al. 2008). Recognizing the importance of vegetation feedback for explaining past climate change (Gaillard et al. 2010; Strandberg et al. 2014) motivated quantitative estimates of global vegetation cover change (Harrison et al. 2020). However, while pollen diagrams are becoming more readily available globally (Williams et al. 2018), estimates of relative pollen production for major plant groups are hitherto not available for most regions.

In South-America, a large number of local and regional pollen surface sample studies have been conducted generally to assist in the qualitative interpretation of pollen diagrams

(Flantua et al. 2015, Marchant et al. 2009). Little of that data is available and/or linked to environmental parameters allowing quantitative reconstructions (Montade et al. 2019). This shortcoming is represented by the small number of studies available from South America providing any kind of quantitative reconstruction based on pollen, as visible in the distribution of global pollen-based climate reconstructions by Bartlein et al. (2011). Quantitative estimates of past vegetation cover in South America have so far only been attempted for Southwestern Amazonia, reducing the landscape to two vegetation types: forest and non-forest (Whitney et al. 2018). This lack of quantitative vegetation reconstructions is partly due to the shortage of detailed information on the pollen representation of South American vegetation types (Whitney et al. 2018). To date, no study has been published for South America estimating relative pollen productivity following approaches developed in Europe and North America based on individual field studies (Bunting et al. 2013) or using available data (Dawson et al. 2016).

Pollen vegetation relationship studies indicating overrepresented and underrepresented taxa are available for specific vegetation types such as saltmarsh (Medeanic et al. 2016), coastal vegetation (Fontana 2005; Masciadri et al. 2013) and Cerrado (Ledru 2002). Studies explicitly estimating the pollen vegetation ratio using pollen traps and forest inventory data have been published for Barro Colorado Island, Panama (Bush and Rivera 1998; Haselhorst et al. 2020) as well as Noel Kempff Mercado National Park and Beni Basin in Bolivia (Gosling et al. 2005, 2009; Jones et al. 2011). Montade et al. (2016) published averaged pollen vegetation ratios for three isolated mountains in Ceará, north-eastern Brazil, based on a collection of surface soil samples and botanical surveys. Analyzing the pollen composition of moss pollsters collected in a private forest reserve compared to vegetation survey and long-term monitoring data, Cárdenas et al. (2019) provide ratios of average pollen versus vegetation proportions. Overall quantitative pollen vegetation studies are indeed rare and have so far not developed beyond the R-value approach. These are generally based on averaging pollen and vegetation information, rarely calculating the ratio of values, making them comparable between sites. While these values are informative general problems of the R values need to be considered (Parsons and Prentice 1981).

Reconstructing changes in vegetation cover in South America is of interest in understanding the impact of pre-Columbian societies (McMichael et al. 2012) and climatically driven forest cover changes (Rodrigues et al. 2016). This is of particular interest in the *Araucaria* forest-grassland mosaic of southern Brazil, where pollen diagrams document a stepwise shift from open grasslands to dense forests during the Holocene (e.g. Behling et al. 2004). The area is part of the Atlantic Forest biome, a global biodiversity hotspot (Colombo and Joly 2010) and understanding its natural dynamics will contribute to securing its future survival. Before European arrival, this landscape was home to the southern Jê, which had semi-sedentary lifestyles and might have contributed to the afforestation as their diet included the seeds of *Araucaria* (Iriarte and Behling 2007). Several fossil pollen diagrams exist from the region, and their interpretation has so far been qualitative, relying on expert knowledge.

This study aims to analyze the pollen vegetation relationship in the *Araucaria* region of southern Brazil to improve our ability to reconstruct local forest cover changes, both qualitative and quantitatively. Going beyond the simple R-value approach, we aim to estimate relative pollen productivity for a few dominant pollen taxa with a special focus on *Araucaria angustifolia*. We also investigate the general applicability of these values by selecting two study regions with contrasting climate.

4.2 Environmental setting and methods

4.2.1 Geography and climate

The two study regions are located in southern Brazil and differ in relation to their proximity to the Atlantic Ocean, resulting in differences in precipitation. Vila Velha State Park (25°12' S, 50°02' W) in Paraná state is situated more inland with a stronger seasonal climate. Aparados da Serra National Park (29°10' S, 50°07' W) in Rio Grande do Sul is located at the edge of the high-land with strong Atlantic influence (**Fig. 7**). The study areas are situated at an elevation of 850-960 m a.s.l. and ca. 900-1000 m a.s.l. respectively. The climate in Vila Velha is characterized by a mean annual temperature of 17,4°C and annual precipitation of 1554 mm with more moisture availability during January and February. In Aparados da Serra the mean annual temperature is 14,8°C and annual precipitation of 1807 mm, with September and October as the wettest months (Alvares et al. 2013)

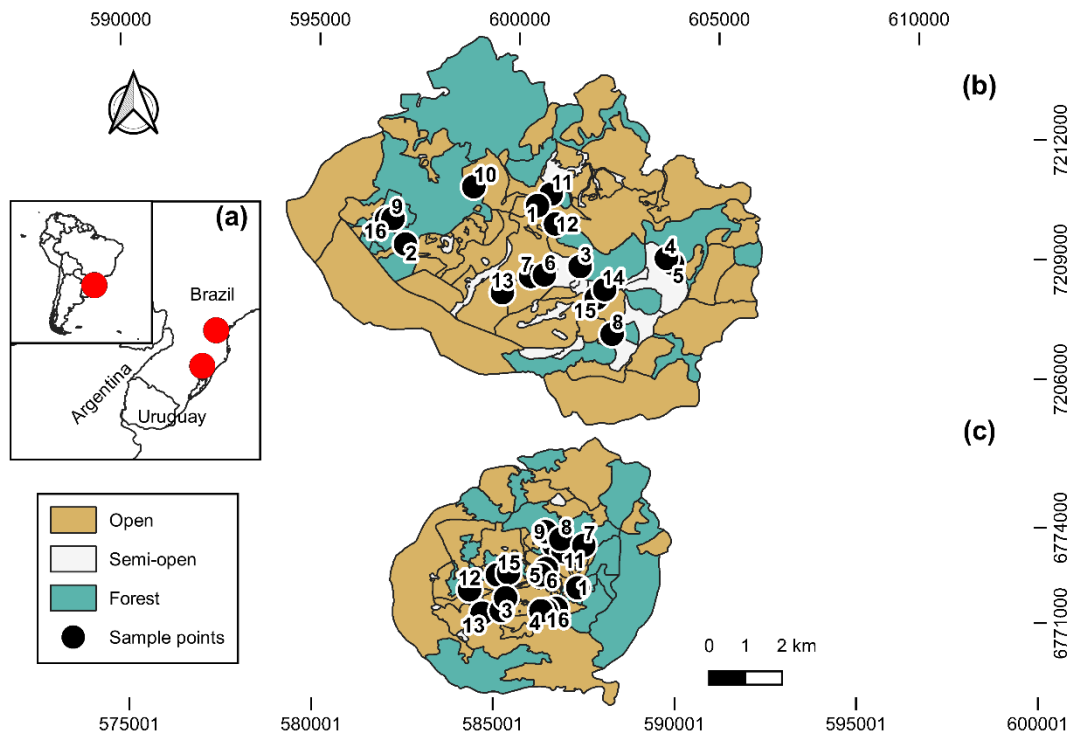


Fig. 7 A) Location of the study area and distribution of the sampling sites in B) Vila Velha State Park and C) Aparados da Serra National Park.

4.2.2 Vegetation

Vegetation in both parks is characterized by a mosaic of *Araucaria* forest and grassland. Species composition of forests and grasslands is different in the two parks. Vila Velha shows elements of the Cerrado vegetation biome. Open grassland areas are mainly related to shallow soils on the sandstone, while woodlands and semi-open areas dominated by large shrubs occupying the valleys and locations with deeper soils. Small groups of *Araucaria angustifolia* trees occur in open areas, and the tree is dominating some forest patches. However, the majority of the woodlands are dominated by taxa of the Myrtaceae, Fabaceae, Melastomataceae, Lauraceae and Asteraceae families, *Araucaria angustifolia* is usually sub-dominant.

The grassland vegetation is also highly diverse, including Cyperaceae, *Dicksonia* sp., Poaceae and Asteraceae. The most abundant species are the grasses *Aristida jubata*, *Andropogon bicornis* and *Trachypogon canescens*. The most diverse plant family is the

Asteraceae with 208 species, including 34 in the genus *Baccharis* (Cervi et al. 2007; Dalazoana et al. 2007; Mocoehinski and Scheer 2008).

In contrast, in Aparados da Serra the forest patches are dominated by *Araucaria angustifolia* in the emergent layer, usually accompanied by *Mimosa scabrella* and *Pictocarpa angustifolia* in the canopy layer and by arboreal elements such as *Lamanonia speciosa*, *Ilex microdonta*, *Podocarpus lambertii*, *Sapium glandulatum* and, *Myrsine* spp in the understory. Small trees and shrubs from the families Melastomataceae (*Tibouchina*, *Leandra*, *Miconia cinerascens* and *Miconia sellowiana*) and Myrtaceae (*Myrceugenia euosma* and *Siphoneugena reitzii*) are common, the woody bamboo *Merostachys multiramea* is also present but less frequent (Rambo 1956; Baptista et al. 1979; MMA and IBAMA 2007).

A semi-open vegetation type is rare in Aparados da Serra. Here, the vast valleys are often filled with wetlands. Open vegetation patches are dominated by Poaceae, *Baccharis* spp. or *Eryngium* spp. Other important herbaceous taxa are *Polygala* spp., *Euphorbia* spp., *Cyperus* spp., *Bulbostylis* spp., *Rhynchospora* spp., *Sisyrinchium* spp., *Dicksonia sellowiana* and *Cyathea* spp. *Acaena eupatoria*, *Tradescantia* spp., *Desmodium* spp., *Oxalis* spp., and *Chaptalia* spp. In this park, Asteraceae family is highly diverse, with 133 species, including 34 belonging to the genus *Baccharis* (Rambo 1956; Baptista et al. 1979; MMA and IBAMA 2007).

4.2.3 Pollen sampling and vegetation surveys

Vegetation surveys were carried out together with the collection of samples for pollen analysis in July 2018. Sites were selected in a way to obtain a good representation of the different vegetation types and cover a gradient from fully open to fully forested situations. If possible, pollen samples were taken in small wet spots with mosses present. Here, the green parts of the mosses were sampled, assuming that it would contain at least one year of pollen deposition. Where no mosses were present, we sampled the soil litter. In all situations, several samples were collected from within about one square meter and mixed. The centre point for the collection of the pollen sample was taken as the centre for the vegetation sampling. The location was recorded with a GPS (**Appendix 1**).

The vegetation was surveyed following the general strategy proposed by Bunting et al. (2013). Out to 10 m from the sampling points, the vegetation survey was conducted as

walking-in-circles spaced 2 m apart, estimating and mapping vegetation cover (Broström et al. 2004). The radius of the innermost circle was 1 m. The area out to 50 m from the sampling point was sketched and described based on transects in the four directions of the compass. Only mature, pollen-producing trees were included. A general vegetation map was constructed out to 2000 m from the sampling points based on satellite images and field notes (Fig. 1). Mapping was done using QGIS 3.4.0 software.

4.2.4 Samples and data treatment

All samples were treated with 10% hot KOH, 10% hot HCL, 70% cold HF, and three minutes of hot acetolysis in the laboratory. After the KOH treatment, the samples were sieved using a 150 µm mesh size to remove larger organic and inorganic remains. Mounted samples were analyzed at 400X and 1000X magnification, a minimum of 300 pollen grains per slide were counted. The identification of palynomorphs was carried out using the references collections of the Department of Palynology and Climate Dynamics of the University of Göttingen as well as catalogues of pollen and palynological keys by Bauermann et al. (2013), Roubik and Moreno (1991) and Silva et al. (2016) and the online Neotropical Pollen Key (Bush and Weng 2007).

Sites were classified as open, semi-open or forested vegetation types based on the vegetation data within a 100 m distance from each pollen sample. The classification carried out using unconstrained cluster analysis with the squared chord distance and Ward's method for linking samples. The Dufrene-Legendre Indicator Species Analysis (indval) was performed on the pollen data using the vegetation classification to explore whether individual pollen taxa may identify the different vegetation types. PCA was performed to visualize the major differences in pollen composition and explore the similarities between pollen and vegetation data. Analyses were performed in R using the “vegan” and “labdsv” packages (Dufrene and Legendre 1997; Oksanen et al. 2017).

We calculated the representation factor (R-value sensu Davis 1963) to compare to other studies from South America using this simple ration and evaluate the results obtained with the more sophisticated Extended R-Value model (ERV). Representation factors have

been estimated for single sites as well as mean values over all sites in each study area, following Eq. (1):

$$R = p/v_i = \frac{\text{Pollen abundance}(\%) \frac{\text{averaged}}{\text{all}} \text{sites}_i}{\text{Vegetation abundance}(\%) \frac{\text{averaged}}{\text{all}} \text{sites}_i}, \quad (1)$$

4.2.5 Relative pollen productivity estimates (PPEs)

Estimates of the relative pollen productivity for *Araucaria angustifolia*, Asteraceae, *Baccharis*, Cyperaceae, Poaceae and Forest were obtained with the Extended R-Value model, as implemented in ERV.Analysis.v2.5.3.exe software (Sugita 2017 unpublished) and ERV Analysis in R (Theuerkauf & Couwenberg, under review). Analyses were initially run with all sub-models, however, ERV sub-model 1 gave the most consistent and logical results and analyses with sub-models 2 and 3 were not perused further. We used taxon-specific distance-weighting assuming a Gaussian plume diffusion model (GPM) of small particles in the air (Prentice 1985) as well as the Lagrangian stochastic model (LSM) (Kuparinen 2006). Following previous ERV studies (Broström et al. 2004), we set basin radius to 1 m. The GPM predicts very high pollen deposition near the pollen source, resulting in an unrealistically high weight of the vegetation in the first meter. In the case of *Araucaria angustifolia*, the GPM predicts that 98% of all pollen released would be deposited within 1 m from the tree.

Pollen productivity was initially computed relative to Poaceae as species of this family occur in all vegetation types. However, the lag of a strong gradient in the abundance of grasses led to spuriously high PPEs in some analysis. Therefore, we also performed the analyses with Cyperaceae as a reference taxon. The fall speed of pollen was estimated using Stoke's law (Gregory 1973) based on measurements of the diameter of at least 30 pollen grains. The “forest group” is used as a single pollen taxon but represents a large mix of trees from different plant families with various pollen types. Different pollen types pertained in that group were measured in a typical sample, and the average weighted by the proportional abundance of these pollen types was used to estimate the fall speed for this group.

4.3 Results

4.3.1 Modern pollen and vegetation data

The overall cover abundance of the vegetation within a buffer of 2000 m around all surface samples yielded similar vegetation proportions in Vila Velha and Aparados da Serra (**Table 1**), with *Araucaria angustifolia* (12% and 13%), Poaceae (23% and 24%) Cyperaceae (13% and 15%), and *Baccharis* (9% and 5%). The largest difference was found for “Forest taxa” with 26% and 19% in Vila Velha and Aparados da Serra respectively. The vegetation composition in the 100 m around each surface sample was used in a cluster analysis and compared to the assignment samples in the field to one of three classes “open” and “semi-open” and “forest”. Results of this cluster analysis yielded two main groups in both regions (**Fig. 8**). The cluster “semi-open” vegetation is related to samples from the “open vegetation” in Vila Velha, and to “forest” in Aparados da Serra. In Vila Velha the cluster analysis is not fully separating sites from open and semi-open areas. One group collects all semi-open vegetation sites (3, 4, 8, 14), but includes sites 5 and 10 from open environments. Both sites 5 and 10 are situated near rock outcrops, which reduces the overall vegetation cover and might be the reason for assigning the samples to this group.

Table 1. Vegetation composition within 2000 m radius, data given in percentage of area.

Name	Vila Velha	Aparados da Serra
<i>Araucaria angustifolia</i>	12.39	12.92
<i>Asteraceae</i>	9.67	13.75
<i>Baccharis</i>	8.99	5.49
<i>Cyperaceae</i>	13.42	14.83
Poaceae	23.02	23.65
Forest taxa	25.96	18.75
Other taxa	6.55	10.60

Pollen analysis of the 34 surface samples yielded a total of 75 different pollen and spore taxa (**Appendix 2**). In Vila Velha (**Fig. 8**) the most abundant pollen type is Poaceae (average 40%; min 18%; max 55%), followed by Cyperaceae (19%; min 2%; max 40%). The proportion of *Araucaria angustifolia* pollen varies between 0% and 18%, with an

average of 5%. All other tree pollen taxa are combined in the forest group (average 16%; min 4%; max 42%), with *Myrsine*, *Mimosa* and *Alchornea* as the most abundant. *Baccharis*-type (average 9%; min 1%; max 34%) is the most abundant Asteraceae pollen, and as plants of the genus were mapped in the field, it is considered separately. *Ambrosia*-type and *Senecio* are the most remaining Asteraceae pollen (average 11%; min 1%; max 27%) that are grouped under Asteraceae p.p. in further analyses.

Pollen percentages from both areas are compared to the results of the cluster analysis of the 100 m radius vegetation data (**Fig. 8**). For Vila Velha, pollen proportions of tree versus herbaceous pollen types do not show a clear difference between sites from the three environments. However, forest sites have higher pollen percentages of *Araucaria angustifolia* and Myrtaceae and lower proportions of *Baccharis*-type. Pollen and vegetation data show better correspondence for the samples from Aparados da Serra. The open vegetation group contains a cluster of three sites (3, 13, 15), which are wetlands within large open areas, and their pollen content reflects this in the dominance of Poaceae and Cyperaceae.

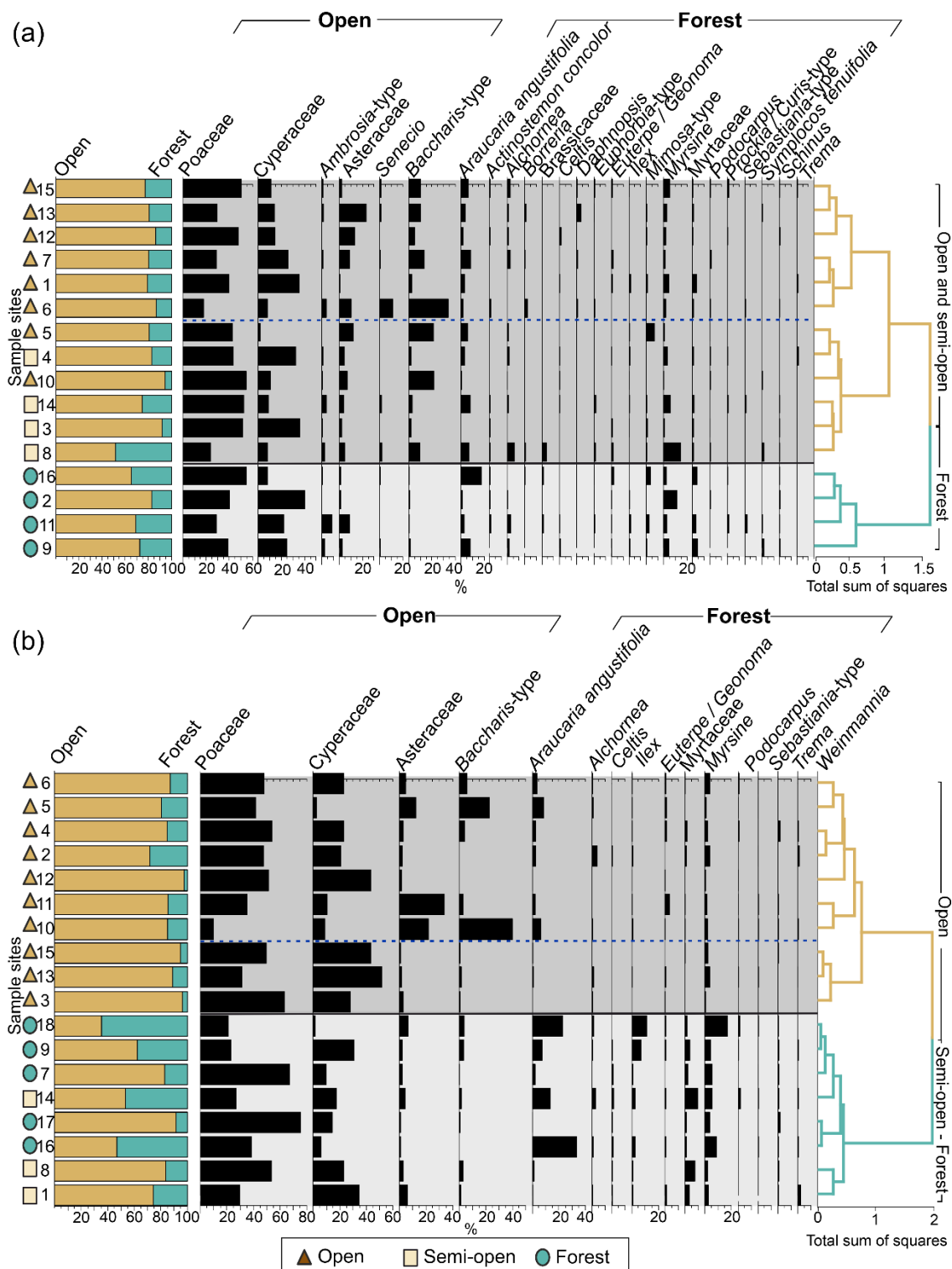


Fig. 8 Pollen diagrams for A) Vila Velha with 16 sampling points and B) Aparados da Serra with 18 sampling points. Dendrogram based on vegetation data.

We used the indicator species analysis (IndVal) to identify the pollen taxa that are characteristic for the vegetation groups identified by the cluster analysis (**Table 2**). In Villa Velha, higher pollen proportions of *Baccharis*-type are a strong indication (IndVal 0.94) that the sample is from open semi-open vegetation, while the occurrence of *Schinus* pollen indicates forest (IndVal 0.72). In Aparados da Serra the open vegetation is not well indicated by a particular pollen type, while tree pollen proportions of Myrtaceae (0.91), *Araucaria angustifolia* (0.79) *Ilex* (0.78) *Celtis* (0.79), *Myrsine* (0.74), and *Trema* (0.78) are robust indicator taxa for forest plots.

Table 2. Indicator Species Analysis. Taxa identified with * have $p < 0.05$ = significant

Region	Taxon	Landscape unit	indval	pvalue	freq
Vila Velha	<i>Baccharis</i> -type	Open and Semi-open	0.94	0.002*	16
	<i>Araucaria angustifolia</i>	Forest	0.64	0.237	15
	<i>Celtis</i>		0.28	0.695	7
	<i>Ilex</i>		0.51	0.304	10
	<i>Myrsine</i>		0.59	0.656	16
	Myrtaceae		0.58	0.267	12
	<i>Trema</i>		0.41	0.447	9
	<i>Schinus</i>		0.72	0.034*	10
Aparados da Serra	<i>Baccharis</i> -type	Open	0.66	0.323	15
	<i>Araucaria angustifolia</i>	Semi-open and Forest	0.79	0.086*	17
	<i>Celtis</i>		0.79	0.004*	8
	<i>Ilex</i>		0.78	0.06*	15
	<i>Myrsine</i>		0.74	0.007*	18
	Myrtaceae		0.91	0.001*	14
	<i>Trema</i>		0.68	0.036*	16
	<i>Schinus</i>		0.16	0.918	6

4.3.2 Pollen-vegetation relationships

4.3.2.1 Multivariate data analysis

Principal component analysis of the vegetation data (**Fig. 9** a,c) separated forested from open vegetation sites. Semi-open sites have different affinities in the two study areas and plot near open sites in Vila Velha and forest sites in Aparados da Serra. In Vila Velha, forest plots are characterized by *Araucaria angustifolia*, which separates these plots from semi-open plots. As mentioned before, plot 5 and 10 differ from other open plots because they are situated near and within rock outcrops and exposed soil, changing the proportion of the mapped vegetation in comparison to the overall open character of these sites. Apart from these two samples, the PCA separates semi-open from open plots. In Aparados da

Serra (**Fig. 9 c**), the vectors for *Araucaria angustifolia* and forest are not strongly separated, indicating similar tree composition in forest and semi-open plots.

The PCA of the pollen data (**Fig. 9 b,d**) does not yield a clear separation of open, semi-open and forested sites, particularly for Vila Velha (**Fig. 9 b**). Five of the open sites (5, 6, 7, 10, 13) with high pollen percentages of *Baccharis*-type and other Asteraceae are separated from semi-open and forested plots. Three open sites (1, 12, 15) instead appear inseparable from semi-open and forested plots because all are characterized by high values of Poaceae and Cyperaceae. In sample 1, for example, Poaceae and Cyperaceae sum up to ~75%, while pollen from the Asteraceae family is rare. Sample 15 comes from open vegetation; however, semi-open vegetation occurs only 100 m from the site. Pollen composition in sample 15 is similar to sample 14 from a site in this nearby semi-open vegetation.

Also, in Aparados da Serra (**Fig. 9 d**), pollen composition does not separate open, semi-open and forested sites. The first axis represents the variance in the pollen proportions of Poaceae versus the forest elements, generally separating open versus forested sites. However, a sample from the forested site 17 and the semi-open site 8 are also high in Poaceae pollen and plot with the open grassland samples. Sample 17 has been taken in a small forest opening with grasses that may have contributed to its high Poaceae pollen proportion. Sample 8 is situated at the forest edge and was therefore classified as semi-open, while the local abundance of grasses may explain the position in the PCA. This comparison of the pollen and vegetation composition in the PCA analysis indicates that the pollen composition at each site is strongly influenced by the vegetation beyond the 100 m radius used here for comparison.

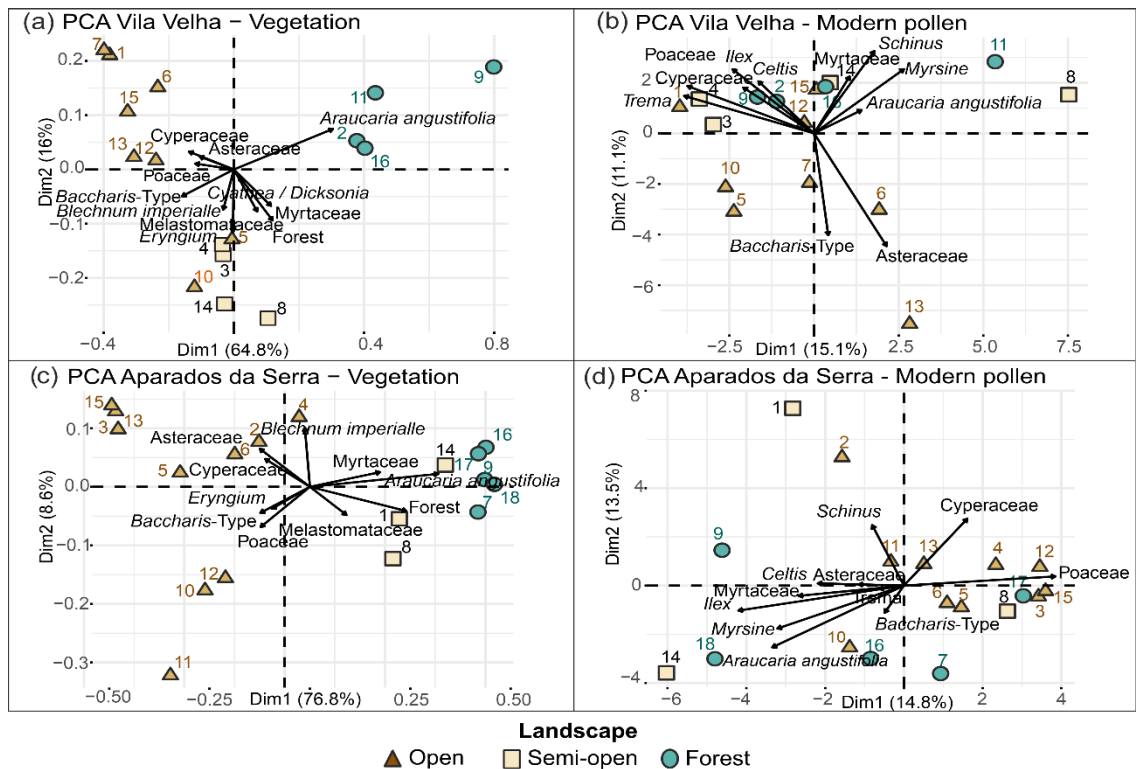


Fig. 9 PCA biplots of pollen assemblages and vegetation for Vila Velha (a, b) and Aparados da Serra (c, d) respectively

4.3.2.2 Representation factors (R-values)

A visual comparison of the average pollen proportions overall study sites with the average vegetation proportions in the 100 m radius of the sampling points (**Fig. 10** a-d) shows that *Poaceae* is the most overrepresented and *Araucaria angustifolia* the most underrepresented taxon. Striking are the similarities in average R-values between the two regions, also when using the vegetation cover in an overall 2 km buffer around all sites (**Fig. 11**). The R-values for the six different taxa follow the same trend in both study regions except for an under-representation of *Asteraceae* p.p. in Aparados da Serra, while this taxon has a near one to one average pollen to average vegetation proportion in Vila Velha. In both regions, the pollen of *Araucaria angustifolia* is strongly under-represented, *Baccharis* and the forest group are under-represented. Pollen from *Cyperaceae* and *Poaceae* are over-represented.

Vegetation and pollen proportions at individual sites show a large scatter. The site-based ratios follow the same pattern as the ratio based on averages (**Table 3**). The scatter of values around the mean is generally higher in Aparados da Serra, particularly for *Asteraceae* p.p. and *Araucaria angustifolia*.

VEGETATION AND FIRE HISTORY IN ARAUCARIA FOREST AND GRASSLANDS, SOUTHERN BRAZIL

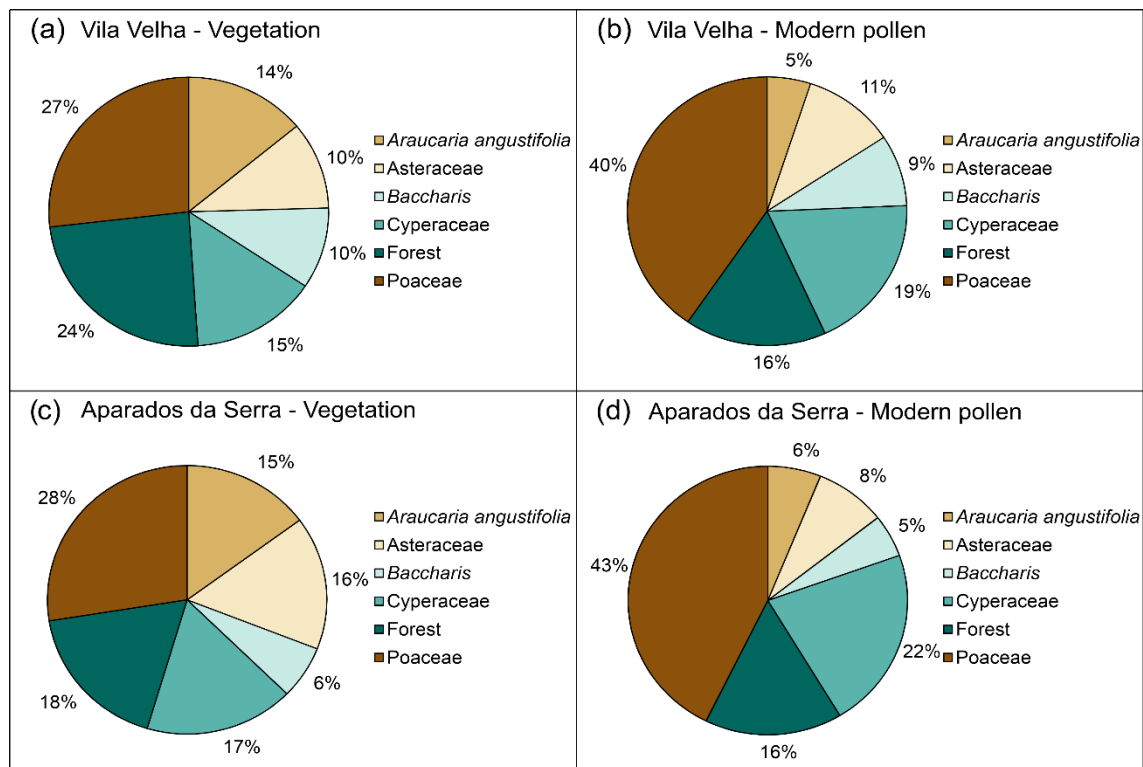


Fig. 10 Percentages of pollen and vegetation cover within 100 m radius in Vila Velha (a,b) and Aparados da Serra (c,d).

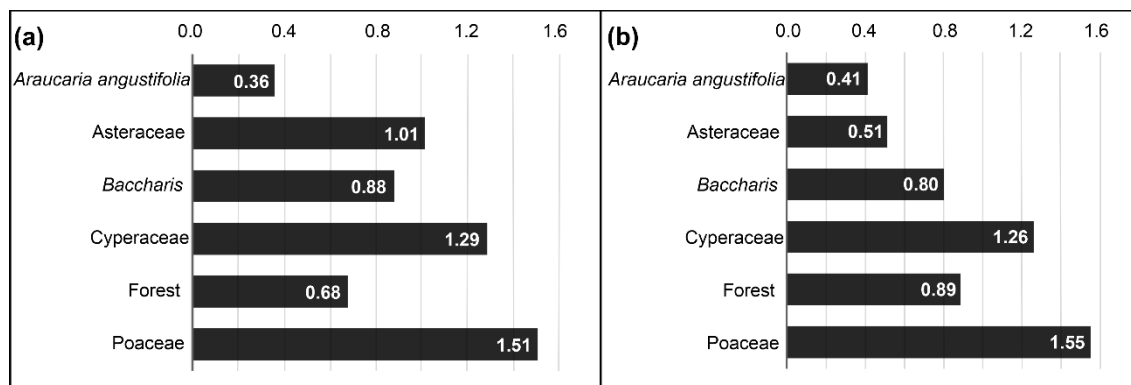


Fig. 11. Mean representation factor (R-values) for the six major taxa as averaged pollen proportions over all sites in one region versus averaged vegetation within 2,000 m of the sample site in **a** Vila Velha and **b** Aparados da Serra

Table 3. Site-based representation factor (p/v values) for the six major taxa in this study in Vila Velha and Aparados da Serra.

Location	Site No.	<i>Araucaria angustifolia</i>	Asteraceae	<i>Baccharis</i>	Cyperaceae	Forest	Poaceae
Vila Velha	1	0.28	0.11	0.28	2.31	0.71	1.47
	2	0.05	0.19	0.13	3.93	0.49	2.51
	3	0.00	0.18	0.17	2.00	0.42	1.58
	4	0.30	0.52	0.18	2.20	0.57	1.53
	5	0.45	1.67	1.91	0.12	0.55	1.53
	6	0.45	2.01	2.80	0.43	0.71	0.51
	7	1.67	0.91	1.08	1.41	0.73	0.82
	8	0.63	1.10	0.82	0.56	1.57	0.87
	9	0.25	1.01	0.39	2.62	0.60	2.60
	10	0.04	0.86	3.09	1.05	0.13	3.35
	11	0.23	1.52	0.04	1.40	1.10	1.06
	12	0.25	1.47	0.48	0.90	0.51	1.64
	13	0.51	2.08	0.87	0.77	1.02	0.86
	14	0.92	0.97	0.21	0.59	0.78	1.76
	15	0.77	0.55	0.76	0.68	0.76	1.66
	16	0.56	0.36	0.09	0.83	0.52	3.55
	Mean	0.46	0.97	0.83	1.36	0.70	1.71
Aparados da Serra	1	0.04	0.83	0.31	2.87	0.78	1.34
	2	0.26	0.14	0.00	0.97	2.86	1.55
	3	0.00	0.18	0.16	1.40	0.30	2.23
	4	0.22	0.18	0.69	1.16	0.98	1.83
	5	0.50	0.91	3.47	0.14	0.69	1.48
	6	0.19	0.70	0.96	1.48	0.51	1.78
	7	0.13	0.61	0.06	0.81	0.46	3.00
	8	0.09	0.42	0.39	1.60	0.61	2.10
	9	0.43	0.38	0.44	1.97	1.51	0.89
	10	0.35	2.07	5.98	0.61	0.40	0.37
	11	0.11	3.17	0.48	0.78	0.49	1.42
	12	0.04	0.10	0.00	1.92	0.29	1.58
	13	0.09	0.23	0.27	2.67	0.67	1.13
	14	1.01	0.39	0.21	0.88	2.92	0.90
	15	0.05	0.05	0.12	2.05	0.45	1.61
	16	2.88	0.12	0.00	0.30	1.30	1.34
	17	0.03	0.06	0.13	0.83	0.41	2.76
	18	1.29	0.72	0.47	0.09	2.12	0.80
	Mean	0.56	0.60	0.74	1.20	1.00	1.55

4.3.2.3 ERV analysis

Relative pollen productivity is expressed in relation to a reference taxon, which needs to occur in all pollen and vegetation samples. Poaceae fulfils this criterion in many study regions and is therefore commonly used as a reference taxon (Broström et al. 2008). However, as presented above, high proportions of Poaceae occur in samples of all vegetation types. The samples from Aparados da Serra do not contain a gradient of Poaceae pollen percentages long enough for successful ERV calculations. This situation led to spuriously high PPEs in some analysis. Thus, we have selected Cyperaceae as an alternative reference taxon, which is also present in all vegetation plots while showing a stronger gradient in the vegetation and pollen data.

In addition to two different reference taxa, PPEs were estimated using two different pollen dispersal models (GPM and LSM) implemented in two different programs (ERV.Analysis.v 2.5.3-D) and ERV Analysis in R-R). ERV results were evaluated considering the vegetation data in circles of different radii from the sampling point. Here we represent the results for the maximum distance of 100 m (**Fig. 12**). Ideally, the accuracy of ERV calculations should improve with more rings added in the analysis, i.e. a larger vegetation sampling area. However, in both study regions, the distance between modelled and empiric pollen values is lowest with the 50-100 m rings (**Fig. 13**), indicating that the ERV model performs best with only rings up to 100 m radius included in the analysis. This observation may indicate that vegetation composition has not been adequately described for rings beyond 100 m radius. Hence, the 100 m radius represents a good compromise of the higher data accuracy of the field-based vegetation survey and the representation of adjacent woodlands. Results are therefore discussed for this distance. Complete results, including spurious values, are presented in **Appendix 3**.

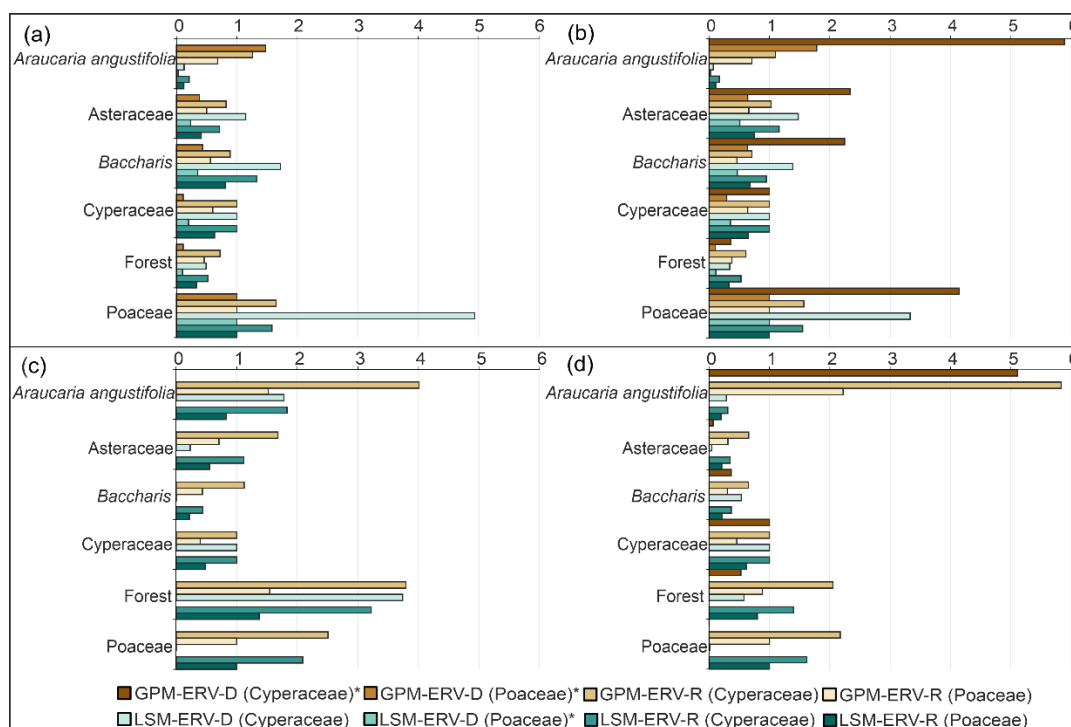


Fig. 12 PPEs results of six major taxa in Vila Velha at 50–100 m radius (**a**) and 1,500–2,000 m radius (**b**) and Aparados da Serra at 50–100 m radius (**c**) and 1,500–2,000 m radius (**d**). *Spurious values resulting from the analysis are not shown in this graphic

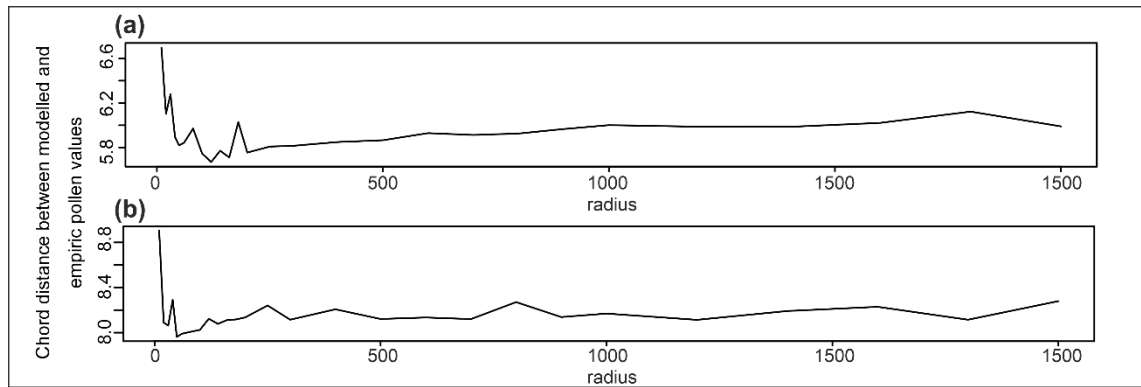


Fig. 13 Chord distances between modelled and empiric pollen values within 2000 m for **a** Vila Velha and **b** Aparados da Serra.

The results of the ERV analysis differ consistently for the dispersal models regardless of the reference taxon. The difference is most pronounced for *Araucaria angustifolia*, the taxon with the largest pollen grains and hence the highest fall speed (**Table 4**). For both study areas, pollen productivity of *Araucaria angustifolia* is as high or higher than pollen productivity of the reference taxon Poaceae or Cyperaceae when calculated with the GPM. In calculations with the LSM, pollen productivity of *Araucaria angustifolia* is much lower. Still, LSM-PPEs of *Araucaria angustifolia* are higher in Aparados da Serra than in Vila Velha. For the other taxa, differences in GPM- and LSM-PPEs are smaller. For the remaining taxa, both models result in different PPEs between regions, which, at least in the case of *Baccharis*-type and the forest taxon can be explained by different species involved and agree with the regional differences in R-values.

Table 4. Estimation of fall speed of common taxa in the study area.

Name	Taxa included	Fall speed (m/s)
<i>Araucaria angustifolia</i>	<i>Araucaria angustifolia</i>	0.140
Asteraceae	Alternanthera, Amaranthaceae, <i>Ambrosia</i> -type, Asteraceae, Cichoroideae, <i>Pfaffia gnaphalioides</i> , <i>Senecio</i> , <i>Solanum</i> , <i>Valeriana stenophylla</i> , <i>Vernonia</i> and <i>Xyris</i>	0.015
<i>Baccharis</i>	<i>Baccharis</i> -type	0.016
Cyperaceae	Cyperaceae	0.027
Poaceae	Poaceae	0.020
Forest	<i>Actinostemon concolor</i> , <i>Acalypha</i> , <i>Alchornea</i> , <i>Celtis</i> , Euphorbiaceae, <i>Ilex</i> , <i>Matayba</i> , <i>Myrsine</i> , Myrtaceae, Mimosaceae, Moraceae, <i>Ranunculus bonariensis</i> , <i>Rhamnus</i> -type, <i>Sebastiania</i> -type	0.020

Scatter plots (**Fig. 14**) of modelled against empiric pollen data indicate for Vila Velha good correspondence between pollen and vegetation abundances for *Baccharis*-type, and poor correspondence for the forest taxon and Poaceae. In Aparados da Serra *Araucaria*

angustifolia and the forest taxon show the best relationship between the variance in vegetation and pollen proportions.

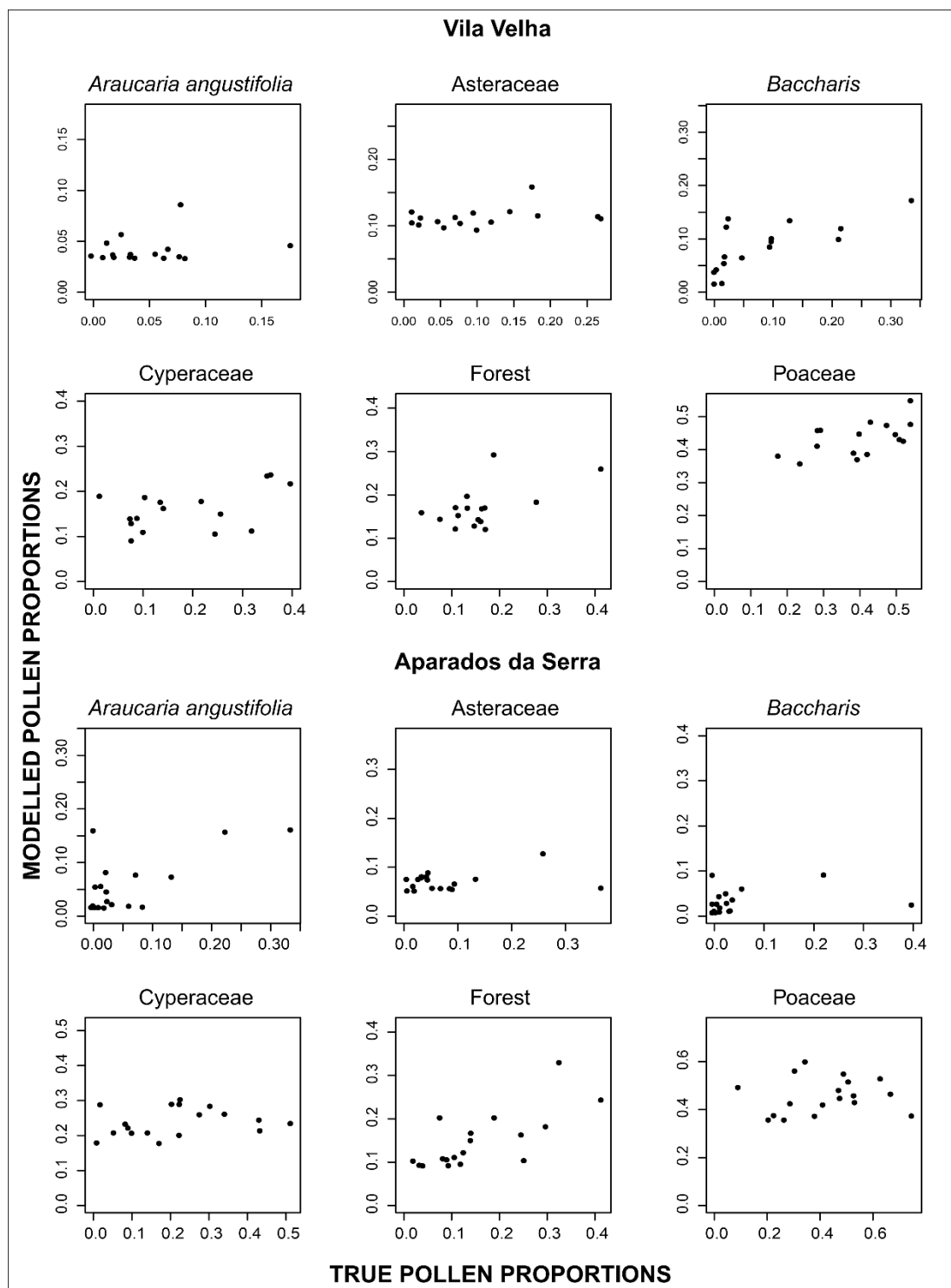


Fig. 14. Scatter plots of true pollen and modelled pollen proportions within 100 m radius from 16 samples in Vila Velha and 18 samples in Aparados da Serra for the six taxa selected in this study.

4.4 Discussion

4.4.1 Representation of openness in the pollen spectra from the *Araucaria* forest-grassland mosaic

The *Araucaria*-Grassland mosaic in southern Brazil is characterized by well defined forest edges, clearly separating open and semi-open vegetation from woodlands. Despite that, it appears challenging to separate these two vegetation types in pollen data using ordination and classification techniques. These difficulties may be due to Poaceae and *Araucaria angustifolia* pollen showing only a weak local signal, corresponding to the vegetation in a 100 m radius. In the case of Poaceae, this could be caused by species of the family frequently growing within the forest and dominating the surrounding grasslands. Both at Vila Velha and Aparados da Serra, the woodlands contained bamboo of the genus *Merostachys* and *Chusquea*.

The other effect obscuring the local separation of the two vegetation types is the different height at which the pollen is released, often described as the “edge effect” of woodlands leading to a spread of tree pollen over a larger area away from the forest (Bunting et al. 2013). *Araucaria* trees often raise their branches over the canopy of other trees so that perhaps a larger proportion of its pollen is transported above the canopy (Rempe 1937). In Aparados da Serra, the pollen of several trees growing below the canopy of *Araucaria* was found more frequently within or close to woodlands and was therefore identified as good indicators for forested sites. *Schinus* is the only tree taxon in Vila Velha consistently more abundant in samples from woodlands, while here, *Baccharis*-type pollen resulted in being a reliable indicator of open vegetation. The different land use activities can explain the lack of abundant *Baccharis*-type pollen in Aparados da Serra, where *Baccharis* shrubs are suppressed by grazing and frequent fires (Rambo 1956).

The above mentioned weak local pollen signal of Poaceae and *Araucaria angustifolia* has been observed in other studies from southern Brazil. For instance, a pollen vegetation comparison in the *Araucaria*-Grassland mosaic in Santa Catarina State (Cárdenas et al. 2019) revealed no correspondence between pollen proportions and local site characteristics, including open and closed vegetation. Jeske-Pieruschka et al. (2010) only indicated small differences in pollen composition inside and outside the woodland in a

study of 18 surface samples crossing an *Araucaria* dominated forest patch in Rio Grande do Sul State.

While grasses are the most abundant taxon in open vegetation types of South America and make up nearly one-third of the plant cover in the two study areas, they also act as high pollen producers being the most abundant pollen type in the air. This high regional deposition of Poaceae pollen results in the pollen type also being abundant in surface samples from woodland patches with low grass cover. In the Neotropics, Bush (2002) observed that Poaceae pollen is dominant where trees with high pollen production are lacking. Nevertheless, Poaceae pollen provide an important measure to separate different ecosystems at the landscape scale (Rodrigues et al. 2016) and an indicator taxon for *Araucaria* forest and high elevation grassland in an analysis of 196 surface samples from eastern Brazil (Montade et al. 2016). In a surface sample study from southern South America, Paez et al. (2002) observed that Poaceae pollen are abundant in samples from *Araucaria araucana* populations, the second species in the genus with similar pollen morphology to *Araucaria angustifolia*.

4.4.2 Representation of pollen taxa and pollen productivity

Campos vegetation is characterized by high abundances of Asteraceae, particularly *Baccharis*, Cyperaceae and the dominating Poaceae. Both Poaceae and Cyperaceae have R-values of above one, i.e. they are over-represented in pollen records. Plants with such high pollen representation are generally anemophilous, with numerous exposed anthers, small pollen grains (30-40 μm), and high pollen production (Davis 1984; Hjelle 1997). Also, conifers are usually over-represented in the pollen record as they are wind-pollinated, as is *Araucaria angustifolia*. However, the tree is dioecious with a rather large (60 μm), non-saccate pollen grains resulting in the highest estimated fall speed among the here investigated taxa.

Pollen trapping in *Araucaria angustifolia* stands of north-eastern Argentina yielded pollen deposition values between 3000 and 14000 grains $\text{cm}^{-1} \text{ year}^{-1}$ in a situation directly below flowering trees (Simón et al. 2018). These values are similar to the average pollen

influx measured in *Araucaria angustifolia* dominated forest in the province Santa Catarina, Southern Brazil (Behling 1997) and compare to pollen deposition of trees in the genus *Pinus* in Europe (Abraham et al. submitted). A gene flow study of an isolated group of 11 *Araucaria* trees documents that the large pollen type is well dispersed and most trees in that group were fertilized by pollen travelling around 2 km from the nearest more extensive woodland (Bittencourt and Sebbenn 2007). In the here presented study, it was not feasible to identify all trees in the woodland. Although species of the genus *Mimosa*, *Myrsine*, *Clethra* and Myrtaceae family were also recorded, their abundance in the small areas mapped was often too low for reliable comparisons to their equally low pollen percentages. The combined forest taxa group yielded higher R-values compared to *Araucaria angustifolia*. This result may be due to these trees producing more pollen than *Araucaria angustifolia*.

The different R-values for the forest group between Vila Velha and Aparados da Serra are likely due to differences in forest composition, with higher abundances of pollen from Myrtaceae, *Ilex* and *Myrsine* in Aparados da Serra in the pollen samples. Cárdenas et al. (2019) indeed estimate higher R-values for several tree taxa, including *Clethra*, *Myrsine* and *Podocarpus*, compared to *Araucaria angustifolia*. Also, taxa including the Myrtaceae family, identified as low pollen producers, revealed high R-values in other studies (Cárdenas et al. 2019, Gosling et al. 2009). These differences indicate that pollen production and dispersion differ substantially among species of this family. Moreover, many forest trees are palynologically silent (Gosling et al. 2009; Cárdenas et al. 2019), which hampers drawing any further conclusion from the forest group taxon.

Gosling et al. (2009) also report small R-values for Poaceae, which may be partially due to the available vegetation data coming mainly from tree inventories. As discussed above, pollen productivity of Poaceae may indeed be low compared to the trees present in a particular study region (Bush 2002). The calculation of R-values does not account for pollen dispersal. Hence, the difference in R-values between taxa may relate to differences in pollen productivity or pollen dispersal. PPE calculation does account for pollen dispersion by distance weighting plant abundances. As long as a suitable dispersal model is applied in the calculations, PPEs quantify differences in pollen productivity between taxa. Only *Araucaria angustifolia* represents a single species in vegetation and pollen data, while even the genus *Baccharis* combines species with different life forms present in different abundances in the two study areas.

The choice and parameterization of the pollen dispersal model is the most important factor influencing the resulting pollen productivity estimates (Theuerkauf et al. 2013). The decrease in pollen contribution of a given plant with distance from the point of reference may be described by simple particle dispersal models such as GPMs (Bunting et al. 2013). For several regions, LSMs (Kuparinen et al. 2007) have shown to describe pollen deposition more realistically than GPMs (Theuerkauf et al. 2013; Mariani et al. 2016). In this study, dispersal model selection strongly affected *Araucaria angustifolia*, with GPM-PPEs being much higher than the LSM-PPEs. This difference is due to the large difference in fall speed. The fall speed of pollen has a significant influence on the predicted dispersal pattern in the GPM but not as strong in the LSM (**Fig. 15**). The GPM model predicts that most *Araucaria angustifolia* pollen would be deposited within meters of the parent tree, which is clearly not observed in the field. Because the GPM underestimated the dispersal distances of *Araucaria angustifolia* pollen, the resulting PPEs are unrealistically high. Both models assume horizontally homogeneous canopies, which is violated in the current study where groups of *Araucaria angustifolia* in the open grassland are more similar to smokestacks with respect to their pollen release. In this parkland situation with pollen being released at different heights and with edge effects occurring at forest margins, also the chosen LSM model may not be fully suited.

Nevertheless, the estimate of a pollen productivity for *Araucaria angustifolia* of 0.8 relative to Poaceae for Aparados da Sierra based on the LSM model may be realistic considering that about half of the trees are female therefore non-pollen-producing. The *Araucaria angustifolia* PPE of 0.1 in Villa Velha instead appears too low. For this study area, the scatterplots do not show the expected 1:1 relationship between modelled and empiric pollen values (**Fig. 14**). This pattern indicates that the relationship between abundances of *Araucaria angustifolia* in the vegetation and pollen deposition is not that close. For example, pollen deposition is highest in site 16 (17.7%), although *Araucaria angustifolia* is only intermediately abundant within 100 m distance from that site. The poor pollen vegetation relationship for *Araucaria angustifolia* in Vila Velha may relate to the location of this area near the distribution limit of the tree. Near this limit, the growth and pollen production of trees may be more variable and influenced by local site

conditions. Also, the age of a tree determines its pollen production (Matthias et al. 2012). Differences in age-structure may hence cause biases in the pollen vegetation relationship.

Similarly, pollen production will be related to the ratio of male versus female tree, which may differ between sites. Regardless, the inadequacy of the dispersal models considering the different release height of pollen is likely the major problem in this mosaic landscape. Developing dispersal models incorporating the effect of release height might improve pollen vegetation relationships in these landscapes.

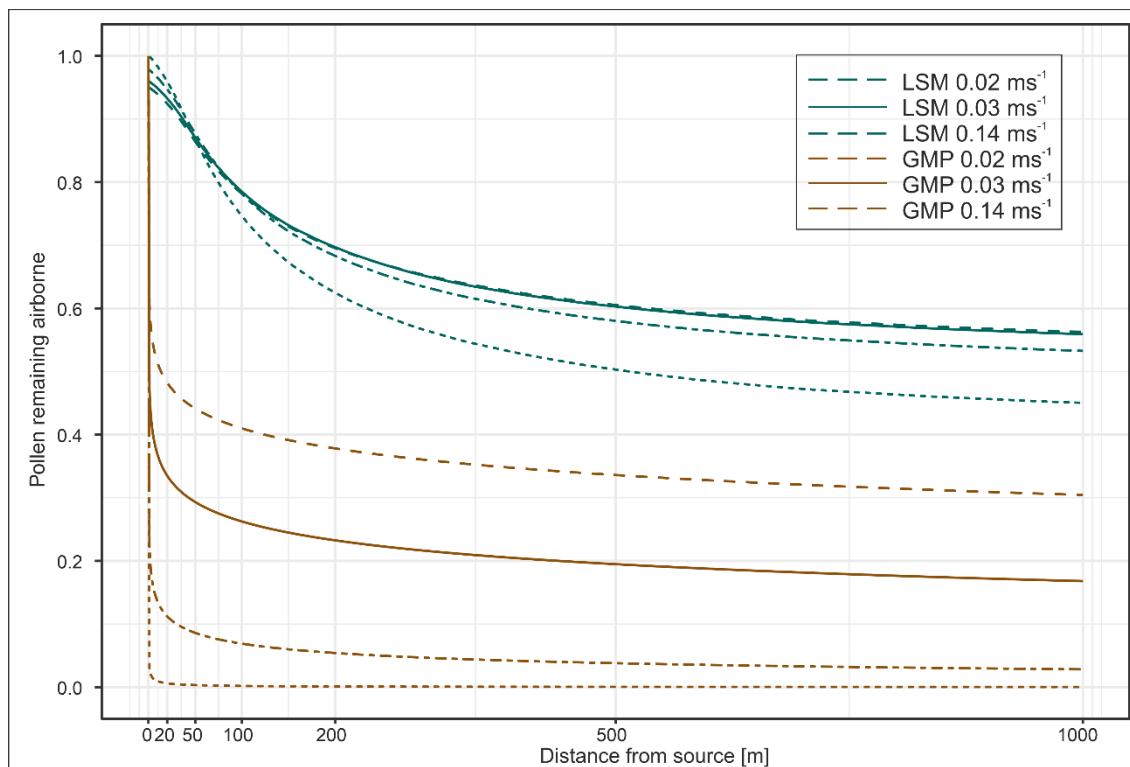


Fig. 15 Proportion of pollen remaining airborne until 1000 m distance from a pollen source, calculated with the GPM (red) and LSM (green) and for three different fall speeds of pollen (0.02, 0.03, 0.14 ms⁻¹). The highest fall speed represents pollen of *Araucaria angustifolia*

4.5 Conclusions

The application of procedures designed in high latitude vegetation types of the northern hemisphere to estimate pollen productivity in the low latitudes of South America is challenging but possible. This study shows that it is possible for the *Araucaria* forest-grassland mosaic of southern Brazil, while documenting several problems for this particular vegetation type. Poaceae is the most overrepresented taxon in the *Araucaria* forest-grassland mosaic of southern Brazil. Grasses occur in all vegetation types with different cover abundance, while their pollen proportion in surface samples is not

providing clear differences between forest and open areas. Locally open vegetation types can be detected by *Baccharis*-type pollen indicating open conditions and *Araucaria* and *Celtis* pollen indicating woodland.

Similarities in R-values and PPEs between regions document that pollen production of individual species within the large plant families of Poaceae and Asteraceae is similar, allowing the application of resulting PPEs on the broader region. Conversely the forest group consisting of trees from different families showed a different behaviour between the study areas. Here it seems necessary to develop PPEs for at least groups of trees with similar pollen dispersal syndrome. The dioecious nature of *Araucaria angustifolia* hampers estimating pollen productivity of this iconic tree. The obtained productivity of 0.8 with respect to Poaceae is lower than pollen productivity of the general forest, resulting in the tree being underrepresented by its pollen even though it is wind-pollinated.

The application of pollen dispersal models designed for closed canopies in the natural parkland situation with pollen released at different levels may explain some difficulties in estimating PPEs. Further model development needs to include the effect of pollen release at different heights.

The insights and obtained PPEs for 6 major pollen taxa are now available to explore the increasing number of pollen diagrams from the region and perhaps refine previous interpretations.

Data availability

After publication pollen data will be submitted to the Latin American Pollen Database.

Author contribution

TG designed the study and with DPB carried out the field work. DPB counted the pollen, compiled the vegetation data and lead the data analysis and writing. MT carried out the ERV analysis. All authors discussed the results and contributed to the writing.

Competing interests

The authors declare that they have no conflict of interest.

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5. LATE QUATERNARY

PALAEOECOLOGICAL CHANGES IN

SOUTHERN BRAZIL: A MULTI-PROXY

AND HIGH-RESOLUTION RECORD

5.1 Introduction

The Atlantic Rainforest biome once covered around 1.5 million km² along South American Atlantic coast (Ribeiro et al., 2011), it has now been reduced to 7.5% of its original area and is considered as one of the most important biodiversity hotspots and target for conservation priorities (Myers et al., 2000; Scarano, 2002). Characterized by high levels of endemism, species richness and heterogeneity, it encompasses vegetation types such as dense ombrophilous forest, semi-deciduous forest (Atlantic rainforest), deciduous forest, marshals, swamps, mangroves, *Araucaria* forests, savannas (Cerrado), grasslands (Campos) and high-altitude grasslands (Campos de altitude) (Ribeiro et al., 2011).

The extension of the Atlantic Rainforest Biome in southern Brazil, reach and cover the states of Paraná, Santa Catarina and more than a half of Rio Grande do Sul including all its coastal extension. In this region, the vegetation is mainly represented by *Araucaria* forest and Grasslands mosaics, together with dense ombrophilous forest, semi-deciduous and deciduous forests (IBGE, 2004, 2012). However, the woodland-grassland vegetation that once dominated the landscape at the beginning of the 20th century, have been severally reduced and nowadays less than 25% of the original area still exist (Machado Mello & Peroni, 2015; Rodrigues Salgado et al., 2019). Studies in southern Brazil in the *Araucaria* and Campos region attempting to reconstruct the vegetation and climate history document that Campos vegetation was dominating and covering extensive areas in the highland region during the Late Pleistocene until the Middle Holocene (Behling, 1995, 1997, 2006; Behling et al., 2004; Behling & Negrelle, 2001; Jeske-Pieruschka et al., 2010, 2013).

The initial expansion of *Araucaria* has been recorded in the highlands of Santa Catarina, Paraná and Rio Grande do Sul, at different time periods and it has been hypothesized that *Araucaria* forest initially expanded by spreading out of the gallery forests along the rivers (Behling et al., 2004). In Rio Grande do Sul in São Francisco de Paula region and in Cambará do Sul the expansion is recorded at ~4000 cal yr BP (Behling et al., 2004; Jeske-Pieruschka & Behling, 2012). For the highlands of Santa Catarina state, Behling (1995) found the first expansion at ~3460 cal yr BP in Serra da Boa Vista and ~2390 cal yr BP in Serra do Rio Rastro. While in Paraná state, in Serra do Araçatuba the expansion is documented after ~2000 cal yr BP (Behling, 2006) and in Serra do Campos Gerais at ~2930 cal yr BP (Behling, 1997). A second and marked expansion of the *Araucaria* forest is documented in the highlands of Santa Catarina and Rio Grande do Sul for the last 1000 years (Behling, 1995; Behling et al., 2001, 2004), and at about 1400 cal yr BP in the highlands of Paraná (Behling, 1997).

This study aims to improve our understanding of the causes and dynamics of past vegetation changes in the Atlantic Rainforest biome. Based on a multi-proxy study of the sedimentary record of the small lake Lagoa Dourada in the highlands of Vila Velha State Park.

5.2 Geological and environmental setting

5.2.1 Geology and geomorphology

The studied lake, Lagoa Dourada, is located in the highlands of Paraná state in the State Park of Vila Velha at an altitude ca. 850 m a.s.l. (25°12' S, 50°02' W) (**Fig. 16**), about 25 km southeast of Ponta Grossa. The lake is classified as a silted up Furna, placed among the most remarkable landforms in the Furnas Formation. Furnas are roughly vertical cylindrical hollows formed up to the surface where the rocky roof of deep subterranean cavities has collapsed, as a consequence of the chemical dissolution of the clay diagenetic cement (kaolinite, illite) which release the quartz grains and a subsequent remove them by mechanical erosion (Melo et al., 2015; Stevanović, 2015). They are considered key

structures in the groundwater flow of the region (Melo et al., 2015). In this system, karstification processes are widespread in the outcropping area in non-carbonate rocks (Melo et al., 2003, 2015; Melo & Fonseca, 2007).

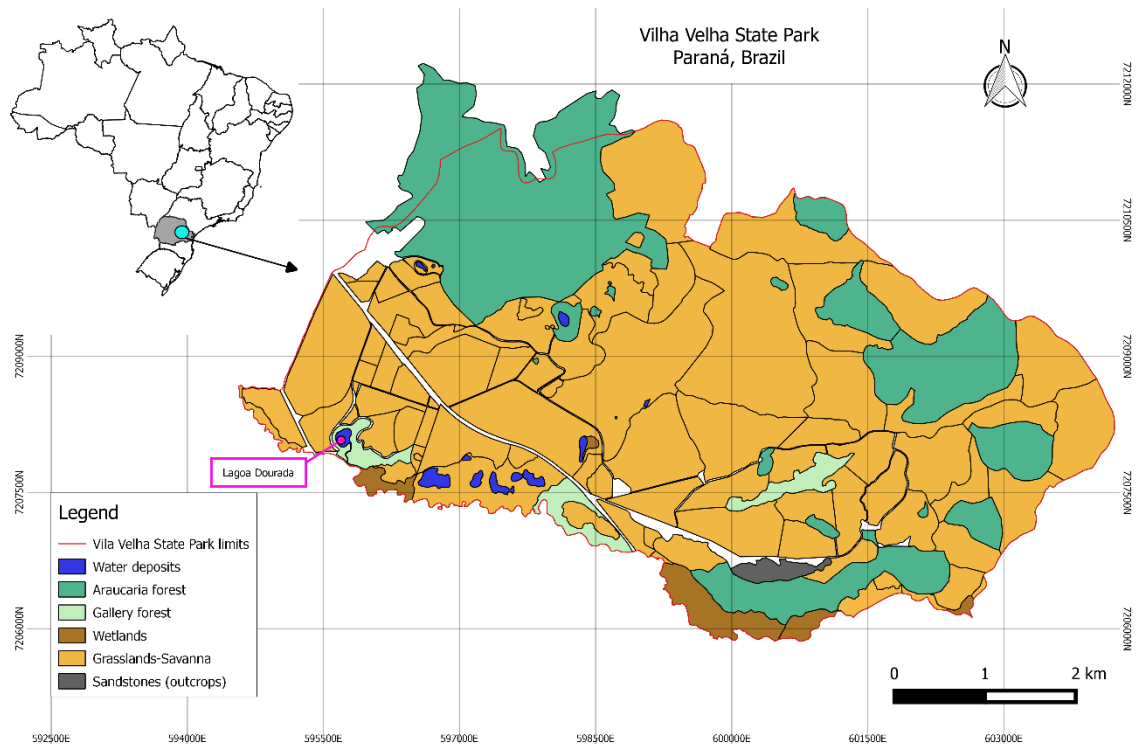


Fig. 16 Map showing the location of the study site referred in this study. In gray Paraná State, zoom in the current vegetation units present in the Vila Velha State Park and in red Lagoa Dourada Furna. Elaborated based on the available information from “Plano de Manejo Vegetacao Parque Estadual Vila Velha” (Governo do Estado de Paraná, 2004).

5.2.2 Present-day climate and vegetation

Information on the climate in Vila Velha comes from the meteorological station Ponta Grossa, documenting annual precipitation of 1554 mm with a minimum between April and August, but without a dry season. Mean annual temperature is 17,8°C, January and February are the warmest months of the year with a mean monthly temperature of 21.4°C and the coldest month is July with 13.8°C (IAPAR, 2020). Frost occurs in Vila Velha, between May and August with an average of five or more frosts events per year, these limit the growth of plants sensitive to low temperatures (Melo et al., 2000).

Framed under the Atlantic Forest (IBGE, 2004), Vila Velha contains several ecosystems such as Mixed Ombrophilous Forest (*Araucaria* forest), Alluvial Mixed Ombrophilous Forest (Gallery forest), Grasslands (Campos), open Savanna (Campo limpo/sujo) and

Fluvial Influence Pioneer formations (wetlands, marshlands or várzea) (**Fig. 16**) (Cervi et al., 2007).

Araucaria angustifolia is present both in forest patches as well as in open landscapes, it predominates in the emergent layer, but is not the dominant tree in the majority of the woodlands. It is accompanied in the canopy by species like; *Ocotea porosa*, *O. puberula*, *O. pulchella* (Lauraceae), *Capsicodendron dinisii* (Canellaceae), *Gochnatia polymorpha* (Asteraceae) *Podocarpus lambertii* (Podocarpaceae), *Ilex paraguariensis*, *Cedrela fissilis*, *Campomanesia xanthocarpa* (Myrtaceae), *Matayba elaeagnoides* (Sapindaceae), *Sloanea lasiocomia* (Elaeocarpaceae), *Luehea divaricata* (Tiliaceae), *Mimosa scabrella* (Mimosaceae), *Dalbergia brasiliensis* (Fabaceae), *Jacaranda puberula* and/or *Tabebuia alba* (Bignoniaceae) (Rodrigues Salgado et al., 2019). The understorey is dominated by Myrtaceae (*Myrcia*, *Eugenia*, *Calyptanthus* and *Gomidesia*), Flacourtiaceae (*Casearia* and *Xylosma*), Sapindaceae (*Allophylus* and *Cupania*), Rutaceae, Symplocaceae and Aquifoliaceae (Roderjan et al., 2002). Besides, *Dicksonia sellowiana* and *Cyathea* tree ferns are characteristic and cespitose grasses such as *Chusquea* and *Merostachys* occur.

In the Gallery forests, *Sebastiania commersoniana* is the most characteristic species, with more complex associations in which even *Araucaria angustifolia* has an important participation in the physiognomy. In the canopy are *Schinus terebinthifolius*, *Allophylus edulis*, *Blepharocalyx salicifolius* and *Vitex megapotamica*, being less frequent *Luehea divaricata*, *Syagrus romanzoffiana*, and *Salix*. Common in the lower strata *Myrciaria tenella*, *Myrceugenia euosma*, *Calyptanthus concinna*, *Daphnopsis racemosa* and *Psychotria carthagenensis* (Roderjan et al., 2002). Open vegetation (Campos) is characterized by the dominance of Poaceae and Cyperaceae where about 40% of all of the taxa is shared with the Cerrado Biome (Savana). Poaceae taxa in particularly shares nearly 63% with Cerrado Biome. This vegetation type is known as a “Savana gramíneo lenhosa” in Portuguese (Cervi et al., 2007).

The present vegetation is strongly affected by large-scale afforestation with *Pinus* and *Eucalyptus* that took place a few decades ago which has been monitored and controlled

in the last ~30 years. The study site is surrounded by a Gallery forest and located near an *Araucaria* forest patch, covering a low hill and adjacent remnants of natural grasslands.

5.3 Methods

5.3.1 Chronology, particle grain size, pollen and geochemical analyses

A 1440 cm long sediment core was collected in 2017 from the centre of Lagoa Dourada using two different piston cores. The first 10 m were collected in a lightweight Livingstone-type corer (Livingstone, 1955; Nesje et al., 1987) and a square-rod Livingstone-type corer (Wright, 1967) was used to extract the deeper parts of the lake deposits (4.50 m). A total of 23 samples (8 macrofossils and 15 bulk samples) from the entire core were submitted to radiocarbon dating by Accelerator Mass Spectrometry (**Table 4**). The age-depth model was constructed in rbacon (Blaauw et al., 2020) prescribing approximate sedimentation rates estimated based on changes in pollen concentrations. Visual description of the sediments and general lithology was performed using the Munsell Soil Colour Chart (Munsell Color (Firm), 1954). A total of 171 samples along the core were taken and the sediments from exactly the same depth were analyzed for pollen, major element geochemistry and particle grain size.

VEGETATION AND FIRE HISTORY IN ARAUCARIA FOREST AND GRASSLANDS, SOUTHERN
BRAZIL

Table 5. Radiocarbon dates of Lagoa Dourada core. Calibrated ages (two standard deviations (2σ) ranges) were obtained from Calib 7.0.4

LabCode	Depth	14C yr BP	Age range (cal yr BP) 2σ	Age median prob (cal yr BP)	Description	Comments
Poz-119117	172.6	990 \pm 30	791 - 925	856	Macrofossil	-
Poz-111295	204.8	1470 \pm 30	1289 - 1369	1326	Macrofossil	-
UBA-29240	387.3	2332 \pm 37	2159 - 2271	2317	Macrofossil	-
Poz-121537	517.7	3205 \pm 35	3252 - 3298	3388	Macrofossil	-
Poz-119118	633.2	4300 \pm 35	4629 - 4636	4836	Macrofossil	-
Poz-107807	716.1	4355 \pm 35	4828 - 4973	4879	Macrofossil	Used for mean offset calculation
Poz-122526	730	9700 \pm 40	10788 - 10971	11074	Bulk	Used for mean offset calculation
Poz-119119	731.1	4635 \pm 35	5055 - 5187	5311	Macrofossil	Used for mean offset calculation
Poz-119120	732	9870 \pm 40	11182 - 11315	11234	Bulk	Used for mean offset calculation
Poz-122527	779	8530 \pm 50	9425 - 9546	9497	Bulk	Excluded
Poz-119121	793.8	7930 \pm 50	8582 - 8814	8712	Bulk	Excluded
Poz-116232	826.8	8330 \pm 40	9132 - 9429	9297	Bulk	Excluded
Poz-122528	862.8	10590 \pm 50	12421 - 12653	12521	Bulk	Excluded
Poz-119122	891.2	11630 \pm 60	13293 - 13551	13415	Bulk	Excluded
Poz-111296	914.2	11380 \pm 60	13074 - 13298	13186	Bulk	Used for mean offset calculation
UBA-29241	925.2	6237 \pm 34	6982 - 7181	7089	Macrofossil	Used for mean offset calculation
Poz-107808	997.9	12020 \pm 60	13614 - 13678	13832	Bulk	Mean offset
Poz-119188	1003	11620 \pm 50	13286 - 13496	13407	Bulk	Mean offset
Poz-107809	1149	14540 \pm 80	17445 - 17918	17671	Bulk	Excluded
Poz-116234	1185	14660 \pm 80	17569 - 18010	17795	Bulk	Excluded
Poz-111297	1233	12930 \pm 60	15166 - 15646	15389	Bulk	Mean offset
Poz-107810	1320	13750 \pm 70	16276 - 16853	16545	Bulk	Mean offset
Poz-107815	1432.6	13850 \pm 70	16410 - 16986	16704	Bulk	Mean offset

For pollen analysis, *Lycopodium* tablets (9666 ± 212 , Batch Nr. 3862) were added as a marker, to calculate pollen concentration and pollen influx. Samples were treated with 10% hot KOH, 10% hot HCl, 70% cold HF, and three minutes hot acetolysis. Subsequently, the samples were mounted and counted under an optical microscope at 400X magnification. The total pollen sum (minimum of 300 pollen grains) includes pollen from herbs, trees and shrubs. Ferns spores were counted and expressed in percentages of the total pollen sum. The identification of palynomorphs was carried out using the references collections of the Department of Palynology and Climate Dynamics of the University of Göttingen, atlas, catalogues of pollen fossil and recent and palynological keys by Bauermann et al. (2013), Behling (1993), Roubik and Moreno (1991) and Silva et al. (2016) were used as well as the online Neotropical Pollen Key (Bush & Weng, 2007). Pollen diagrams were plotted with C2 software (Juggins, 2007) and zonation was based on stratigraphically constrained cluster analysis (CONISS) obtained with Tilia 2.6 software (E. Grimm, 2015). Pollen data were summarized in a cumulative diagram using four curves: Grassland, *Araucaria* forest, Atlantic rainforest and other trees and shrubs taxa.

The content of total Carbon (TC), Total Nitrogen (TN) and Total Sulphur (TS) was measured using a CNS elemental analyzer (EuroEA, Eurovector). The elemental analyzer combusts the sample at high temperatures which oxidizes the organic matter. The resulting gases are then detected by chromatography (Meyers and Teranes, 2002). Biogenic silica (BSi) was analyzed for all the samples according to the leaching method of Müller and Schneider (1993). Extracted with 1M NaOH at 85°C and cycled by a continuous-flow system to an autoanalyzer, where the dissolved silicon is measured by spectrophotometry.

Fifteen samples along the whole core were selected for determining total organic carbon content (TOC), measurements were carried out in the EuroEA, Euvector machine after removing carbonates with 3 % and 20 % HCl at 80°C. Total inorganic carbon content (TIC) was calculated as the difference between TC and TOC (Ohlendorf et al., 2014). For particle grain size analysis, organic matter and diatoms were removed from the samples with H₂O₂ and NaOH respectively. For dispersion, the samples were filled up with 20 ml Calgon ((NaPO₃)₃n) and shaken overnight. Analyses were performed with a Beckman Coulter LS 200 laser diffraction analyzer. Each sample was measured at least three times for 60 seconds until a stable distribution was reached. An average value was calculated

for each sample from all runs, thereafter the data was analyzed using GRADISTAT program (Blott & Pye, 2001).

Multivariate statistical analyses were carried out to highlight and evaluate the possible relationships of vegetation in response to geochemical variables, to highlight the most important factors driving vegetation dynamics in time. First, a Principal Component Analysis (PCA) was performed to visualize the major differences in pollen composition. Followed this, a constrained ordination (redundancy analysis (RDA)) was done, to extract the variation that is directly explained by the geochemical variables. PCA and RDA were done using CANOCO 5.0 software (ter Braak & Smilauer, 2012).

5.4 Results

5.4.1 Lithology, chronology and temporal resolution

Five distinct lithological units (L1 to L5) were identified in the Lagoa Dourada core (**Fig. 17**). After organic content was removed, the grain size proportions were reported for the inorganic component of the entire core. The lowest part of the sequence from 1440 to 1150 cm – L1 (~11700-8600 cal yr BP), was composed of silt (63%), sand (26%) and clay (11%). Further up, from 1150 to 940 cm – L2 (8600-7030 cal yr BP), a dense sandy (51%) and silt (42%) layer was found, overlaid by an organic layer from 940 to 880 cm – L3 (7030-6780 cal yr BP) that revealed after removing organic matter high percentages of sand (53%) and silt (40%) particles, that is then interrupted by another silt (28%), clay (7%) and sandy (65%) layer from 880 to 760 cm – L4 (6780-5590 cal yr BP). The uppermost section of the sediment core, from 760 to 0 cm – L5 (5590 cal yr BP-present), consists of organic sediments with a high content of silt (40%), sand (33%) and low content of clay (7%).

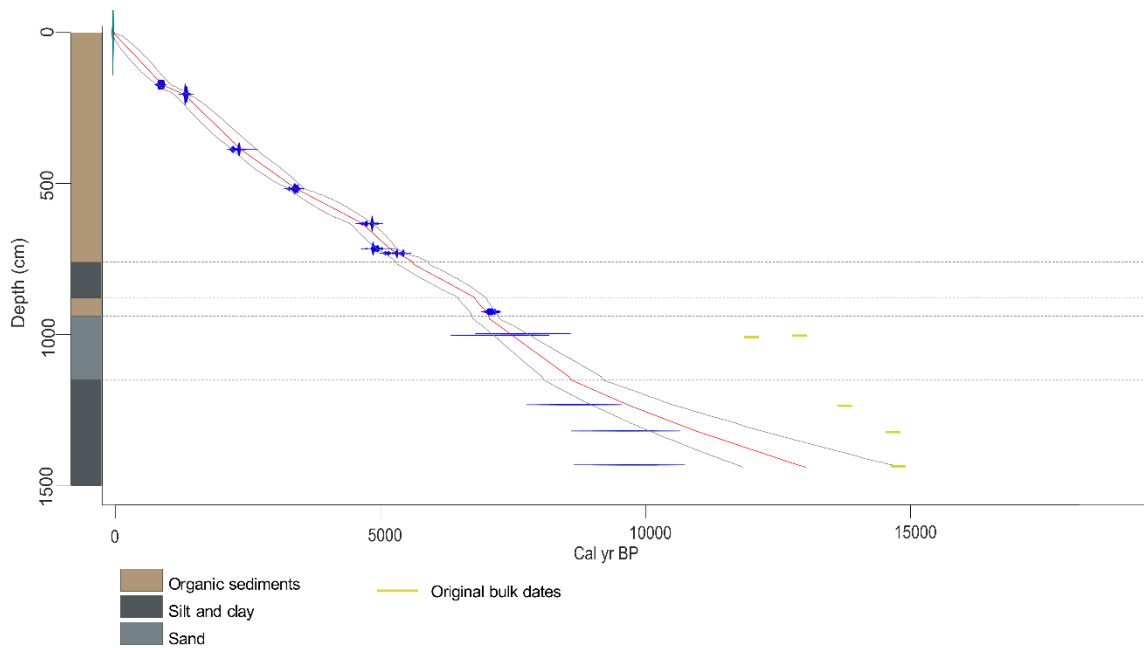


Fig. 17 Lithology and age-depth model of Lagoa Dourada sediment core. Boundaries for accumulation rate calculations were set at the thresholds between different sediment layers (horizontal dashed lines).

Macroscopic plant remains could not be found in the lower part of the core and as carbonates were absent bulk sediment was submitted for radiocarbon dating. The comparison of dates from a macrofossil and bulk resulted in an age difference of about 5100 years (**Table 5**). Most bulk dates are in stratigraphic order, suggesting a relatively constant supply of old carbon to the sediment so that the aforementioned offset of 5100 years was used in age modelling. We used an uncertainty of ± 500 years to represent the scatter of bulk dates. Nevertheless, apart from the two dates used to establish the offset, only 5 bulk dates provided a consistent trend with informing on possible ages for the lower part of the core. To further constrain the ages for the lower part of the core we used pollen concentrations assuming that the total flux of pollen to the sediment did not change in time. Constant pollen concentrations for the upper part of the core with dates on macrofossils support this assumption. Pollen accumulation rates estimated for the upper part of the core were thus used to infer sedimentation rates for the different sediment units. This information was used in the bacon age modelling as prior information together with the five bulk dates with the offset of 5100 ± 500 years. Radiocarbon dates were calibrated with the SHCal13 curve (Hogg et al., 2013) in bacon.

The age-depth model for the first 1000 cm, is relatively linear, which was established by dating macro-fossils found in stratigraphic order. Below, it was not possible to find any macro-fossil. Since there was no carbon, bulk samples were dated and some came in

stratigraphical order, still, a high uncertainty exists under 1000 cm (7500 cal yr BP). With the parameters selected for the age-depth model, a basal age of 12850 cal yr BP for Lagoa Dourada is obtained, nevertheless, due to its high uncertainty (bulk sediments and possible carbon offset), we decided to work under a depth scale for the description of the results. Besides, we assume the core not to be that old, 12850 cal yr BP corresponds closely with the Youngest Dryas (YD) interval (11700 cal yr BP) (Carlson, 2013; E. C. Grimm et al., 2011; Rasmussen et al., 2006), nevertheless, the palynological results evidence no strong change in the vegetation composition and therefore we assume not to cover that period and established based on palynological results and previous research (Melo & Giannini Fonseca, 2000; Moro et al., 2004) a possible basal age no older than 11700 cal yr BP for the following results and interpretations.

5.4.2 Palaeoecological and geochemical history

A total of 150 different pollen and spore taxa were identified (**Fig. 18** and **Appendix 5**). The pollen record is dominated by grassland pollen (average 64%), followed by Atlantic rainforest and other trees and shrubs taxa (24%) and *Araucaria* forest (12%). The representation of tree ferns reached an average of 23%. The most abundant grassland taxa are Poaceae (39%) and Cyperaceae (14%), with low pollen percentages of Asteraceae and *Eryngium*, averaging only 2%. The dominant tree taxa of the Atlantic rainforest, with relative low pollen percentages, are *Alchornea* (3%), *Euterpe/Geonoma* (3%), Moraceae/Urticaceae (1%) and Myrtaceae (1%). Other tree taxa with relevant representation are *Myrsine* (3.5%) and *Phyllanthus* (2%). The main components of the *Araucaria* forest are *Araucaria angustifolia* (6%), *Schinus* (1%), *Sebastiania* (2%) and *Ilex* (1%). Ferns are dominated by *Cyathea* followed by *Lophosoria quadripinnata* and *Osmunda*.

The 15 samples for inorganic Carbon (TIC) along the core yielded on the absence of inorganic Carbon in Lagoa Dourada. Total carbon (TC) is therefore interpreted as total organic carbon (TOC). The geochemical diagram (**Fig. 19**) shows that Biogenic silica presents its highest values in the bottom section of the core (1440 to 1150 cm) when a mix of silt and clay sediments are dominant (first sediment layer). Whilst lower values of

TC, TN and TS prevail. Towards the top a high amount of TC dominates from 760 cm to 0 cm, while TN and TS are still low, increasing just in the last 50 cm. Diagrams are plotted in a depth scale, besides age is also plotted until 7500 cal yr BP. Furthermore, and based on CONISS analysis of the pollen data, the record was divided into five pollen zones:

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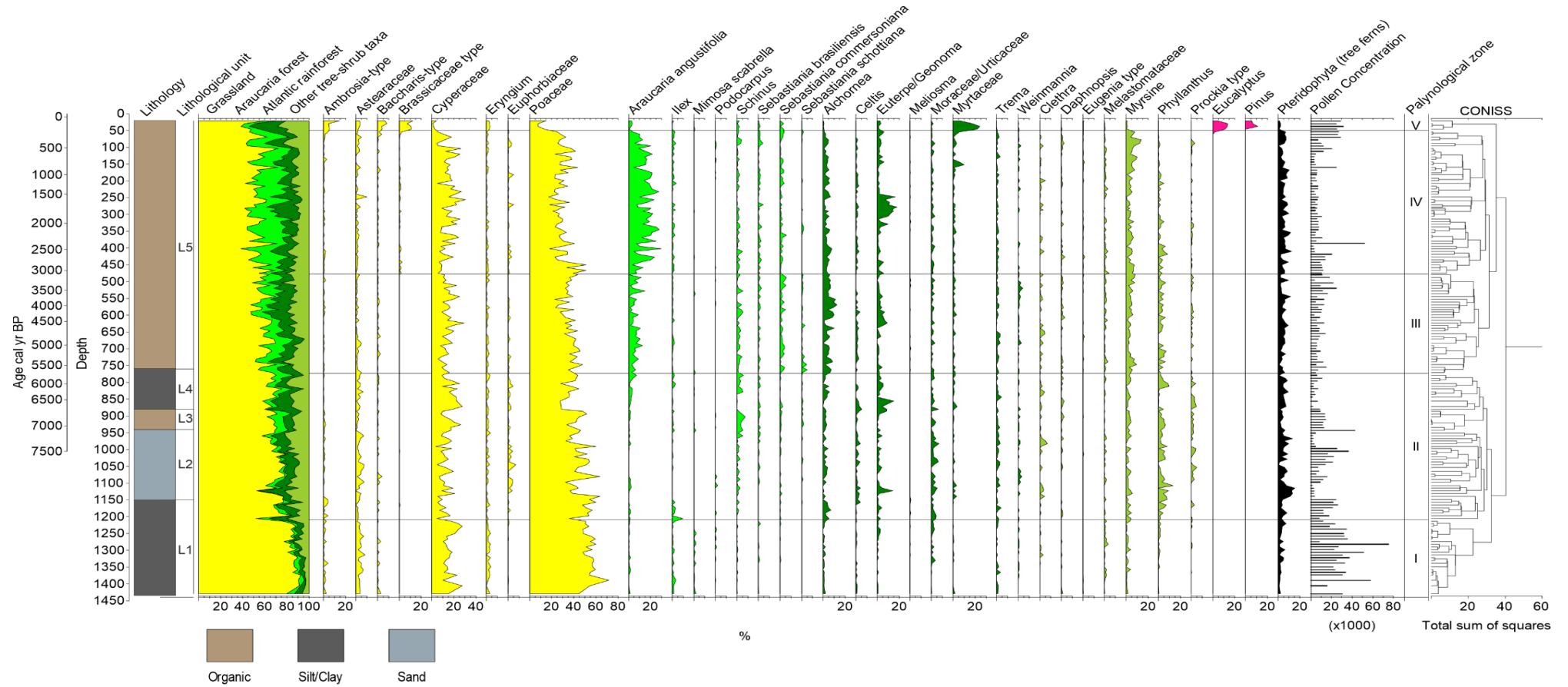


Fig. 18 Summary pollen percentage diagram of Lagoa Dourada core, grouped into Grassland, *Araucaria* forest, Atlantic rainforest and other tree shrubs taxa, tree ferns and CONISS dendrogram.

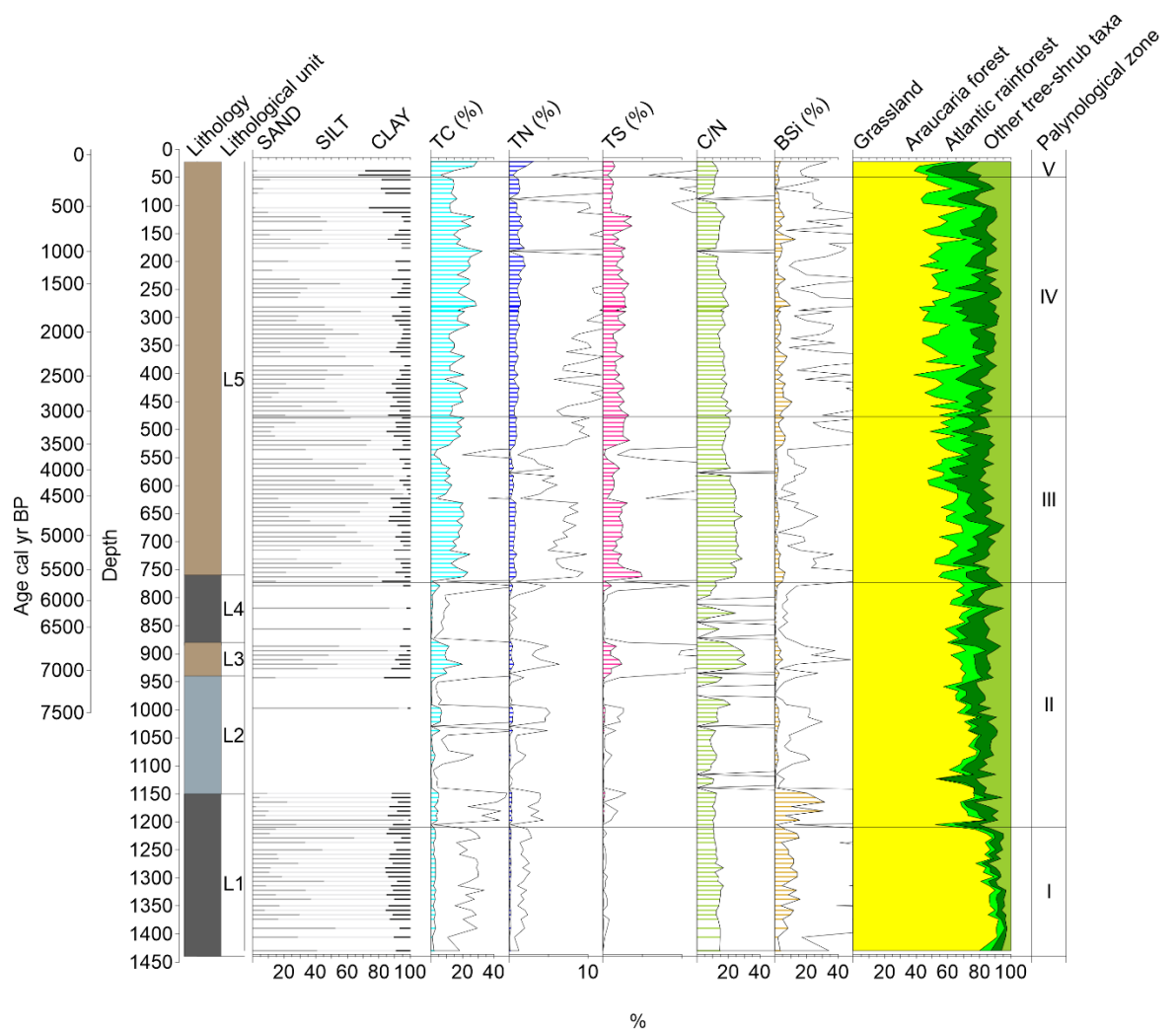


Fig. 19 Particle grain size (Sand, Clay, Silt %), and geochemical diagram of Lagoa Dourada (with Exaggeration = 10 are: total Carbon (TC%), Total Nitrogen (TN%), Total Sulfur (TS%), Carbon/Nitrogen ratio and BSi%), plotted together with cumulative vegetation curves.

Zone LD-I (1440 – 1209 cm; 23 samples): This zone is dominated by grassland pollen (86%), represented mainly by Poaceae (55%) and Cyperaceae (17%). *Araucaria* forest pollen percentage is low (4%), with *Ilex* (1%), *Araucaria angustifolia* (<1%) and *Mimosa scabrella* (<1%). Atlantic rainforest pollen taxa are scarce (4%). Other trees and shrubs (6%) are poorly represented with few pollen grains of *Myrsine* averaging just 1.5%, while the pollen of other trees encountered achieve less than 1% of. Tree ferns (10%) have the lowest representation in the entire core. Geochemical data shows that Carbon content has its lowest values with an average of 2%, Nitrogen and Sulfur are almost absent with less than 1%, C/N ratio is around 13%, while BSi is significantly higher (9%, ranging from 16% to 1.7%). The grain size of the inorganic fraction of the sediment consists of silt (62%), sand (26%) and clay (12%).

Zone LD-II (1209 – 773 cm; 52 samples): This zone is characterized by the decrease of grassland taxa (70%) mainly by Poaceae (44%); the slight increase of *Araucaria* forest (6%) with a low and sporadic representation, especially from *Araucaria angustifolia* (averaging 1%), increasing just towards the top of this period; the increase of vegetation in the Atlantic rainforest (11%) and other trees and shrubs (14%); as well the notorious increase in tree ferns (25%). Between 8490 – 8360 cal yr BP peaks in the percentages of *Osmunda* (30%) and *Euterpe/Geonoma* (7% with a maximum of 14%) are detected, followed by an increase in *Dicksonia* and *Lophosoria quadripinnata*, but just averaging less than 4%. There are no other important fluctuations in the percentages of the taxa identified, nevertheless, a gradual and general change in the forest composition is observed. in this zone Carbon content (3%) increased, Nitrogen (<1%) and Sulfur (<1%) remain at very low values. The C/N ratio (11.5%) decreased, as well as BSi (4%), nonetheless, the latest reaches its highest levels in the bottom of the zone (ranging from 31.6% to 6.8%) section that still belongs to the first sedimentary layer; particle grain size analysis identified an increase in sands (44%), and a decrease in silt (48%) and clay (8%).

Zone LD-III (773 – 477 cm; 37 samples): In this zone, grasslands (60%) decrease further with Poaceae (37%) and Cyperaceae (14%). *Araucaria angustifolia* was found constantly among the samples analyzed with are higher representation than the previous periods

(average 6%), indicating the establishment of the tree in the area around 7000 cal yr BP. *Sebastiania* species as a component of the *Araucaria* forest occurs with its highest values reaching altogether in average 4%. Atlantic rainforest taxa (13%) kept increasing with *Alchornea* (6%) and *Euterpe/Geonoma* (3%) as the most abundant plants. Other trees and shrubs taxa reached 14% with *Myrsine* (4%). Tree ferns (23%) slightly decreased but no significant change is recorded. CNS values increased (14%, <1% and 2%, respectively); in consequence C/N ratio (22%) is also higher, while BSi (2.5%) is lower. Sand (51%) content is higher, silt (41%) lower and clay 8% content maintain the same proportion as the previous zone.

Zone LD-IV (477 – 50 cm; 56 samples): During this period the dominance of grasslands is not as strong as before averaging now 53%, while the rapid increase of other vegetation types is noticed. *Araucaria angustifolia* (averaging 15%, ranging from 27% to 4%) became the most dominant tree with its highest representation throughout the entire core. Among the Atlantic rainforest taxa, *Alchornea* (4%) decreased and the palms *Euterpe/Geonoma* (4%) slightly increased, towards the top of this zone Myrtaceae tends to increase, reaching maximum values of 10% a trend also documented in other taxa like *Myrsine* (8%) with maximum values of 14%. Besides, tree ferns (27%), mainly *Cyathea* (17%) slightly increased. Geochemical data are characterized by a general increase in Carbon content (18%) and Nitrogen (1%); Sulfur (2%) does not present variations; C/N ratio (16%) is lower; BSi (4%) is slightly higher and the proportion of clay particles (54%) and silt (9%) have raised, while sands decreased (37%).

Zone LD-V (50 – 0 cm; 4 samples): During this zone grasslands (47%) mainly Poaceae (11%) and Cyperaceae (2%) recorded the lowest average values throughout the entire core, whilst *Ambrosia*-type (7%) and *Baccharis*-type (6%) had increased. *Araucaria angustifolia* (2%) considerably dropped down as well as tree taxa from woodlands. Human indicating taxa are recorded, peaks are especially detected in *Eucalyptus* (11%) and *Pinus* (6%) and *Brassicaceae* (10%). Myrtaceae (18%) strongly increased as a main component of the Gallery forest that surrounded Lagoa Dourada, while tree ferns (20%) decreased. Carbon content (12%) have slightly decreased and small variations are registered in Nitrogen (1%) and Sulfur (1%) percentages; C/N ratio (12%) and BSi (2%) decreased. The most significant change is observed in particle grain size analysis, where after removing organic content, silt (68%) particles are dominant, and a reduction in clay (27%) and sand (5%) is recorded.

5.4.3 PCA and RDA

The principal component analysis indicates that 24% of the total variance in the vegetation data is explained by the first (16%) and second (8%) axes (**Fig. 20**). Shows that in the first axis of the PCA samples are separated according to their proportion of Poaceae and Asteraceae versus *Araucaria angustifolia*, *Sebastiania commersoniana*, *Myrsine* and *Alchornea*. Samples from the zones I and II are represented by Poaceae, Asteraceae *Eryngium* and Cyperaceae, whilst the ones from zone III and IV are characterized by tree taxa, as has been described in the pollen diagram. Therefore, the first component can be considered as a representation of open versus forest environments in this case Grasslands versus *Araucaria* forests. The second axis, in contrast, separates the samples according to the proportions of human indicator taxa such as; *Eucalyptus*, *Pinus* and Brassicaceae with Myrtaceae as a reflection of the present vegetation (Gallery forest) as well as taxa like *Baccharis*-type and *Ambrosia* versus Cyperaceae, in which zone V encloses the samples from the most recent period where plantations of *Eucalyptus* and *Pinus* were established. Supplementary variables from geochemical data were passively included in the PCA, where CNS contents show correlation within forested environments while plotting opposite to BSi contents in open scenarios. The results from the RDA analysis (**Table 6**) reveals that 32.8% of the variation can be explained with the geochemical data. All the variables are significantly correlated with the variance in taxa composition, the largest part of the variance is explained by sedimentary Carbon, Nitrogen and Sulphur contents.

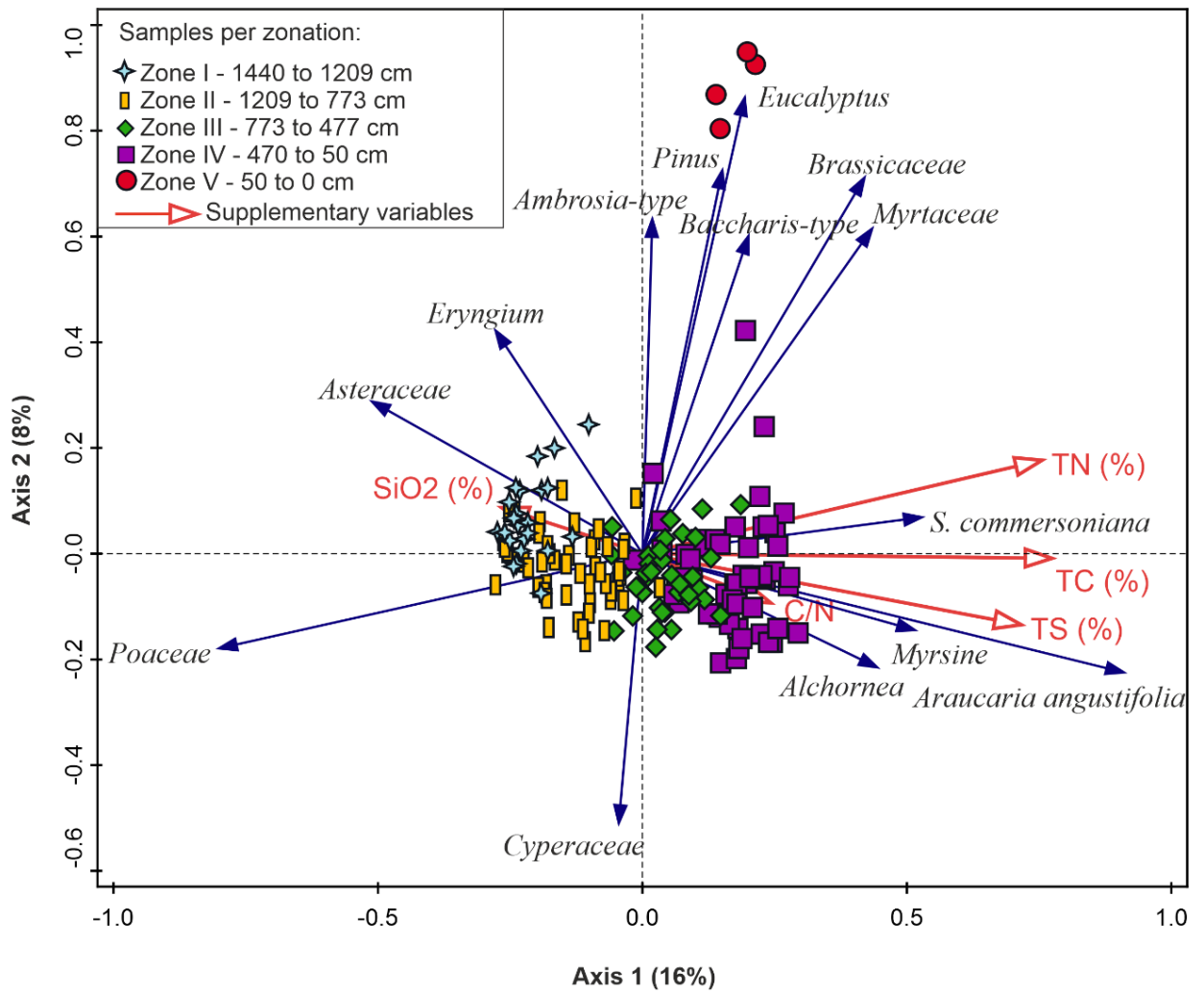


Fig. 20 Principal Component Analysis (PCA) of pollen percentage data after square root transformation of Lagoa Dourada.

Table 6. Results from the redundancy analysis (RDA)

Name	Explains %	pseudo-F	P
TC (%)	9.8	18.5	0.002
TN (%)	9.7	18.2	0.002
TS (%)	8.7	16.2	0.002
BSi (%)	2.4	4.3	0.002
C/N	2.2	3.8	0.002

5.5 Interpretation and Discussion

The observed changes in sediment composition and pollen aspects of Lagoa Dourada record describe significant changes in the pond and the surrounding vegetation. Lacustrine deposition at Lagoa Dourada could have begun at around ~11700 cal yr BP. A crucial process in silting-up the pond are the floodwater of Guabiroba River (Melo et al., 2003) and thus can perhaps explain the accumulation of sands in such a quantity in the entire profile and especially in the lowest meters of the core. The bottom of the core, which is mainly composed by silt sediments and sand, revealed no significant variation in sediment composition.

At around 1320 cm depth pollen proportions changed; trees and shrubs taxa remained in low quantities but few new pollen taxa appeared; a small increase in tree ferns is noticed, those represented mainly by *Cyathea* and *Dicksonia* species indicate a stepwise change toward a warmer climate. A similar trend was also documented by Behling and Negrelle (2001) in Volta Velha record in the Atlantic Lowland of Santa Catarina in which *Ilex* showed a stepwise change before other forest taxa incremented and warmer conditions prevail, suggesting that those changes are an expression of regional climatic variations.

From 9350 to 5770 cal yr BP warm and dry conditions were dominant nevertheless the pollen assemblages indicated the beginning of somewhat wetter and warmer conditions than before. The slight increase of several tropical trees, shrubs and ferns taxa standing out *Alchornea*, *Euterpe/Geonoma*, *Moraceae/Urticaceae*, *Myrsine* and *Cyathea/Dicksonia* tree ferns that slowly spread; the somewhat more frequent appearance of *Araucaria angustifolia* and the decrease of *Eryngium* support this interpretation, revealing that variations in climate were determinant for the plant communities. In the Atlantic lowlands of Santa Catarina state Behling and Negrelle (2001) documented a similar trend in the vegetation during the Mid-Holocene with the increase of *Alchornea*, *Myrsine* and *Arecaceae*. Moreover in south-eastern Brazil, Bernal et al., (2016) documented in Botuverá Cave, through the analysis of $\delta^{18}\text{O}$ that a gradual change with more moisture availability due to the increase of rainfall occurred from the early to the Late Holocene. Those results also indicate that from ~7500 cal yr BP there was an

intensification of the South American Monsoon System (SAMS) from early to Late Holocene with a higher amount of seasonal rainfall.

Even though our study site is not directly placed under the strong influence of the SAMS an important pattern was detected at around 7000 cal yr BP. During this time *Araucaria angustifolia* is for the first time stable before this, there were only scattered occurrences of this pollen type in the record. Here *Araucaria angustifolia* expansion started, increasing gradually towards the Late Holocene. The scattered occurrence of the conifer earlier than 7000 cal yr BP may imply that it was probably only present in small scattered stands, supporting the hypothesis that its initial expansion happened by spreading out of the gallery forests along the rivers and wet areas (Behling et al., 2004; Jeske-Pieruschka et al., 2013), detected in here during the Mid-Holocene.

Between 5770 to 3080 cal yr BP, the increase and expansion of *Araucaria* forest stand out, characteristic trees such as; *Araucaria angustifolia*, *Schinus*, *Sebastiania brasiliensis*, *Sebastiania commersoniana* and *Sebastiania schottiana* increased synchronously. Also, tree ferns remain present with an important representation and typical Atlantic rainforest and other trees taxa continue increasing in the pollen record like *Alchornea*, *Euterpe/Geonoma* and *Myrsine*. Those vegetation changes all indicate wetter and cooler climatic conditions. The decrease of herbs and grasses also reflects the expansion of the forest. The expansion of *Araucaria* forest has been documented at different times in the region, for instance, Behling (2006, 1997) recorded this event for Serra dos Campos Gerais at about 2930 cal yr BP and in Serra do Araçatuba after 2000 cal yr BP.

We also evidenced in this period that the availability of Carbon, Nitrogen and Sulfur increased, this could be related to weathering processes that took place on the sediments, perhaps due to the underground water system of the Furnas in this area (Melo & Giannini Fonseca, 2000). Thus changes in the sediments, were congruent with changes in the vegetation, a correlation that has been noticed before in the *Araucaria* Forest-Grassland mosaics in Rio Grande do Sul.

From 3080 to 220 cal yr BP the ecosystems became more even, meaning that the taxa present start maintaining similar proportions without showing extreme changes (drops or peaks), suggesting that the climatic conditions were stable allowing the forest growth without strong disturbances. Here, the greatest expansion of *Araucaria angustifolia* took place, averaging 15% of representation and reaching maximum values of 27%. The

marked establishment of this tree suggests and evidences its colonization in places that initially were grasslands, leaving as a consequence their decrease. Fact, supported by the pollen accumulation rates that increased from 1585 in the previous period to 1741 grains $\text{cm}^{-2} \text{yr}^{-1}$ in here.

Between 1880 to 1530 cal yr BP peaks in the palm trees, *Euterpe/Geonoma* are detected with an average of 11% of representation, these changes might suggest a wetter climate for those periods that perhaps was too wet for *Araucaria* trees or that happened in a different area, as *Araucaria angustifolia* reflects a decrease during the same period but slowly recover after it, with the remarkable decrease of palm trees.

The introduction of *Pinus* and *Eucalyptus* plantations in Paraná region is uncertain, nevertheless, it should have happened after the arrival of Europeans, documented for 1703 in Ponta Grossa. In this region, the *Tropeiros* (troops or commissions drovers of horse, cattle and mule) travelled with their wares towards São Paulo (Dias de Mello, 2017; Silveria Silva, 2015) but they had not colonized the land for that time. Possession of the land, colonization and settlement occurred later in 1800 (Ferreira, 1996). Our results match pretty well with that information, here we documented that the plantations of *Pinus* and *Eucalyptus* in Paraná state started 220 years ago. For Vila Velha State Park is well known that plantations also occur in 1964 as a reforestation measure and due to poor management, they rapidly became invasive (Governo do Estado de Paraná, 2004). This is also supported by the palynological record, in which an increase from 7% to 12% in *Eucalyptus* and from 5% to 7% in *Pinus* is recorded.

Nowadays despite some efforts for controlling these populations, mainly by local authorities, national parks and some governmental entities, southern Brazil is documented as the region with the highest forest cover of those trees with 239.448 ha occupied by *Pinus* and 143.849 ha by *Eucalyptus* (de Loyola Eisfeld & Ferreira do Nascimento, 2015). The introduction of these trees together with grazing activities rapidly affected the natural ecosystems. In the pollen record the *Araucaria* forest, Grasslands, and Atlantic Rainforest in which *Araucaria angustifolia*, *Alchornea*, *Myrsine*, *Moraceae/Urticaceae*, *Cyperaceae*, *Phyllanthus* and *Poaceae* revealed a very low representation as well tree ferns. The

decrease of those species in the forest at the same time allowed the fast spread of Myrtaceae, considered a high species richness family characterized by pioneer species (Higuchi et al., 2012). Meanwhile in the grasslands pioneers' herbs and shrubs grew fast, among them stand out *Ambrosia*, Asteraceae, *Baccharis* and also Brassicaceae.

5.6 Conclusions

We identified changes from drier Early Holocene conditions to wetter Mid-Holocene climate, through a slow vegetation shift into *Araucaria* forest at about 7000 cal yr BP showing stable tree cover since then until the 19th century. This first establishment of *Araucaria* forest is recorded much earlier of what other records suggest for the entire region (average 4000 cal yr BP) and it seems to be related to more moisture availability after ~7500 cal yr BP as Botuverá cave record indicates.

Besides, *Araucaria* forest revealed a stepwise increase strongly recorded first at about 5700 cal yr BP and second at 3000 cal yr BP in which wetter and moister conditions prevailed. Those results support the hypothesis that *Araucaria* forest initially expanded by spreading out of the gallery forests along the rivers. Human impact in the last 220 years caused a significant change on the vegetation composition in the region, with the introduction of *Pinus* and *Eucalyptus* a complete reorganization of natural ecosystems. We also noticed that the variations registered in the sediment composition such as the availability of Carbon, Nitrogen and Sulfur are significantly correlated with changes in the vegetation and with the variance in taxa composition in which a general increase in their abundances is notice.

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6. HIGH-RESOLUTION MID-HOLOCENE FIRE HISTORY IN THE *ARAUCARIA* FOREST GRASSLAND (CAMPOS) MOSAICS IN SOUTHERN BRAZIL

6.1 Introduction

The long-term fire history of southern Brazil and its relationship to past vegetation and environmental changes is still unknown. Palaeoecological investigations in the region carried out in sediments recovered from peat bogs have focused on vegetation dynamics and few also studied fire history. Proving trends for the overall change in fire activity and indicating that high burning periods started at different times during the Holocene (Behling, 1997, 2007; Behling et al., 2004, 2005; Jeske-Pieruschka et al., 2010; Jeske-Pieruschka & Behling, 2012). However, despite their potential to reveal regional patterns in climate, fire and vegetation history, those sites are less suited for high-resolution analyses due to their slow sediment accumulation rate. Hence, sub-decadal not either decal high-resolution records are hitherto available.

Filling this knowledge for south Brazil is important for the following reasons. First, because natural vegetation dynamics in the *Araucaria* and Campos region and its response to disturbances are poorly known. Then a long-term perspective will allow better temporal scales of observation and thus better understanding for biotic processes and species responses to changing climate and disturbances (Finsinger et al., 2017; Tinner et al., 2013). Second, *Araucaria* forest and grassland mosaics are among the ecosystems that belong to the Atlantic Forest biome, considered as one of the most important biodiversity hotspots and target for conservation priorities (Myers et al., 2000; Scarano, 2002) hosting several species that are identified under risk of extinction as is the case of *Araucaria*

angustifolia (Paraná pine) (Thomas, 2013). Here long-term records will help to evaluate the current state of the *Araucaria* forest and grasslands in comparison to their past situations. This will help to provide essential information to consider while implementing management and conservation strategies in the *Araucaria* and Campos region. Third, the use of fires for land management is controversial and here fire frequency is an issue, some studies suggested that grasses seem to be adapted to frequent burning, i.e. annually or every few years (Overbeck & Pfadenhauer, 2007; Quadros & Pillar, 2001). The here study will help to understand how frequent a fire can be and this will provide the basis for land management strategies.

This investigation focused on the Mid-Holocene ~7500 cal yr BP to present charcoal and vegetation history in the highlands of Paraná State (southern Brazil) in the silted-up Forna Lagoa Dourada. Detailed vegetation history of this particular site is presented in the previous chapter. Located in the State Park of Vila Velha within the actual distribution of the *Araucaria* and Campos region in which a protected population of *Araucaria angustifolia* is found, Lagoa Dourada provides a unique potential in revealing its Holocene history. *A. angustifolia* is a critically endangered conifer (Thomas, 2013) distributed in Brazil, primarily in the states of Paraná, Santa Catarina, Rio Grande Do Sul, and locally in São Paulo, Minas Gerais and Rio De Janeiro and in Argentina at the north-eastern side of the country in the Province of Misiones (Bittencourt, 2007; Earle, 2020). It is recognized as a highly flammable conifer (Duarte et al., 2006; Silva & Anand, 2011), and its relationship with fire has been of special interest for more than 40 years. Soares (1979) hypothesised that the tree is a fire-dependent species that needs fire (or another disturbance) to regenerate naturally and succeed, however, this hypothesis has so far not been tested in a long-term perspective.

We, therefore, conducted macro-charcoal and pollen analysis at a high-resolution (sub-decadal and decadal) to reconstruct changes in past fire regimes and its relationship with vegetation and climate to estimate long-term trends in the *Araucaria* forest and grassland mosaics. We specifically aimed to answer two questions: **1)** How did the fire regime change since the Mid-Holocene (7500 cal yr BP) until present in the open grassland? and **2)** what are the leads and lags between fire and *Araucaria angustifolia*?

6.2 Environmental setting

6.2.1 Geography and climate

Lagoa Dourada (25°14'25.55" S, 50°2'58.21" W) situated 25 km southeast of Ponta Grossa in Vila Velha State Park, Paraná State, southern Brazil (**Fig. 16**). The lake is located at 815 m a.s.l. it is a small and round (100 m diameter) and is formed on the Furnas Formation containing Holocene sediments (Moro et al., 2004).

The meteorological station of Ponta Grossa, document annual precipitation of 1554 mm with a minimum between April and August, but without a dry season. Mean annual temperature is 17,8°C, January and February are the warmest months of the year with a mean monthly temperature of 21.4°C and the coldest month is July with 13.8°C (IAPAR, 2020). Frost occurs in Vila Velha, between May and August with an average of five or more frosts events per year, these limit the growth of plants sensitive to low temperatures (Melo & Giannini Fonseca, 2000).

6.2.2 Vegetation

Vila Velha is framed under the Atlantic Forest Biome (IBGE, 2004), in the park several ecosystems are encountered such as Mixed Ombrophilous Forest (*Araucaria* forest), Alluvial Mixed Ombrophilous Forest (Gallery forest), Grasslands (Campos), open Savanna (Campo limpo/sujo) and Fluvial Influence Pioneer formations (wetlands, marshlands or várzea) (**Fig. 16**) (Cervi et al., 2007). *Araucaria angustifolia* is present both in forest patches as well as in open landscapes, it predominates in the emergent layer, but is not the dominant tree in the majority of the woodlands. It is accompanied in the canopy by *Mimosa scabrella*, small trees and shrubs from the families Melastomataceae and Myrtaceae and arboreal elements from Lauraceae, Fabaceae and Asteraceae are common together with ferns such as *Dicksonia sellowiana* and *Cyathea* sp. The most characteristic species of the gallery forests is *Sebastiania commersoniana* forming complex associations with species from Anacardiaceae, Sapindaceae, Lamiaceae families, among others (Roderjan et al., 2002). Open vegetation (Campos) is

characterized by the dominance of Poaceae and Cyperaceae where about 63% of the grasses are shared with the Cerrado Biome (Savana).

6.3 Materials and Methods

6.3.1 Sediment collection, core treatment and chronology

A 1440 cm long sediment core was collected in 2017 from the centre of Lagoa Dourada using two different piston cores. The first 10 m were collected in a lightweight Livingstone-type corer (Livingstone, 1955; Nesje et al., 1987) and a square-rod Livingstone-type corer (Wright, 1967) was used to extract the deeper parts of the lake deposits (4.50 m). Visual description of the sediments and general lithology was performed using the Munsell Soil Colour Chart (Munsell Color (Firm), 1954). A total of 23 samples (8 macrofossils and 15 bulk samples) from the entire core were submitted to radiocarbon dating by Accelerator Mass Spectrometry (**Table 5**). The age-depth model was constructed in rbacon (Blaauw et al., 2020) prescribing approximate sedimentation rates estimated based on changes in pollen concentrations (see the previous Chapter for a detail description). Ages estimated for the lower sections of the core are uncertain due to an old carbon effect on the bulk ^{14}C dates. The chronological control for the first 1000 cm of the core, revealed a relatively linear tendency (**Fig. 17**) based on dated terrestrial macrofossils and deemed reliable. While the age model suggests a bottom age around 12800, this does not coincide with known patterns in vegetation history and therefore a basal age of 11700 cal yr BP is assumed here. We, therefore, present the results of the fire history for the last 7500 cal yr BP, comprising four out of five palynological zones (II (partially), III, IV and V) established in the pollen diagram.

6.3.2 Macro-charcoal and pollen analyses

We used macroscopic charcoal influx as a proxy for local fire activity (Whitlock & Larsen, 2001). Volumetric subsamples of 0.25 cm^3 (organic sediment), 0.5 cm^3 (clay-silt sediment) and 1 cm^3 (sand sediment) taken along the core every 1 cm were prepared for macro-charcoal analysis by treating them with NaPO_3 5% and H_2O_2 10% to concentrate charcoal particles (Schlachter & Horn, 2010). Afterwards, subsamples were washed and sieved through $125\text{ }\mu\text{m}$ mesh and analyzed in the stereomicroscope to separate charcoal particles. Charcoal fragments were classified into two morphological types; grass or

wood, providing additional information on fuel type (Wu et al., 2019). Charcoal derived from grass is usually thin, large, flat, black-grey colour, and characterized usually by the presences of stomata in the epidermal walls (Jensen et al., 2016). Woody charcoal produced by trees and shrubs can be identified by its sheen and thick, layered and prismatic structure as well as its black dark colour (Enache & Cumming, 2006; Wu et al., 2019). The identified particles were then measured by area and size (length and width) with an image analyzer software (WindSeedle, Regent Instruments Canadá, Inc.) following Finsinger et al., (2014). This allowed to express charcoal data as charcoal number-influx, (called CHAR_C: number of particles cm⁻² yr⁻¹), charcoal area (CHAR_A: total area mm² cm⁻² yr⁻¹), and as concentrations (# cm³) for morphological type.

For pollen analysis, we used the data presented in the previous Chapter and increased the resolution with a special focus on two time periods (**Appendix 4**); at 450 cm to 488 cm (2870 to 3170 cal yr BP) and 880 cm to 921 cm (6780 to 6970 cal yr BP) with samples every 1 cm. In total 117 pollen samples were added in the present study for a total of 288 samples along the core. For their analysis *Lycopodium* tablets (9666±212, Batch Nr. 3862) were added as a marker, to calculate pollen concentration and pollen influx. Samples were treated with 10% hot KOH, 10% hot HCl, 70% cold HF, and three minutes hot acetolysis. Subsequently, the samples were mounted and counted under an optical microscope at 400X magnification. The total pollen sum (minimum of 300 pollen grains) includes pollen from herbs, trees and shrubs. Ferns spores were counted and expressed in percentages of the total pollen sum (**Appendix 6**). The identification of palynomorphs was carried out using the references collections of the Department of Palynology and Climate Dynamics of the University of Göttingen, atlas, catalogues of pollen fossil and recent and palynological keys by Bauermann et al. (2013), Behling (1993), Roubik and Moreno (1991) and Silva et al. (2016) were used as well as the online Neotropical Pollen Key (Bush & Weng, 2007).

6.3.3 Numerical analysis

For fire history reconstructions we followed the methods outlined in Higuera (2009) and used the software package CharAnalysis (Philip Higuera, 2009). First, a temporal median

resolution of 7 years per cm^2 (CHARi) was used, then data was broken down into a low-frequency background component (CHARback) and a peak component (CHARpeak). For the background component, we used a locally weighted polynomial regression (LOWESS) with robust outliers and a moving window of 1000 years. This resulted in a robust signal-to-noise index (SNI) (Kelly et al., 2011). The CHARpeak component was estimated by residuals and evaluated with a Gaussian mixture model that aimed at separating peak samples representing actual fire episodes from surrounding noise in the CHARpeak series. For each 1000-yr window, CHARpeak values exceeding the locally defined threshold were identified as potential fire episodes. Thereafter, the CHARpeak records were screened with peak-screening tests (Finsinger et al., 2017; Philip Higuera, 2009). This allowed us to interpolate and calculate charcoal accumulation rates (CHAR, $\text{pieces cm}^{-2} \text{ yr}^{-1}$), isolate charcoal peaks, and estimate mean fire return interval (mFRI), fire frequency, and fire-episode (peak) magnitude to regularly spaced time intervals. Besides, we used CHARback as a proxy for biomass burning (Finsinger et al., 2017; P Higuera et al., 2007; Kelly et al., 2011).

The pollen diagram was plotted with Tilia 2.6 software (E. Grimm, 2015) and zonation was based on stratigraphically constrained cluster analysis (CONISS). Pollen data were summarized in a cumulative diagram using four curves: Grassland, *Araucaria* forest, Atlantic rainforest and other trees and shrubs taxa. Palynological richness (ET(n)) (H. J. B. Birks & Line, 1992) was determined by rarefaction analysis to the smallest sample size (here $n = 263$) using the “vegan” package in R software (R Core Team, 2013). In here, the complete pollen diagram is presented in an age-depth scale,

To assess regional patterns of vegetation variability multivariate statistical analyses were carried out. First, a Principal Component Analysis (PCA) was performed to explore the relationships between vegetation communities in the different palynological zones for the entire record. Second, a constrained ordination (redundancy analysis (RDA)) was done, to visualize the major differences in pollen composition and to extract the variation that is directly explained by the charcoal variables (charcoal accumulation rates, mean fire return interval, fire magnitude, fire frequency) for the last 7500 cal yr BP. PCA and RDA were done using CANOCO 5.0 software (ter Braak & Smilauer, 2012). Even though this core expands more than 11700 cal yr BP, we present fire activity results for the time between 7500 cal yr BP and present for which the chronological control is best.

Furthermore, to identify links between fire disturbance and vegetation dynamics, and to study the long term fire ecology (Tinner et al., 1999), cross-correlation coefficients of macroscopic charcoal and *Araucaria angustifolia* were calculated using the R software (R Core Team, 2013). Pollen and charcoal concentrations were used to avoid influx biases from the age-depth model (Clear et al., 2013). To enable calculation of cross-correlation, continuous sedimentation has to be assumed, therefore we ran this statistical analysis in two high-resolution sections; one at 450 cm to 484 cm (2870 to 3135 cal yr BP) and the other at 880 cm to 921 cm (6780 to 6970 cal yr BP), those sections were sampled every 1 cm with a temporal resolution of 8 years and 6 years respectively.

6.4 Results and interpretation

6.4.1 Charcoal-inferred fire history

Charcoal concentration records by morphotypes and by area generally are covariant, indicating that the charcoal particle size distributions are homogeneous among samples. Charcoal concentrations and the CHAR record show similar trends, indicating little influence of the variations in sediment accumulation rates. The trends within concentrations and charcoal accumulation rates differ in some periods during the last 7500 cal yr BP (**Fig. 21**) and are described as follow.

In Zone II, from ~7500 to ~7000 cal yr BP woody and grass charcoal concentration are low, with slightly higher charcoal concentrations observed at 7000 to ~6750 cal yr BP, following a posterior decrease. The charcoal concentration of both morphological types rapidly increases in zone III at ~5700 cal yr BP. A High concentration of woody charcoal is observed between 4620 to 3990 cal yr BP. Large size charcoal particles observed at ~4135 cal yr BP (585 cm depth) in the sediment core contain both woody and grass charcoal. In Zone IV a decrease in grass charcoal concentration occur from ~3000 to ~2000 cal yr BP while the woody charcoal concentration remains high. At ~1800 until ~750 cal yr BP grass charcoal concentration is higher than woody charcoal and as a

consequence, a decrease in the concentration per area (CHARa) is noticed. During Zone V a remarkable decrease in grass charcoal and the increase in woody charcoal is recorded.

The charcoal accumulation rate record (CHAR) based on the sum of both morphotypes ranges between 0 and ~ 28.1 particles $\text{cm}^2 \text{yr}^{-1}$. In zone II at ~ 7000 cal yr BP one of the highest peaks in CHAR is detected, followed by a decline that lasts until ~ 5700 cal yr BP. CHAR increases abruptly after this period, peaks and changes are detected. A total of 69 fire peaks were detected during the past ~ 7500 cal yr BP within Lagoa Dourada catchment. Only six additional CHARpeaks failed the charcoal-area peak-screening test. This suggests that almost all the CHARpeaks are robust indicators of past local fire events (Finsinger et al., 2017).

Four of the 69 fire peaks occur in zone II during 7030 to 6850 cal yr BP, with almost all the fire events (65/69; 94%) occurring during the interval between 5660 cal yr BP to the present. The frequency of fire peaks in zone II is low and it varies from 0.66 to 4.79 peaks/ka (average 2.85 peaks/ka). Zone III and IV are characterized by a much higher fire frequency, ranging respectively from 3.02 to 15.49 peaks/ka (11.37 peaks/ka) and from 6.07 to 14.22 (11.87 peaks/ka), relative to that of zone II as well as zone V in which in average 5.25 peaks occur every 1000 years. The interval with the highest fire frequency value (average 15.12 peaks/ka) throughout the core, corresponds to the period between 4950 to 4550 cal yr BP. Fire peak magnitude, providing a reference for fire severity or proximity, show five peaks, among them the highest value is encountered at 1600 cal yr BP ($1259.83 \text{ pieces cm}^2 \text{ peak}^{-1}$). Followed by slightly lower values of fire peak magnitude (i.e. 781.64, 702.11, 970.11 and 950.5 pieces $\text{cm}^2 \text{ peak}^{-1}$) at ~ 5600 , ~ 4825 , ~ 3390 and ~ 1380 cal yr BP, respectively.

CHARback was used as an indicator of local biomass burning (Tinner et al., 1999). CHARback values and trends are easily recognized, in which a clear differentiation occurs for the periods of ~ 7500 to ~ 5700 cal yr BP when values were in their lowest and from ~ 5700 to the present where CHARback values are higher and two lower-amplitude maxima are centred on ~ 7000 , ~ 5000 and ~ 1600 cal yr BP. The CHAR record also shows a similar trend during these periods. Thus, suggest distinct periods of local biomass burning in the surroundings of Lake Dourada.

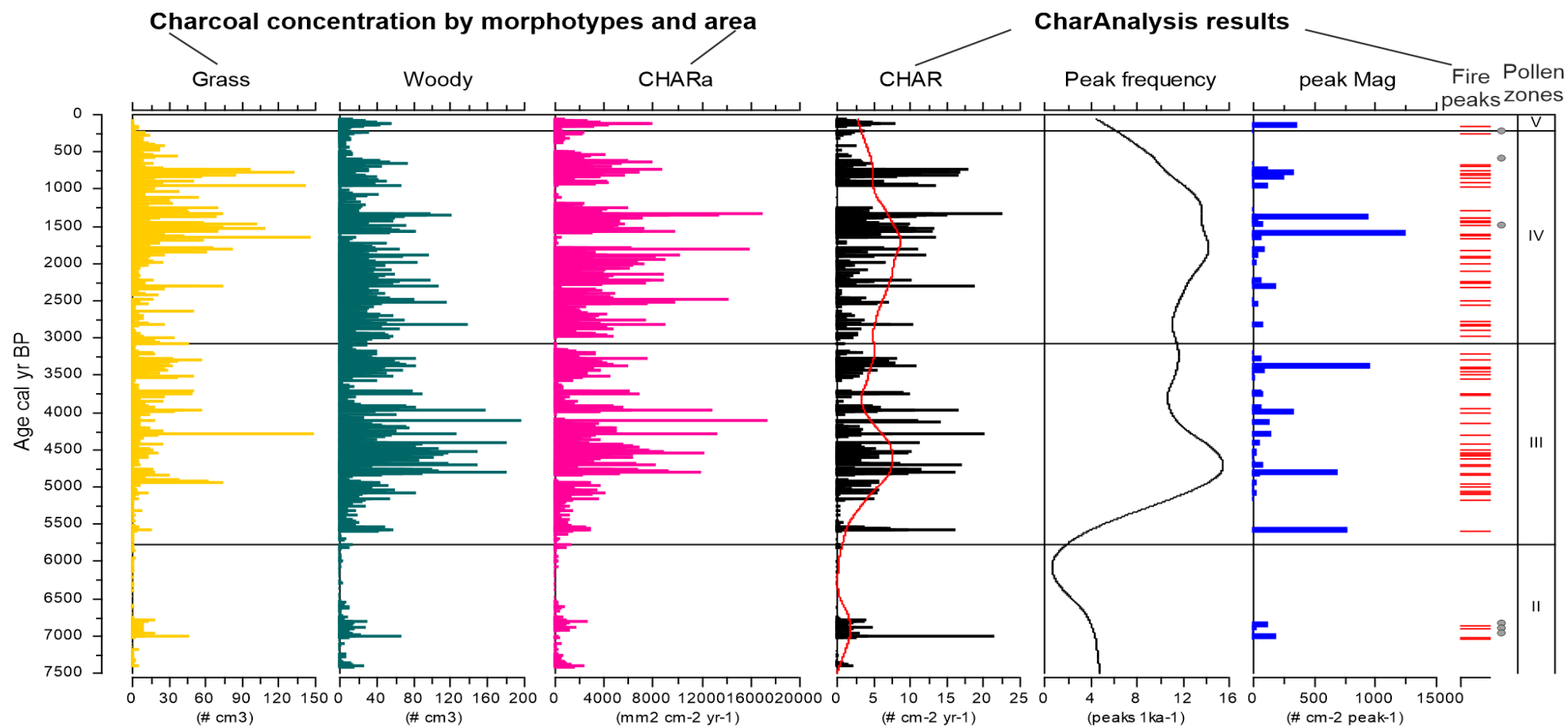


Fig. 21 Charcoal concentration, charcoal accumulation rate (CHAR) and CharAnalysis results for Lagoa Dourada. Charcoal concentration is calculated for grass and woody morphotypes. CHAR is based on the sum of both morphotypes, red line indicates CHARback. Palynological zones are also plotted.

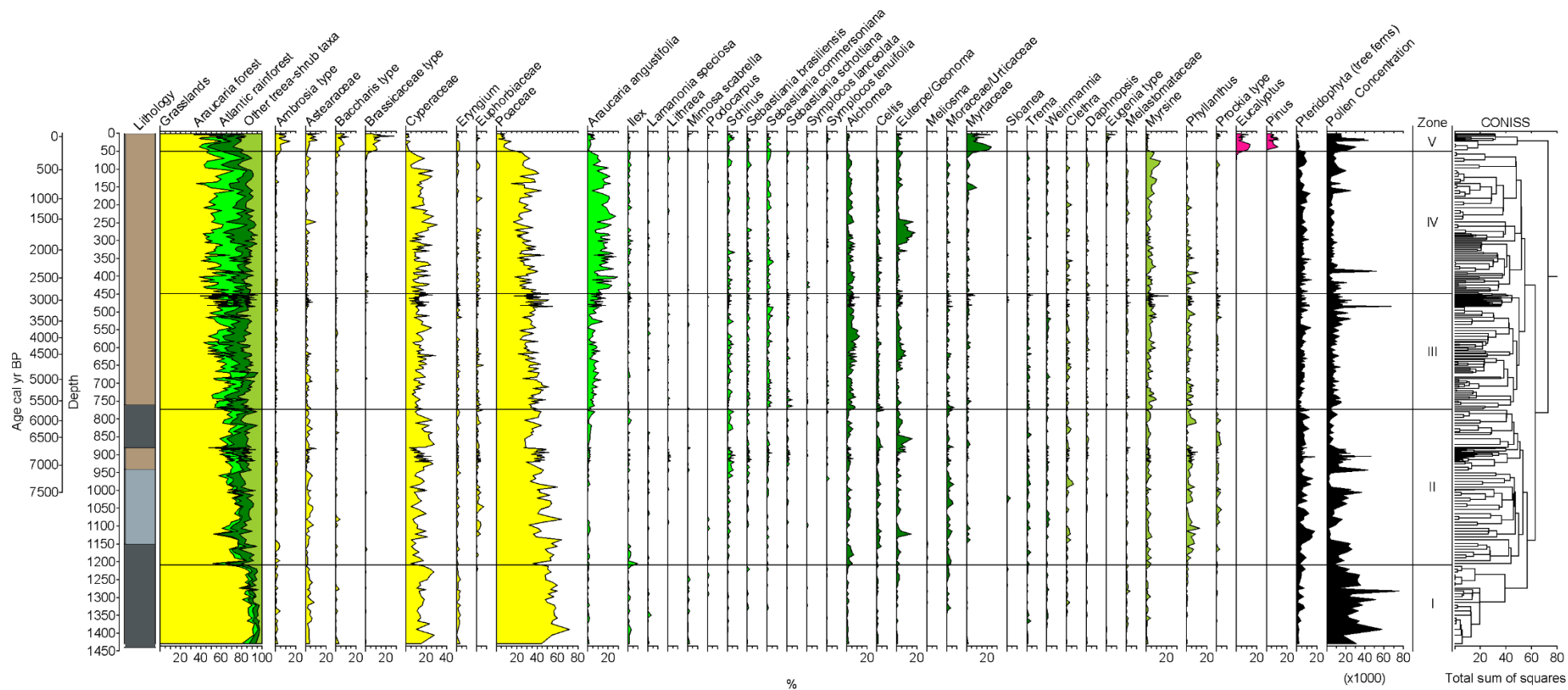


Fig. 22 High-resolution summary pollen percentage diagram of Lagoa Dourada core, grouped into Grassland, Araucaria forest, Atlantic rainforest and other tree shrubs taxa, tree ferns, PCA Axis 1 and 2 and CONISS dendrogram

6.4.2 PCA, RDA and cross-correlation

In the PCA (**Fig. 23**) a total of 18% of the variance in the vegetation data is explained in the first two axes (12% and 6%, respectively). The first axis of the PCA separates the samples according to the proportions of Poaceae and Asteraceae versus *Araucaria angustifolia*, *Myrsine* and *Verbena*, which reflects the separation of woodlands versus grasslands. The second axis separates the samples according to the proportions of Cyperaceae and *Euterpe/Geonoma* versus Euphorbiaceae and *Sebastiania brasiliensis*. The samples arrangement on the PCA shows the vegetation phases through time from Mid-Holocene (right) to Early Holocene (left).

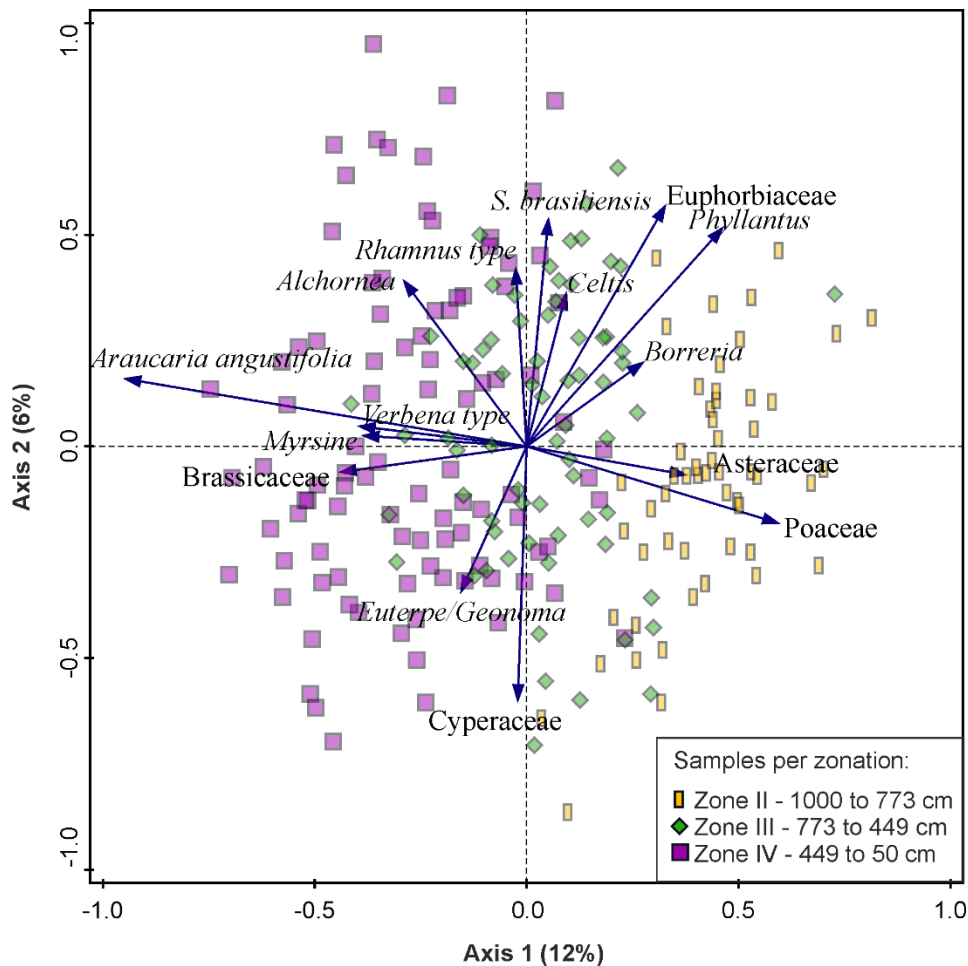


Fig. 23 Principal Component Analysis (PCA) of pollen percentage data from the last 7500 cal yr BP after square root transformation of Lagoa Dourada. In here samples for zone I, are excluded.

The results from the RDA analysis performed for the last ~7500 cal yr BP in the vegetation data and fire variables (**Table 7, Fig. 24**) reveals that 10.5% of the variation can be explained by the charcoal data, three out of the four variables used are significant, they are correlated with the changes in vegetation, as follows; fire frequency, mean fire return interval (mFRI) and charcoal accumulation rates (CHAR), while fire magnitude is not significant. Results also show a positive correlation between *Araucaria angustifolia* and fire frequency in the first axis (80%) of the RDA analysis.

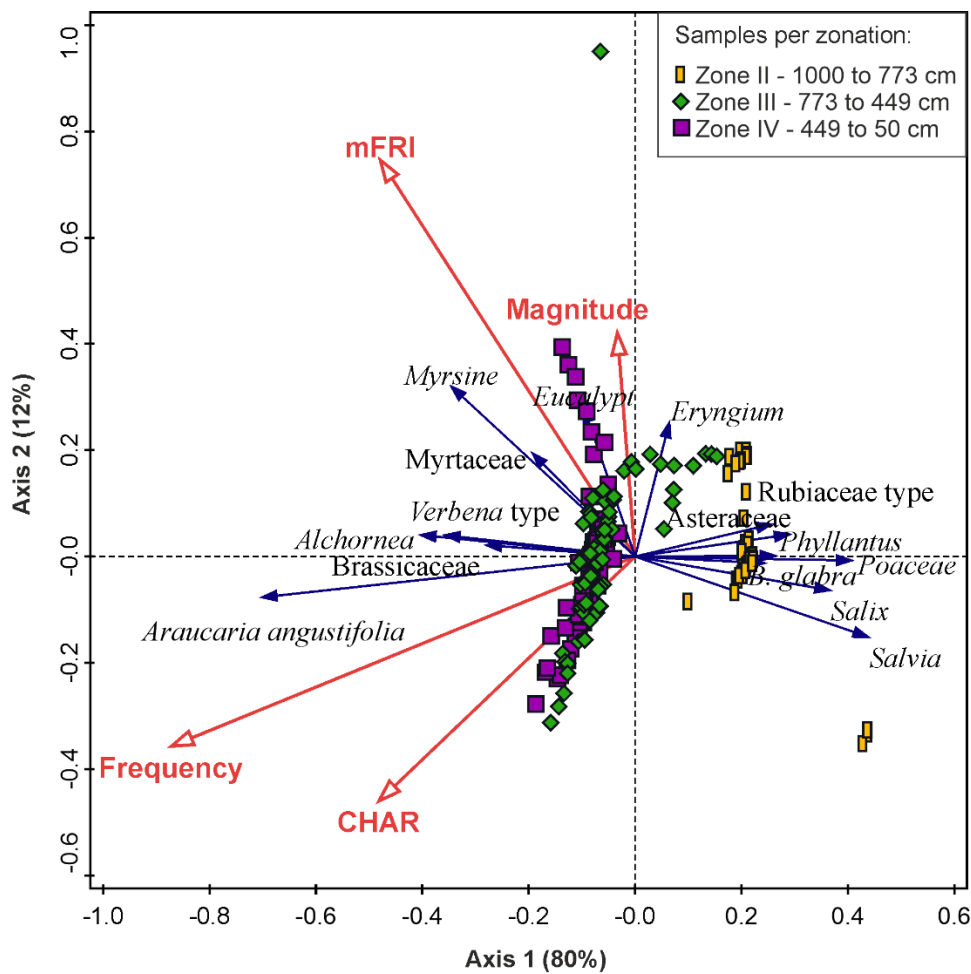


Fig. 24 Redundancy analysis (RDA) biplot of samples, species and environmental variables (mean fire return interval – mFRI, fire magnitude, fire frequency and charcoal accumulation – CHAR) of Lagoa Dourada. The best 15 fitting species indicated by the ordination analysis are plotted.

Table 7. Results of redundancy analysis (RDA)

Name	Explains %	pseudo-F	P
Fire frequency (peaks 1ka-1)	5.2	13	0.002
Mean Fire Return Interval (mFRIs) (yr*fire-1)	2.3	5.2	0.002
CHAR (# cm-2 yr-1)	2.1	4.7	0.002
Fire magnitude (# cm-2 peak-1)	0.5	1.2	0.18

Cross-correlation coefficients (**Fig. 25**) of macro-charcoal and pollen for the two high-resolution periods revealed, first for the period ~7000 cal yr BP *Araucaria angustifolia* does not show a significant correlation not positive or negative, Poaceae present a significant positive correlation (peak at lags -1 to +4) later a negative correlation is detected (peak at lags +8 to +10), Myrtaceae in contrast, shows a positive correlation in negative lags (peak at lags -10 to -5) indicating that changes in *Myrtaceae* happened before the fire which can mean that this taxon was somehow setting the conditions (pre-fire) for a well burnable landscape.

Meanwhile, during the period of the strongest expansion of *Araucaria angustifolia* ~3000 cal yr BP a positive correlation is observed (peak at lags +3 to +6) for this taxon, meaning that fires resulted in increased abundance of *Araucaria*. Poaceae in this period presents a positive correlation in negative lags and thereafter a negative correlation in positive lags, which can be interpreted as a precursor taxon as was the case of Myrtaceae earlier, however, the negative correlation in the positive lags indicate that after the fire the abundances of Poaceae are reduced. Myrtaceae in this period does not show any significant correlation. The differences presented in both periods could be possibly related to the local biomass burning, as indicated by the CHARback in peaks detected ~7000 cal yr BP and between ~3000 to ~3500 cal yr BP.

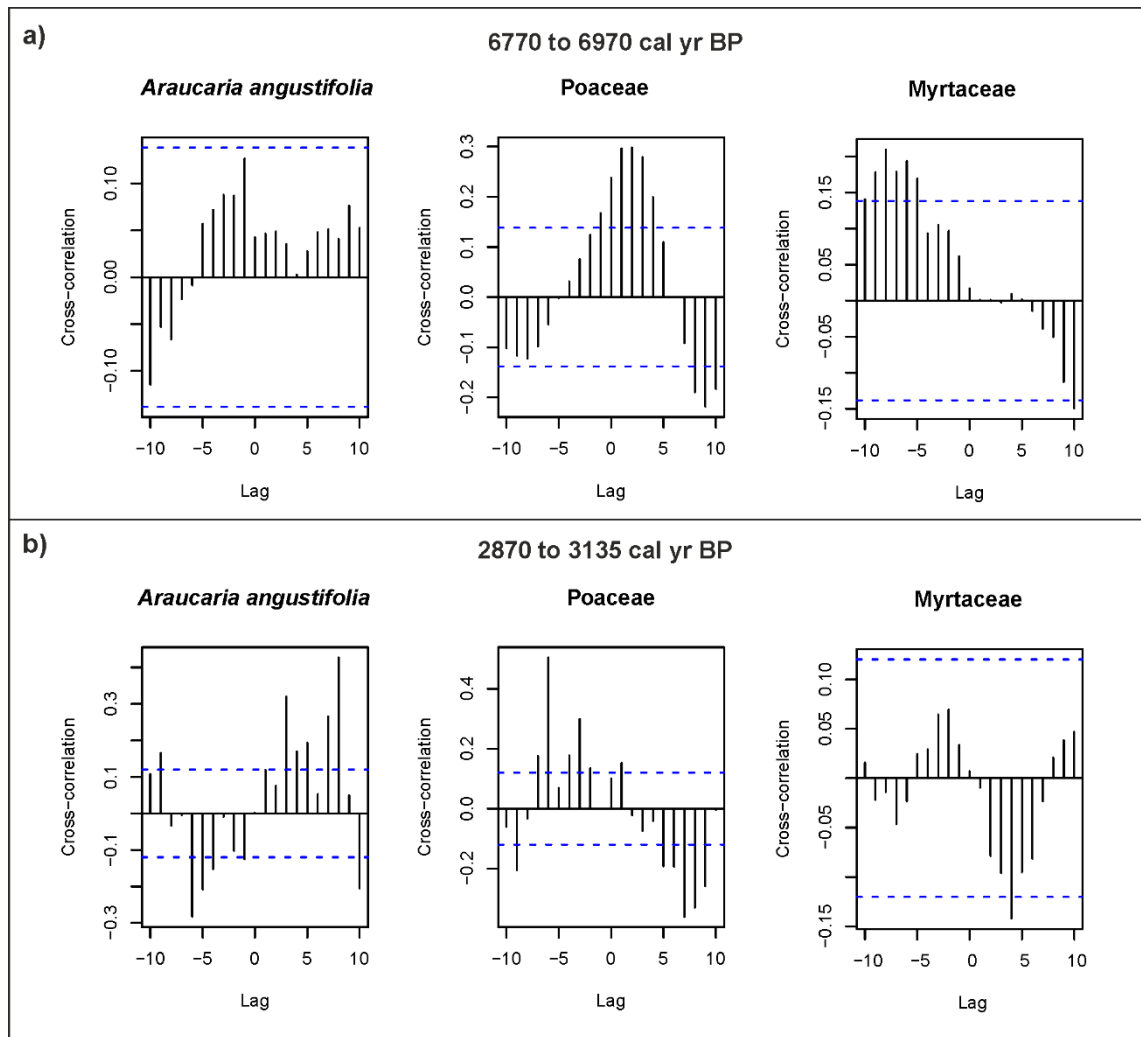


Fig. 25 Cross-correlograms: charcoal vs pollen of selected taxa in two time periods **a)** 6770 to 6970 cal yr BP and **b)** 2870 to 3135 cal yr BP. Vertical axis shows the correlation coefficients; those outside the horizontal blue lines are significant at $p = 0.05$.

6.5 Discussion

6.5.1 Fire-climate relationships and its comparison with prior paleorecords in southern Brazil

The changes in fire frequency during the last 7500 cal yr BP and showed in the time series analysis presented in **Fig. 21** indicate a Mid-Holocene (pollen zone II) characterized by low-frequency fires (28.85 peas/ka) with a moderate magnitude as well as relatively low CHAR values compare to those of Early Holocene times (**Appendix 7**). A general decrease in fire activity during the Mid-Holocene, in comparison to that one of the Early Holocene (higher), is documented among some of the previous investigations in southern

Brazil. For instance, Behling (1997) registered a decrease in CHAR values between ~7000 to ~6000 cal yr BP in Campos Gerais, in which the vegetation suggest a warm environment with shifts of dry and wet climatic conditions. In Serra do Araçatuba (~170 km southeast of Vila Velha) from ~9000 to ~4000 CHAR values decreased and the climatic conditions inferred from the vegetation such as the frequency of *Eryngium* and low proportions of *Araucaria* and Atlantic rainforest taxa, suggest a dry period.

In contrast, Jeske-Pieruschka et al. (2013, 2010) reported for Serra do Tabuleiro (430 km southeast Vila Velha) an increase in fire activity during the Mid-Holocene, this probably due to its isolation to other mountain ranges in which probably microclimatic conditions favoured the increase of burnings, making this particular site act as a refugium. In Cambará do Sul further to the south in the Rio Grande do Sul state, Behling et al. (2004) established that fires since the Mid-Holocene (~7400 cal yr BP) for the first time became frequent as a consequence of climate change that perhaps led to an accumulation of flammable biomass. Behling et al. (2005) also detected for the Campos region in the lowlands of São Francisco de Assis and increase in CHAR values from ~6000 to ~5000 which the authors linked to anthropogenic influence.

Despite the differences encountered in fire history among southern Brazil, it is still possible to identify a regional pattern at least for Paraná state, in which the decrease of fire activity in Mid-Holocene times can be attributed to the dry and warm climatic conditions with wet/dry shifts periods as here proposed and also by the proposals across southern Brazil, especially in Paraná (Behling, 1997; Jeske-Pieruschka et al., 2013), Santa Catarina (Behling, 1995) and Rio Grande do Sul (Behling et al., 2001, 2004) (**Fig. 26**). Supported also by the data obtained in stalagmite record of Botuverá cave, that indicates that between ~7500 to ~5500 cal yr BP there was less moisture availability (compare to the Late Holocene) due to the decrease of rainfall.

Botuverá cave isotope record suggests in general, that for the Late Holocene the total amount of rainfall was higher when compared to the Mid-Holocene, though its variability was smaller (Bernal et al., 2016). Lagoa Dourada reveals for the period between ~5600 to ~3000 (pollen zone III) a reduction of Campos which can be interpreted as changes in

climate from dry to wet conditions as suggested also by Behling (2006, 2007) for Paraná state. However, our results show that also fire played an important role in here, we documented a marked increase in fire frequency (11.37 peas/ka), a higher magnitude and more or less stable trend in CHAR values.

Behling (1997) proposed for Campos Gerais that the increased fire frequency in that area could be explained due to a long annual dry season which seems to have limited the expansion of *Araucaria angustifolia* in there, as the conifer needs somewhat wet and cool environments to be able to establish and grow. Our results suggest that in Lagoa Dourada area the dry season was rather shorter and wetter and cooler climate conditions started earlier than in other areas such as Campos Gerais. The increased abundances of the Atlantic rainforest and *Araucaria* forest taxa support this observation.

A different scenario is the one pictured in the mountain regions of Serra do Araçatuba in where a dry climate prevails with low fire activity (Behling, 2006), making this site an exception of the general trend. Those results along the paleorecords available in Paraná state, in which different trends are identified, suggest that locations, altitude, mountain ranges and proximity to the Atlantic are determinant for variations in moisture (dry and wet), perhaps due to different microclimatic conditions in isolated regions or in deep valleys.

The following period from about 3000 to 220 cal yr BP (zone IV) was characterized by a humid climate without a marked annual dry period as reported by Behling (2006) and detected in here by the presence of taxa such as the palms *Euterpe* and *Geonoma*, indicators of permanent humid conditions. This humid climate allowed the here greatest expansion of *Araucaria*. Fires were also frequent (11.85 peaks/ka) and presented high magnitude and the CHAR values were more or less constant. Our results suggest that fires occurred in the grasslands. In here two relevant peaks are detected, one at 1600 cal yr BP and the other one at 1380 cal yr BP in which a decrease of grasslands taxa, particularly Poaceae is detected. Those periods are concurrent with the suggested human influence documented by Iriarte & Behling (2007) in which the marked expansion of *Araucaria* forest in the region during the Late Holocene is strongly associated to the traditions and agricultural practices carried out by the called Taquara/Itararé groups. The spread of these groups is dated from the period between 1500 to 1000 cal yr BP. Their economy is thought to be based mainly in the exploitation of *Araucaria* seeds and traditionally are characterized by the construction of pithouses (habitation sites) in the highlands.

Furthermore, around 1250 cal yr BP CHAR values drastically reduced and charcoal concentration indicates that the biomass burning belonged to grass elements, this probably indicates a short dry period in where the Campos vegetation was burning but the magnitude of those fires was rather insignificant, in here no fire peaks were detected. These particular events are not registered in other locations in the region, probably due to the resolution that other studies cover which is not greater than 200 years between samples analysed (Behling et al., 2004), but also due to the slow sedimentation rate that those locations captured (Behling, 1997, 2006; Behling et al., 2005; Jeske-Pieruschka et al., 2013). In contrast, during the Late Holocene between 1500 to 1000 cal yr BP, Behling (1997) reported for Serra Campos Gerais a decrease in fire activity, suggesting as stated before particular variations that occur locally and not regionally.

The fire history for the last 220 years (zone V) in Lagoa Dourada shows a decrease in fire activity, with just one peak detected (157 cal yr BP). This is likely a consequence of human occupation in the area by the *Tropeiros* in 1800 (Ferreira, 1996), an arrival that can be also reflected with the appearance of human indicator taxa like *Pinus* and *Eucalyptus*. Besides, the climate in this period is identified as drier and warmer and results (woody charcoal concentration) indicate that fires occur in forested environments, particularly in *Araucaria* forest which is palynologically speaking more reduced than other environments, possibly related to the colonization and occupation practices of *Tropeiros* in Paraná state.

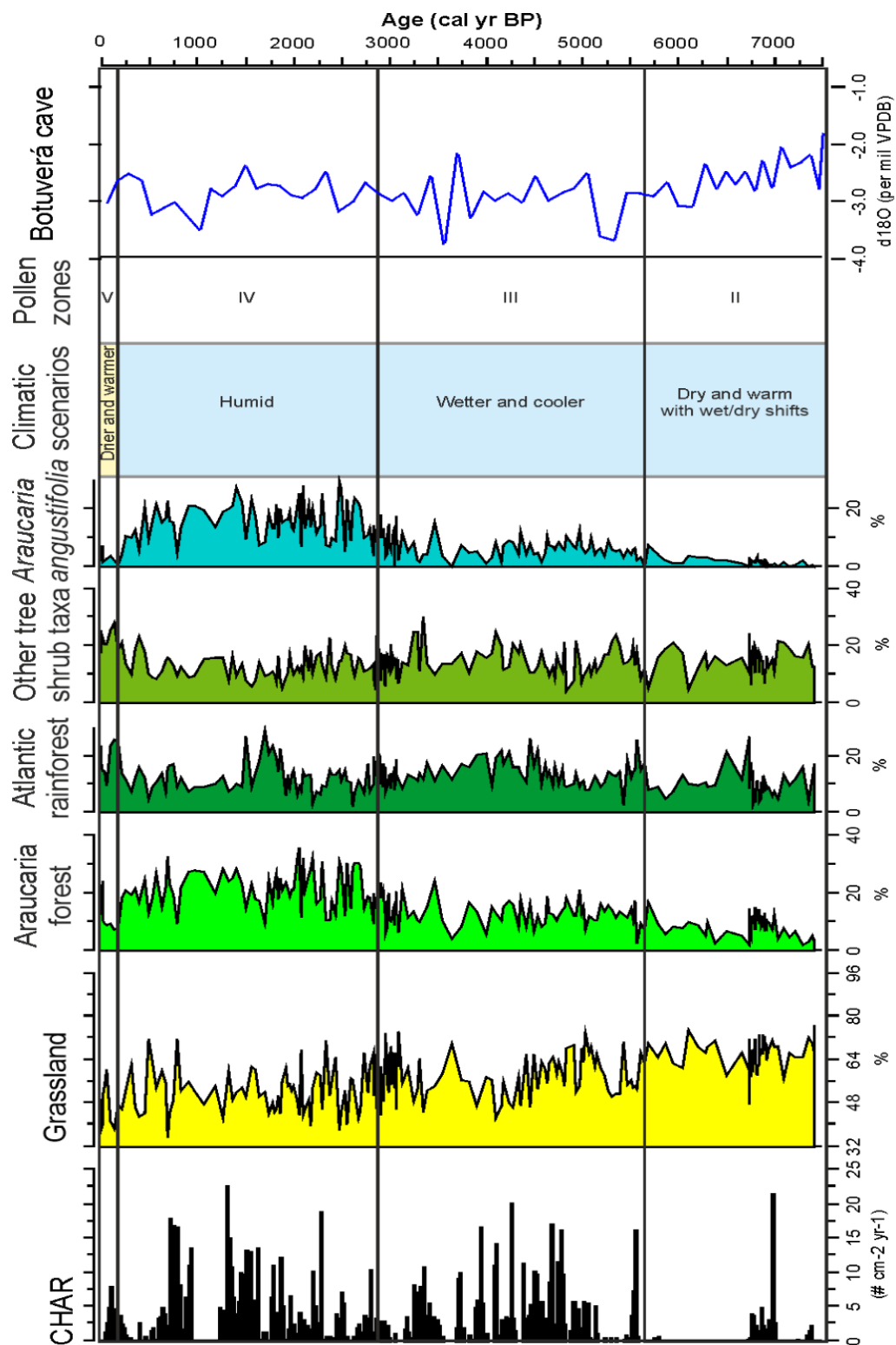


Fig. 26 Comparison of vegetation cover variability in Lago Dourada and the Botuverá Cave σ O18 speleothem record (27°S) (Wang et al., 2007). Main vegetation curves; Grassland, Araucaria forest, Atlantic rainforest, Other tree-shrub taxa and *Araucaria angustifolia*, along with climatic scenarios proposed in here and based on Behling (2006) for each palynological zone and charcoal accumulation rates for the last 7500 cal yr BP at Lagoa Dourada.

6.5.2 Is fire a precursor for *Araucaria angustifolia* establishment and expansion?

Periods with higher or less occurrence of *Araucaria angustifolia* have been identified during the last 7500 cal yr BP in Lagoa Dourada record, in fact, times of approximate establishment and subsequent stepwise expansion of the tree in southern Brazil are documented in here at ~7000, ~5700 and ~3000, respectively. These periods fall in the ending phase of local biomass-burning peaks, suggesting a causal relationship between *Araucaria angustifolia* population expansions and disturbance by fire in the surroundings of the pond. Already Soares (1979) hypothesised that the conifer is a fire-dependent species that needs fire (or another disturbance) to regenerate naturally and succeed and that should be successional placed as a seral species, instead of pioneer or climax, as other authors proposed, due to its lack of natural regeneration among other characteristics that support belongs to this intermediate successional stage.

We tested that hypothesis further with our ultra-high resolution analysis of vegetation and fire dynamics presented in **Fig. 25**, this allowed us to better understand the direct relationship between fire as a trigger of *Araucaria angustifolia* trees in two time periods every 8 and 6 years; one of 191 years and other of 264 years long, for the time of the establishment of the tree and its greatest expansion, respectively. Cross-correlation analysis results proved the importance of fire for the conifer as a fire-dependent species, that regenerates and survive low-moderate fires.

Several conifers in other latitudes have been identified to be resilient to relatively frequent low-moderate fires and in some cases high-intensity fires, such as *Araucaria araucana*, *Pinus nigra*, *P. palustris*, *P. contorta*, *Eucalyptus* spp (Burns, 1993; Ford et al., 2010; Hodgson, 1968; Morales-Molino et al., 2015; Turner et al., 2019). Among the key-tolerance traits that determinate the sensitivity of fire-dependent trees are bark thickness and flammability (Frejaville et al., 2013; Pellegrini et al., 2017). Despite *Araucaria* being highly flammable, its bark thickness makes it a good candidate to survive fire disturbances (Duarte et al., 2006; L. C. R. Silva & Anand, 2011).

6.6 Implications

Based on the findings presented in this research, we advise for the management of the endangered species *Araucaria angustifolia* that fire should be considered as a natural component that plays an important role for the regeneration and success of the tree when the severity of it keeps low. In this sense, the use of low-moderate intensity fires for the competent authorities could be asses through conservation and management programs with prescribed-burning strategies, that allow controlling the intensity and extension of the fires. In this respect, our historical reconstruction of fire and vegetation dynamics provide some useful insights into the long-term fire ecology of the species.

6.7 Conclusions

This study provided for the first time a sub-decadal and decadal resolution analysis to reconstruct the long-term vegetation and fire history in the highlands of Vila Velha in Paraná State. We documented that the changes in forest cover response to climatic conditions as well to fire activity, suggesting that those factors play an important role in vegetation turnover in the *Araucaria* region in Brazil.

The extended results revealed and proved the importance of fires as a trigger for regeneration and expansion of the conifer *Araucaria angustifolia*, suggesting that prescribed-burning strategies may be beneficial for restoration and conservation measurements aimed at reducing the extinction risk of its natural populations in southern Brazil.

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7. SYNTHESIS AND CONCLUSIONS

The *Araucaria* forest grassland mosaic in the highlands of southern Brazil is a unique vegetation type with high floristic diversity. Several palaeoecological studies document that the abundance of woodland patches characterized by *Araucaria* has increased through time, while the causes and mechanisms of this increase remain debated. Fire may be an important agent regulating the balance between grassland and woodland patches, however detailed knowledge on the natural fire dynamics of this system is lacking. The here presented research contributes to closing this knowledge gap with a high resolution pollen and charcoal analysis from a small lake “Lagoa Dourada”. To improve our ability to interpret the pollen signal in terms of area covered by different vegetation types. This project also investigates the representation and relative pollen production of the vegetation in two areas.

Pollen vegetation relationships in the *Araucaria* region

Pollen percentages provide a biased representation of the vegetation. By comparing modern pollen deposition to the current vegetation cover it is possible to reduce that bias. Much research effort has focussed on this problem in Europe and North America, which lead to the development of models of pollen transport and deposition. These models require estimates of the relative pollen productivity of the main vegetation types, which are hitherto lacking for South America. This investigation is the first to use the general methodology for estimating relative pollen productivity developed for temperate vegetation types in Europe and apply it to subtropical Vegetation in South America. The validity of the results was explored by selecting two study regions with contrasting climate: Vila Velha State Park (VV) in Paraná state is situated more inland with stronger seasonal climate and is the location from which the sediment core for palaeoecological reconstructions was obtained. Aparados da Serra National Park (AdS) in Rio Grande do Sul is located at the edge of the high-land with strong Atlantic influence (**Fig. 7**). Six taxa or groups were selected to represent the major components of the vegetation mosaic:

Araucaria angustifolia, Asteraceae p.p., *Baccharis*, Cyperaceae, Poaceae and a group collecting all forest taxa other than *Araucaria*. The vegetation was mapped in the two areas during a field campaign in July 2018. The overall vegetation composition resulted similar in the two regions, *Araucaria angustifolia* (VV: 12% and AdS: 13%), Poaceae (23% and 21%) Cyperaceae (13% and 15%), Asteraceae p.p. (10% and 14%) and *Baccharis* (9% and 5%). The largest difference occurs in the group of “forest taxa” with 17% and 11%, respectively. Similarities were also encountered in the average pollen proportions obtained from 16 and 18 samples in Vila Velha and Aparados da Serra respectively. Poaceae resulted as the most abundant pollen type (in average VV: 40%, AdS: 43%), followed by Cyperaceae (19% and 22%) and the forest group (16% and 16%). While the other taxa showed differences between the two regions. Despite similar average cover of 5-6% for *Araucaria angustifolia* the pollen has a lower range of values in samples from VV (min 0%; max 18%) compared to AdS (min 0%; max 33%). A similar situation occurs with *Baccharis*-type from VV (min 1%; max 34%) to AdS (min 0%; max 40%) and with Asteraceae p.p. from VV (min 1%; max 27%) to AdS (min 1%; max 37%).

The vegetation within a 100 m distance from each pollen sample was classified as open, semi-open or forested and compared to the pollen proportions. Indicator Species Analysis (indval) in Villa Velha revealed that high pollen proportions of *Baccharis*-type are a good indicator for open and semi-open vegetation, while *Schinus* pollen indicate forested situations. In Aparados da Serra on the other hand, no pollen type was identified to indicate open vegetation while for forested scenarios several taxa were recognized, such as Myrtaceae, *Araucaria angustifolia*, *Celtis*, *Myrsine* and *Trema*. To visualize the major differences in pollen composition and explore the similarities between pollen and vegetation data a PCA was performed. The ordination on the vegetation data (**Fig. 9**) clearly separated forested from open vegetation sites, in contrast the ordination on pollen data does not yield a clear separation. These results indicate that the pollen composition at each site is strongly influenced by the vegetation beyond 100 m radius.

The relationship observed between pollen and vegetation percentages provide insights into the general understanding of the landscape, the representativeness and the pollen productivity of the taxa analysed. So far, this visual comparison of pollen and vegetation percentages indicates that Poaceae is the most over-represented taxon and *Araucaria angustifolia* the most under-represented for the entire region. However, for a better

comprehension of this relationship we estimated R-values (sensu Davis 1963) and relative pollen productivity estimates (PPEs) for these taxa.

The R-values for the six different taxa follow the same trend in both study regions except for an under-representation of Asteraceae p.p. in Aparados da Serra, while this taxon has a near one to one average pollen to average vegetation proportion in Vila Velha. In both regions, pollen from Cyperaceae and Poaceae are over-represented. While *Araucaria angustifolia* is strongly under-represented, together with *Baccharis* and the forest group. Estimating the relative pollen productivity requires the use of a reference taxon that all other taxa are compared to and the commonly used Poaceae reference taxon (Broström et al., 2008) was initially also used here. While the vegetation data captures a gradient in the abundance of Poaceae around the sample sites the pollen data is not reflecting this which caused some models to produce unreasonable PPEs particularly in AdS. Hence, we also used Cyperaceae as alternative reference taxon, which is showing a stronger gradient in the vegetation and pollen data (**Fig. 14**). We used a maximum distance of 100 m to estimate PPEs, through the implementation of two different pollen dispersal models; the Gaussian plume diffusion model-GPM and the Lagrangian stochastic model-LSM in two different programs (ERV-D and ERV-R).

The obtained PPEs ERV results differ between the dispersal models regardless of the reference taxon. The difference is most pronounced for *Araucaria angustifolia*, the taxon with the largest pollen grains and hence highest fall speed. For both study areas, pollen productivity of *A. angustifolia* is as high or higher than the one of the reference taxa when calculated with the GPM. For the remaining taxa, both models result in different PPEs between regions, which at least in the case of *Baccharis*-type and the forest taxon can be explained by different species involved, matching with the regional differences in R-values.

This study shows that despite the sharp boundaries that characterizes the mosaic of *Araucaria* and Campos vegetation, in Paraná and Rio Grande do Sul states (study regions) it was difficult to separate these two very distinct vegetation types in the pollen data. In the state of Santa Catarina, Cárdenas et al. (2019) also compared pollen and vegetation in

this mosaic of vegetation and found no correspondence between pollen proportions and local site characteristics including open and closed vegetation. The difficulties using ordination and classification techniques are perhaps due to Poaceae and *Araucaria* pollen showing only a weak local signal. Two other effects might be considered to have an impact in the separation of woodlands and grasslands: First, the occurrence of the bamboo genus *Merostachys* and *Chusquea* in forested environments obscuring the clear separation of open grassland taxa. Grasses in total make up nearly one-third of the plant cover in the two study areas and in South America they are the most abundant plants in open vegetation. Second, the height of pollen released of woodlands compared to grasslands violates the general assumptions of the models used to estimate pollen productivity (Bunting et al., 2013).

We found similarities in R-values and PPEs between regions, suggesting that pollen production of the plant families of Poaceae and Asteraceae are similar, allowing the application of resulting PPEs in the wider region. Reversely, the forest group showed a different behaviour between the two regions, perhaps for its composition in which different families were grouped together. Regarding pollen productivity Poaceae is among the highest pollen producers in this forest-grassland mosaic and despite being a wind-pollinated tree with heavy pollen grains *A. angustifolia* resulted to have lower pollen productivity than the one found for the general forest. In addition, even with the complexity of the forests in the region a number of tree pollen types were identified as indicators of the local forest and *Baccharis*-type pollen as a good indicator of open vegetation types.

Vegetation and fire history of the *Araucaria* forest Grassland mosaics of southern Brazil

In the state of Paraná in the protected area of Vila Velha, we obtained a sediment core recovered from a silted up furna called Lagoa Dourada (**Fig. 16**). Furnas are defined as vertical cylindrical hollows or sinkholes formed up to the surface where the rocky roof of deep subterranean cavities has collapsed, as consequence of a chemical dissolution and karstification processes in the rocks (Melo et al., 2003, 2015; Melo & Fonseca, 2007). Hydrographically Lagoa Dourada is located on the basin of the Guabiroba River (**Fig. 4**), which watershed is the source area of Lagoa Dourada sediments. In Lagoa Dourada pond pollen and charcoal particles were used in order to reconstruct the past vegetation and fire history of the woodland-grassland mosaic. The sediments recovered correspond to the

Holocene, while obtaining a reliable date for the oldest samples was so far not possible. The pollen diagram reveals that the vegetation composition has changed gradually and no abrupt change occurred.

Lagoa Dourada sediment core contain a significant amount of sand, especially in the lowest most meters from 1150 to 940 cm, this can be related to the geological and hydrological system of the Furnas Formation as suggested by Melo et al. (2003), they proved that the floodwaters of the Guabiroba River are crucial in the process of silting-up the pond, thus in consequence might explain the accumulation of sands in such a quantity. Higher up of this sand layer overlaid an organic layer from 940 to 880 cm, that is then interrupted by a silt, clay and sandy layer from 880 to 760 cm. The uppermost section of the sediment core, from 760 to 0 cm, consists of organic sediments with a high content of silt, sand and low content of clay.

From 1440 to 1209 cm (possibly ~11700 to 9350 cal yr BP), Lagoa Dourada surroundings were characterized by the dominance of Campos vegetation, mainly by Poaceae and Cyperaceae, this dominance is attributed to the warm and dry climatic conditions that prevailed during that time (Behling, 2006; Behling et al., 2005; Jeske-Pieruschka & Behling, 2012) which is also supported by the scarce occurrence of plants that require wet soils, either for short or long periods of time, better known as wet indicator taxa, such as tree ferns and some Atlantic rainforest plants. The poor organic content of the sediments also reflects that grasslands were dominant over woodlands, as less biomass is produced in open vegetation environments. Besides, the sediments were mainly composed by silt (63%), sand (26%) and clay (11%). The fire history documented that the Early Holocene was characterized by fires of moderate frequency but with high magnitude as well as high charcoal concentration of both grass and wood particles (**Appendix 7**).

From about 1209 to 773 cm (possibly 9350 to 5770 cal yr BP) the record reveals that warm and dry conditions were still dominant, however, the pollen assemblages indicate the beginning of somewhat wetter and warmer conditions than before. In here shifts of wet/dry conditions are identified based on to the sudden increase and subsequent decrease of wet indicator taxa like palms and tree ferns, probably related to longer rainy periods

and short dry summers. Changes on the amount of seasonal rainfall during the Holocene period have been documented in south-eastern Brazil by Bernal et al., (2016), through the analysis of $\delta^{18}\text{O}$ in an stalagmite cave. Results show that a gradual change with more moisture availability due to the increase of rainfall occurred from the Early to the Late Holocene with an intensification of the South American Monsoon System (SAMS) starting around ~7000 cal yr BP but becoming stronger after about ~5500 cal yr BP.

Vegetation history of Lagoa Dourada tells us that ~7000 cal yr BP a stable population of *Araucaria angustifolia* established. Sporadic occurrences of this pollen type in older sediments indicates that the conifer was probably only present in small scattered stands, supporting the hypothesis that its initial expansion happened by spreading out of the gallery forests along the rivers and wet areas (Behling et al., 2004; Jeske-Pieruschka et al., 2013). In the surroundings of Lagoa Dourada, the mentioned establishment of *Araucaria* was detected during the Mid-Holocene at about ~7000 cal yr BP with a gradual increase towards the Late Holocene.

The period from 7500 to 5800 cal yr BP is characterized by low fire frequency (28.85 peas/ka) with a moderate magnitude as well as relatively low CHAR values compared to those during the Early Holocene. This decrease of fire activity is also reported for southern Brazil, for instance in Paraná state at Serra dos Campos Gerais Behling et al. (2005) reconstructed a warm environment with shifts of dry and wet climatic conditions between ~7000 to ~6000 cal yr BP. In Serra do Araçatuba Behling (2006) found a decrease in fire activity for the period from ~9000 to ~4000 and inferred a dry and warm climate based on a high frequency of *Eryngium* pollen and low proportions of *Araucaria* and Atlantic rainforest taxa. These changes, particularly the documented wet periods, could have influenced burning activity, in the sense of extinguish the fires, reducing them or slowing them down.

Cross-correlation analyses (**Fig. 25**) for the period of the expansion of *Araucaria angustifolia* shows no significant correlation between *A. angustifolia* pollen proportions and charcoal. This may be due to the short period analysed (<200 years), which seems to be insufficient to show the potential responses of the tree population. A significant correlation was found for Poaceae, in which its rapid response to fire was evident. Myrtaceae, shows a positive correlation in negative lags indicating that changes in this taxon happened before the fire, which can mean that Myrtaceae plants were somehow setting the conditions (pre-fire) for a well burnable landscape.

From the period between 5770 to 3080 cal yr BP, the decrease of Campos vegetation is notorious and the increase and expansion of *Araucaria* forest stands out. However, the expansion of *Araucaria* forest is documented at different times in the region, where in Serra dos Campos Gerais it occurred at about 2930 cal yr BP (Behling, 1997) and in Serra do Araçatuba only after 2000 cal yr BP (Behling, 2006). As indicated by those studies, somewhat wetter and cooler climatic conditions prevailed and the vegetation changes registered in Lagoa Dourada are congruent with it. In addition, our results revealed that also fire played an important role in here, a marked increase in fire frequency (11.37 peas/ka), a higher magnitude and more or less stable trend in CHAR values can explain the reduction of grasslands. Furthermore, this increased fire activity despite the more wetter conditions seems to be related to agricultural practices as suggested by Iriarte & Behling (2007) defining the onset of human landscape transformation between around 4320 and 2980 cal yr BP in the region in which slash-and-burn agriculture has been documented to occur across the *Araucaria* region.

The sediment composition of the core shows changes that are concurrent with the above described vegetation change (**Fig. 20** and **Table 6**). For instance, an increase in organic matter content as well as Nitrogen and Sulphur was detected, this may be due to several causes. Weathering processes of the rock, that perhaps has been influenced by the underground water system of the Furnas in this area (Melo & Giannini Fonseca, 2000) or the effect in above-ground post-fire regrowth (Van de Vijver et al., 1999).

During the period between 3080 to 220 cal yr BP the general woodland composition maintained similar proportions without abrupt changes, thus indicate that ecosystems were more homogeneous as not abrupt changes in the vegetation were found, therefore it is assumed that the overall vegetation was more or less stable, and this also may indicate stable climatic conditions, which allowed the forest growth without strong disturbances. The main expansion of *Araucaria* forest also occurred at the beginning of this period with the representation and increase of wet indicator taxa, the dominance of woodlands over grasslands indicate that the climate was humid during this period, as also suggested by (Behling et al., 2005; Iriarte & Behling, 2007) for the Late Holocene.

During the here late Late Holocene period, fires were also frequent (11.85 peaks/ka) with high magnitude and CHAR values more or less constant. The results suggest that fires occurred in the grasslands as higher values of grass charcoal are detected compare to those of woody charcoal. Besides, two burning peaks are detected, at 1600 cal yr BP and at 1380 cal yr BP in which a decrease of grasslands taxa, particularly Poaceae is detected. Iriarte & Behling (2007) documented that the marked expansion of *Araucaria* forest in the region during the Late Holocene is strongly associated to human activity, especially the traditions and agricultural practices carried out by the called Taquara/Itararé groups. The spread of these groups is dated from the period between 1500 to 1000 cal yr BP. Their economy is thought to be based mainly in the exploitation of *Araucaria* seeds and traditionally are characterized by the construction of pithouses (habitation sites) in the highlands. Hence, the fire peaks detected in Lagoa Dourada at 1600 cal yr BP and at 1380 cal yr BP are concurrent with the suggested human activity by Taquara/Itararé groups.

The cross-correlation analyses (**Fig. 25**) showed just for the greatest expansion of *Araucaria* (~3000 cal yr BP) that fires resulted in increased abundance of the conifer however, longer periods of time should be analysed that may be more dissident from the response of these trees to fire. Additionally, the analysis also show that Poaceae was a precursor taxon for fire and its abundance was diminished after intense burnings took place. Also, during this period we observed a marked increase especially in Carbon and Nitrogen in the less sandy and clay rich soils.

The last 220 cal yr BP reflect the colonisation of the area by Europeans. The arrival of European settlers called “*Tropeiros*” occurred between 1703 and 1800 (Ferreira, 1996) and the first firm traces of their arrival in the area is the occurrence of pollen from *Pinus* and *Eucalyptus*. The introduction of these trees together with grazing activities rapidly affected the natural ecosystems and we can see that in the pollen record, here the *Araucaria* forest, Grasslands, and Atlantic Rainforest revealed a very low representation as well tree ferns. Fire activity is also lower and indicates that burnings happened in the forest during colonization times as reflected by the woody charcoal concentration. Also noticed by the strong reduction of *Araucaria* forest, due to the exploitation of the tree for timber production initially started by the *Tropeiros*.

Concluding remarks and perspectives

The studied pollen vegetation relationships in this research and the application of methods designed for other part of the world, provided us insights into pollen productivity of the complex mosaics of *Araucaria* forest and grasslands in southern Brazil, which were challenging but possible to be carried out. To highlight, the similarities found between R-values and PPEs in Poaceae and Asteraceae allows the application of the resulting PPEs in a wider region on the south American continent, while complex groups as the here called “forest taxa” requires more research and at least pollen groups with the same type of dispersion should be selected but ideally tree families should be used for the estimation of pollen productivity, the same principle applies for semi-open vegetation types in which a higher taxonomical level will help to obtain better PPEs results.

On the other hand, the palaeoecological history obtained from Lagoa Dourada pond sediments, gave us a deeper understanding of the dynamics of these vegetation mosaics. The response of the vegetation to changes in climate and disturbances like fire activity and human impact were noticed. The Early Holocene was characterized as a dry and warm period with higher fire activity than the rest of the Holocene, in here Campos vegetation dominated and few scattered occurrences of tree pollen grains were registered. At about ~8500 years BP the climatic conditions switched in short periods from wet to dry, however the climate was mainly dry and warm. Changes in the vegetation occurred, particularly the representation of tree taxa pollen slightly increased, indicating somehow changes towards a wetter climate. At ~7000 cal yr BP *Araucaria angustifolia* occurrences were more constant, indicating the establishment of the conifer, while the previous not so frequent values supported the hypothesis that in earlier times the conifer was probably present in few scattered stands and that later its initial expansion happened by spreading out of the gallery forests along the rivers and wet areas. *Araucaria* forest expanded significantly during two phases, the first one at ~5700 cal yr BP and the second one at ~3080 cal yr BP, periods characterized by wetter and cooler and humid climate, respectively, as well by a higher fire activity however lower than in Early Holocene times. Together all these factors prompted the successful expansion of the *Araucaria* forest.

Finally, anthropogenic disturbance also played an important role in the decline of *Araucaria angustifolia* since around 1730, associated to the arrival of the Europeans and the over-exploitation of the tree for timber production.

With this research I highlighted the importance of fires as a trigger for regeneration and expansion of the conifer *Araucaria angustifolia*. I hope that these results serve for prescribed-burning strategies that will be beneficial for restoration and conservation measurements to reduce the extinction risk of this conifer in southern Brazil. However, my results are just one step towards understanding the dynamics of the *Araucaria* forest and grasslands in the region, and future investigations needs to be done, especially in a deeper understanding of the pollen and vegetation relationships and fire impact analyses capturing longer periods of time.

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APPENDIX 1

Appendix 1. Location, description and landscape unit of samples in Vila Velha and Aparados da Serra area, southern Brazil.

No	Location	Longitude	Latitude	Altitude (m a.s.l)	Landscape unit	Sample-type
1	Vila Velha	-50.002875	-25.219693	832.32	Open	Soil
2	Vila Velha	-50.035657	-25.228606	831.52	Forest	Sphagnum
3	Vila Velha	-49.992172	-25.233416	983.76	Semi-open	Soil
4	Vila Velha	-49.970733	-25.231415	883.8	Semi-open	Soil
5	Vila Velha	-49.969221	-25.232539	864.44	Open	Sphagnum
6	Vila Velha	-50.001061	-25.235357	918.32	Open	Sphagnum
7	Vila Velha	-50.004456	-25.235724	891.39	Open	Other moss
8	Vila Velha	-49.984089	-25.248676	900.43	Semi-open	Other moss
9	Vila Velha	-50.038809	-25.222842	860.67	Forest	Other moss
10	Vila Velha	-50.018749	-25.215528	854.57	Open	Soil
11	Vila Velha	-49.99953	-25.21709	839.73	Forest	Soil
12	Vila Velha	-49.998372	-25.223821	956.65	Open	Other moss and soil
13	Vila Velha	-50.011453	-25.239455	847.85	Open	Other moss and soil
14	Vila Velha	-49.986021	-25.238588	949.88	Semi-open	Sphagnum
15	Vila Velha	-49.988093	-25.240571	960.04	Open	Sphagnum
16	Vila Velha	-50.040356	-25.222949	841.36	Forest	Other moss
1	Aparados da Serra	-50.101446	-29.175675	921.37	Semi-open	Sphagnum
2	Aparados da Serra	-50.121861	-29.178493	943.21	Open	Other moss and soil
3	Aparados da Serra	-50.123101	-29.182098	950.97	Open	<i>Sphagnum</i> and other moss
4	Aparados da Serra	-50.111883	-29.182182	960.35	Open	Sphagnum
5	Aparados da Serra	-50.111979	-29.172051	934.99	Open	Sphagnum
6	Aparados da Serra	-50.110355	-29.170224	920.83	Open	Sphagnum

No	Location	Longitude	Latitude	Altitude (m a.s.l)	Landscape unit	Sample-type
7	Aparados da Serra	-50.099717	-29.163641	918.33	Forest	Sphagnum
8	Aparados da Serra	-50.10624	-29.161901	924.39	Semi-open	Sphagnum
9	Aparados da Serra	-50.110606	-29.159777	937.98	Forest	Other moss and soil
10	Aparados da Serra	-50.108187	-29.163627	895.02	Open	Sphagnum
11	Aparados da Serra	-50.105539	-29.165374	922.68	Open	<i>Sphagnum</i> and other moss
12	Aparados da Serra	-50.132089	-29.176228	950.79	Open	Sphagnum
13	Aparados da Serra	-50.128526	-29.182846	937.56	Open	Sphagnum
14	Aparados da Serra	-50.12103	-29.171422	973.05	Semi-open	Sphagnum
15	Aparados da Serra	-50.124207	-29.171987	967.86	Open	Sphagnum
16	Aparados da Serra	-50.110358	-29.182142	948.09	Forest	<i>Sphagnum</i> and other moss
17	Aparados da Serra	-50.107548	-29.181512	941.76	Forest	<i>Sphagnum</i> and other moss
18	Aparados da Serra	-50.110683	-29.160436	944.92	Forest	<i>Sphagnum</i> and other moss

APPENDIX 2

Appendix 2. List of identified taxa from Vila Velha and Aparados da Serra, grouped according to their affinities for vegetation assemblages or major taxa categories. *Taxa listed below each category.

Araucaria angustifolia	Borreria	Luehea	Schinus
Asteraceae*	Brassicaceae	Matayba	Scutellaria
Alternanthera-type	Cecropia	Mimosa-type	Sebastiania-type
Ambrosia-type	Celtis	Moraceae	Serjania
Asteraceae	Clethra	Myrsine	Spondias
Senecio	Cuphea urbaniana	Myrtaceae	Struthantus
Solanum	Daphnopsis	Phrygilanthus acutifolius	Styrax
Valeriana stenophylla	Ephedra	Phyllanthus	Symplocos lanceolata
Vernonia	Eriocaulon	Plantago australis	Symplocos tenuifolia
Xyris	Esenbeckia	Podocarpus	Tetrorchidium rubricenium
Baccharis-type	Euphorbia-type	Polygala	Trema
Cyperaceae	Euterpe/Geonoma	Prockia / Curis-type	Urticaceae
Forest*	Fabaceae	Psycotria	Verbena-type
Acalypha	Fagara	Ranunculus bonariensis	Weinmannia
Actinostemon concolor	Gaultheria	Rhamnus-type	Ferns*
Alchornea	Gomphrena	Roupala	Cyathea/Dicksonia
Allophylus	Ilex	Rubiaceae-type	Blechnum imperiale
Alnus	Iridaceae	Salix	Poaceae
Apiaceae	Lamanonia speciosa	Salvia	
Begonia	Lamiaceae	Sapium glandulatum	

APPENDIX 3

Appendix 3. RRP results for six major taxa, obtained under GPM and LSM analysis through the ERV.Analysis.v2.5.3.exe software (ERV-D) (Sugita 2017 unpublished) and ERV Analysis in R (ERV-R) (Theuerkauf in prep.) with Poaceae and Cyperaceae as a reference taxon. Models with * were excluded from the analysis.

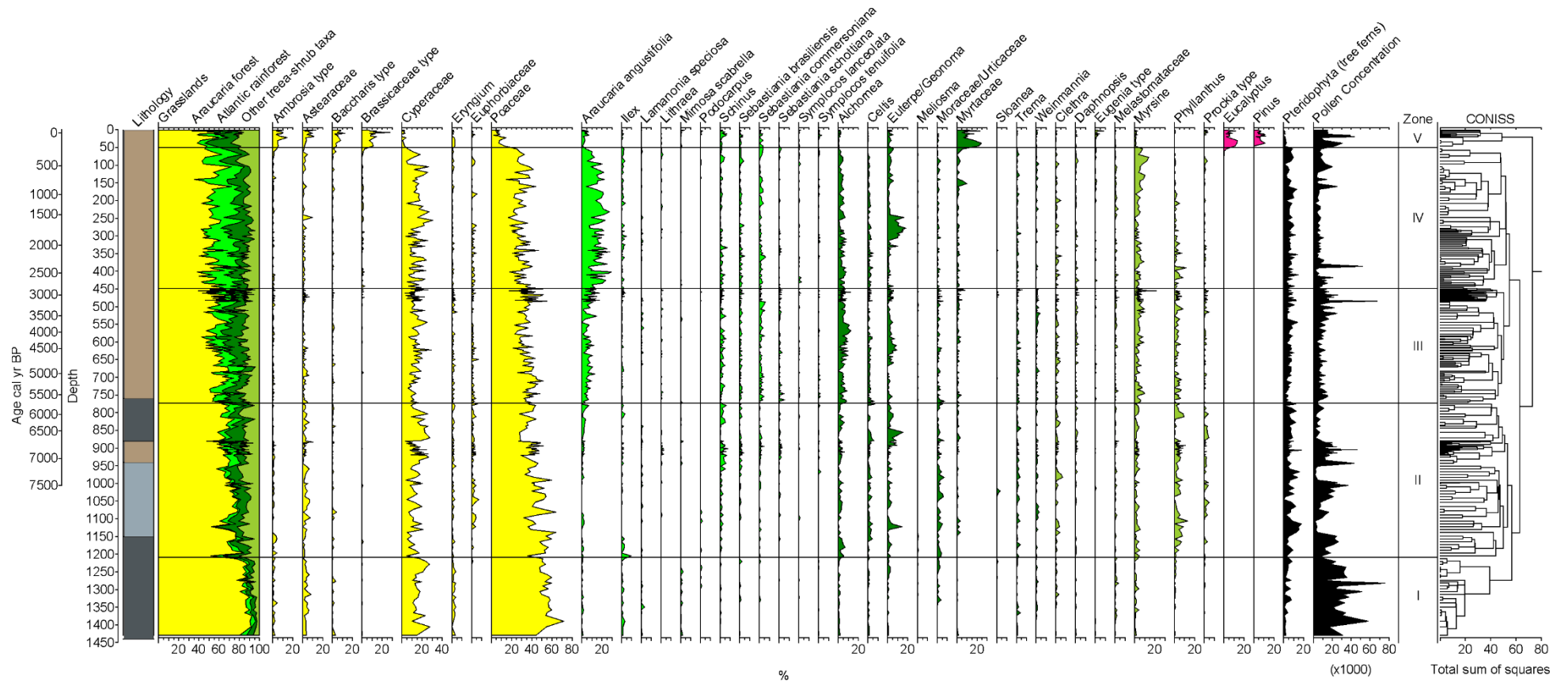
	50-100m	<i>Araucaria angustifolia</i>	Asteraceae	<i>Baccharis</i>	Cyperaceae	Forest	Poaceae
Vila Velha	GPM-ERV-D (Cyperaceae) *	14.29 ± 2.71	3.4 ± 0.04	3.89 ± 0.08	1 ± 0	0.98 ± 0.04	9.41 ± 0.54
	GPM-ERV-D (Poaceae)	1.47 ± 0.27	0.38 ± 0.01	0.43 ± 0.02	0.11 ± 0.01	0.11 ± 0.01	1 ± 0
	GPM-ERV-R (Cyperaceae)	1.26 ± 0.74	0.82 ± 0.29	0.89 ± 0.25	1 ± 0	0.72 ± 0.21	1.65 ± 0.34
	GPM-ERV-R (Poaceae)	0.68 ± 0.41	0.5 ± 0.13	0.56 ± 0.15	0.6 ± 0.12	0.46 ± 0.1	1 ± 0
	LSM-ERV-D (Cyperaceae)	0.13 ± 0.01	1.15 ± 0.01	1.72 ± 0.04	1 ± 0	0.49 ± 0.01	4.94 ± 0.1
	LSM-ERV-D (Poaceae)	0.03 ± 0	0.23 ± 0	0.35 ± 0.01	0.2 ± 0	0.1 ± 0	1 ± 0
	LSM-ERV-R (Cyperaceae)	0.21 ± 0.16	0.71 ± 0.5	1.33 ± 0.67	1 ± 0	0.52 ± 0.23	1.58 ± 0.83
	LSM-ERV-R (Poaceae)	0.12 ± 0.13	0.41 ± 0.27	0.81 ± 0.37	0.63 ± 0.33	0.33 ± 0.12	1 ± 0
	1500-2000m	<i>Araucaria angustifolia</i>	Asteraceae	<i>Baccharis</i>	Cyperaceae	Forest	Poaceae
	GPM-ERV-D (Cyperaceae)	5.89 ± 0.38	2.34 ± 0.07	2.24 ± 0.04	1 ± 0	0.36 ± 0.01	4.14 ± 0.16
	GPM-ERV-D (Poaceae)	1.78 ± 0.13	0.64 ± 0.05	0.64 ± 0.05	0.29 ± 0.03	0.11 ± 0.01	1 ± 0
	GPM-ERV-R (Poaceae)	0.71 ± 0.37	0.66 ± 0.1	0.46 ± 0.07	0.64 ± 0.09	0.38 ± 0.05	1 ± 0
	GPM-ERV-R (Cyperaceae)	1.1 ± 0.66	1.03 ± 0.2	0.71 ± 0.08	1 ± 0	0.61 ± 0.08	1.57 ± 0.22
	LSM-ERV-D (Cyperaceae)	0.07 ± 0	1.48 ± 0.02	1.39 ± 0.01	1 ± 0	0.34 ± 0.01	3.33 ± 0.07
	LSM-ERV-D (Poaceae)	0.02 ± 0	0.51 ± 0.02	0.47 ± 0.02	0.35 ± 0.02	0.11 ± 0	1 ± 0
	LSM-ERV-R (Cyperaceae)	0.17 ± 0.05	1.16 ± 0.36	0.95 ± 0.28	1 ± 0	0.53 ± 0.11	1.55 ± 0.29
	LSM-ERV-R (Poaceae)	0.11 ± 0.03	0.75 ± 0.16	0.68 ± 0.15	0.65 ± 0.14	0.33 ± 0.04	1 ± 0
Apar	50-100m	<i>Araucaria angustifolia</i>	Asteraceae	<i>Baccharis</i>	Cyperaceae	Forest	Poaceae

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GPM-ERV-D (Cyperaceae) *	20.82 ± 3.09	0.54 ± 0.02	0 ± 0	1 ± 0	3.71 ± 0.2	0 ± 0
GPM-ERV-D (Poaceae) *	67230.7 ± 17879.46	5370.94 2983.38	± 91.69 ± 308.9	9509.78 1713.58	± 13196.37 2459.11	± 1 ± 0
GPM-ERV-R (Cyperaceae)	4.01 ± 3.58	1.68 ± 0.59	1.12 ± 0.38	1 ± 0	3.8 ± 0.99	2.51 ± 0.36
GPM-ERV-R (Poaceae)	1.52 ± 1.35	0.71 ± 0.27	0.44 ± 0.15	0.4 ± 0.06	1.54 ± 0.37	1 ± 0
LSM-ERV-D (Cyperaceae)	1.78 ± 0.2	0.23 ± 0.01	0 ± 0.05	1 ± 0	3.74 ± 0.26	0 ± 0
LSM-ERV-D (Poaceae) *	1446.69 ± 773.38	238.92 ± 288.92	4.96 ± 35.2	1521.04 782.24	± 1695.53 ± 3042.32	1 ± 0
LSM-ERV-R (Cyperaceae)	1.83 ± 1.25	1.12 ± 0.91	0.44 ± 0.74	1 ± 0	3.22 ± 1.14	2.09 ± 0.83
LSM-ERV-R (Poaceae)	0.83 ± 0.51	0.55 ± 0.33	0.22 ± 0.25	0.48 ± 0.11	1.37 ± 0.45	1 ± 0
1500-2000m	<i>Araucaria angustifolia</i>	Asteraceae	<i>Baccharis</i>	Cyperaceae	Forest	Poaceae
GPM-ERV-D (Cyperaceae)	5.11 ± 1.06	0.07 ± 0.01	0.37 ± 0.03	1 ± 0	0.53 ± 0.03	0 ± 0
GPM-ERV-D (Poaceae) *	5428.02 ± 3347.79	49.01 ± 75.46	313.73 ± 280	790.88 ± 543.83	335.72 ± 358.37	1 ± 0
GPM-ERV-R (Cyperaceae)	5.83 ± 5.72	0.66 ± 0.14	0.65 ± 0.18	1 ± 0	2.05 ± 0.29	2.17 ± 0.24
GPM-ERV-R (Poaceae)	2.22 ± 2.58	0.31 ± 0.07	0.3 ± 0.08	0.46 ± 0.05	0.89 ± 0.14	1 ± 0
LSM-ERV-D (Cyperaceae)	0.29 ± 0	0.05 ± 0	0.53 ± 0.01	1 ± 0	0.58 ± 0.01	0.02 ± 0
LSM-ERV-D (Poaceae) *	9.79 ± 3.97	1.52 ± 0.85	18.12 ± 7.37	32.68 ± 15.7	18.67 ± 8.21	1 ± 0
LSM-ERV-R (Cyperaceae)	0.31 ± 0.18	0.35 ± 0.11	0.37 ± 0.24	1 ± 0	1.4 ± 0.35	1.62 ± 0.33
LSM-ERV-R (Poaceae)	0.2 ± 0.12	0.21 ± 0.07	0.22 ± 0.13	0.62 ± 0.16	0.8 ± 0.29	1 ± 0

APPENDIX 4

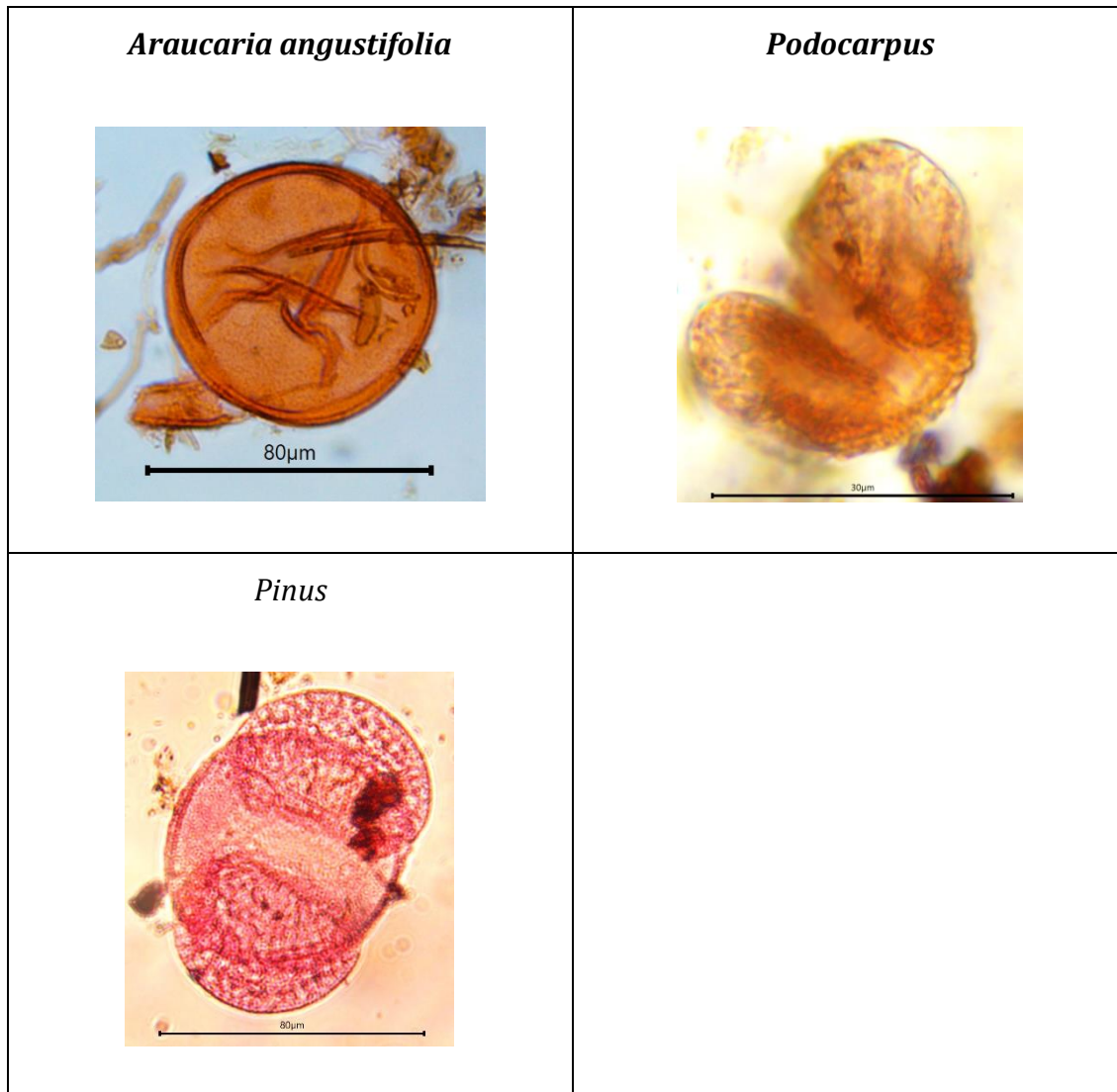
Appendix 4. High resolution summary pollen percentage of Lagoa Dourada record.




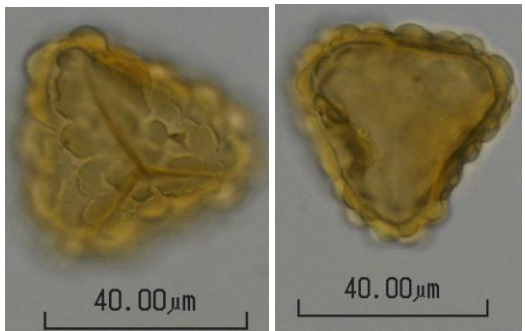
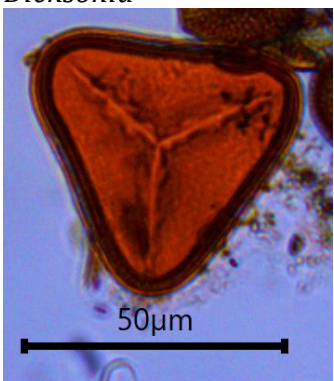
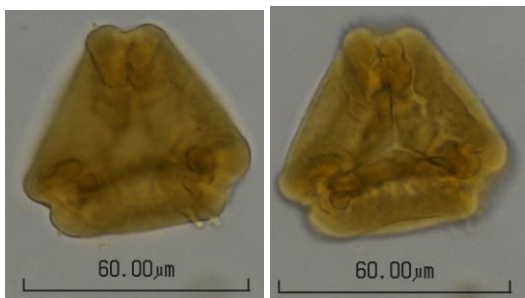
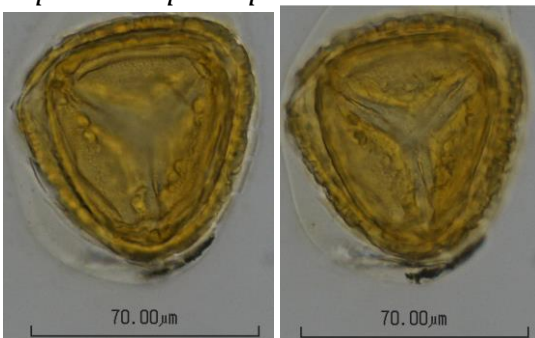
APPENDIX 5

Appendix 5 Photos of selected pollen and spores identified in this research. All photos were taken under 40x magnification microscope.

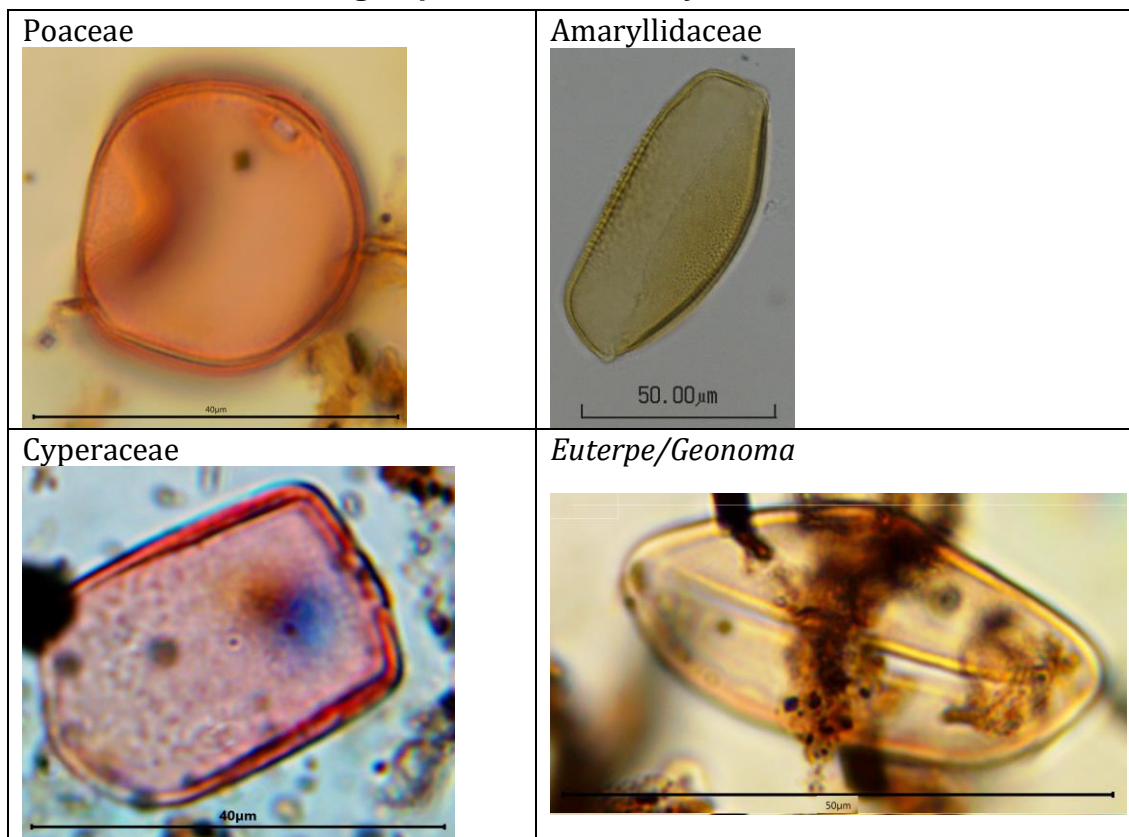
Gymnospermae



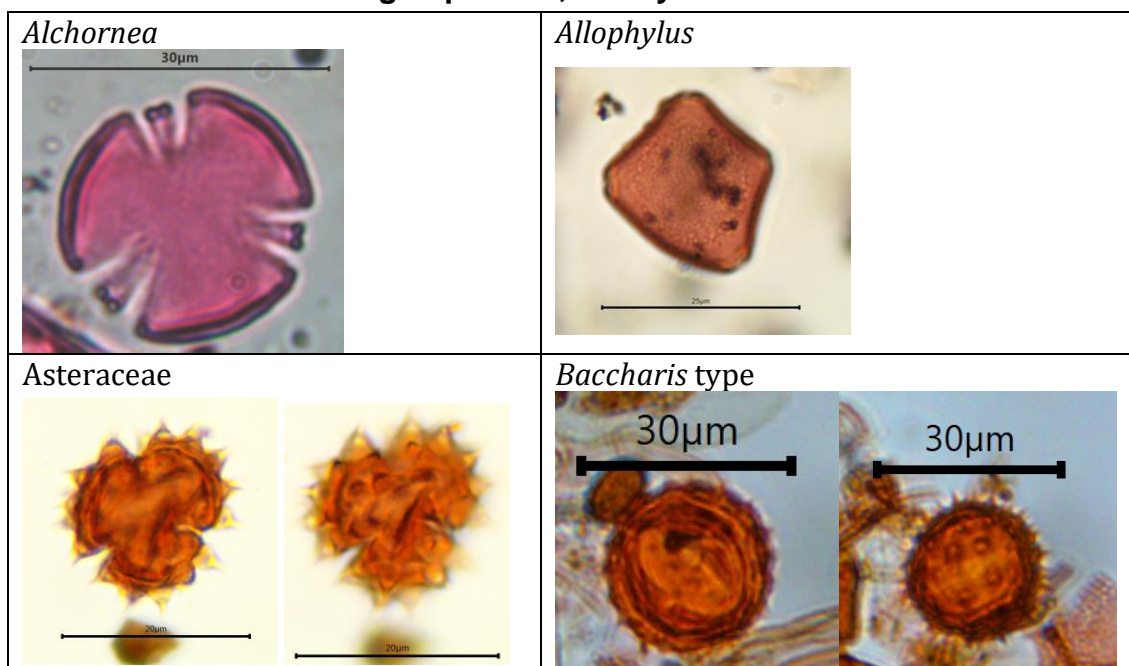
Pterido0phyta

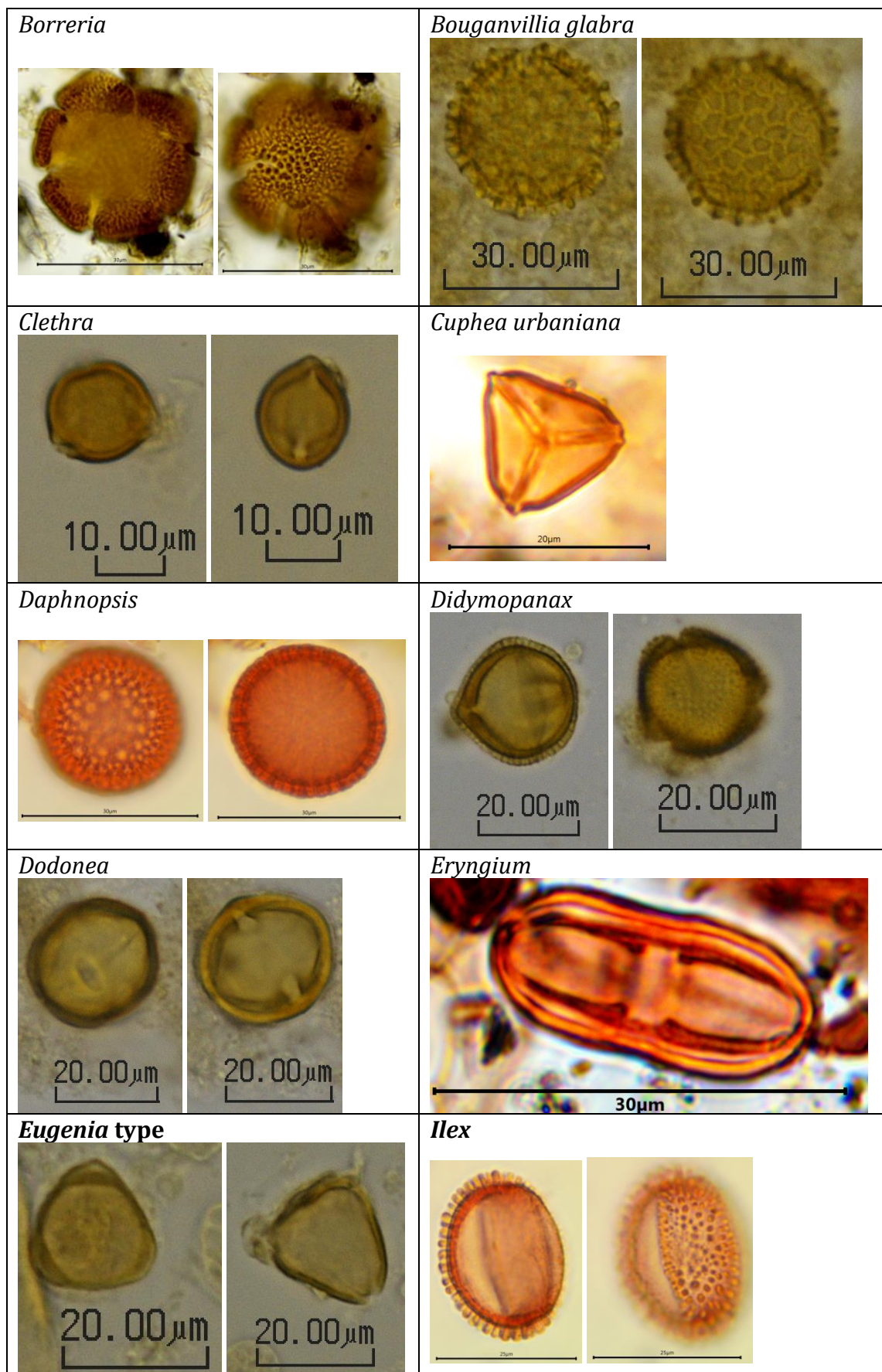
<p><i>Cyathea</i></p> 	<p><i>Cyathea schanschin</i> type</p> 
<p><i>Dicksonia</i></p> 	<p><i>Dicksonia sellowiana</i></p> 
<p><i>Lophosoria quadripinnata</i></p> 	

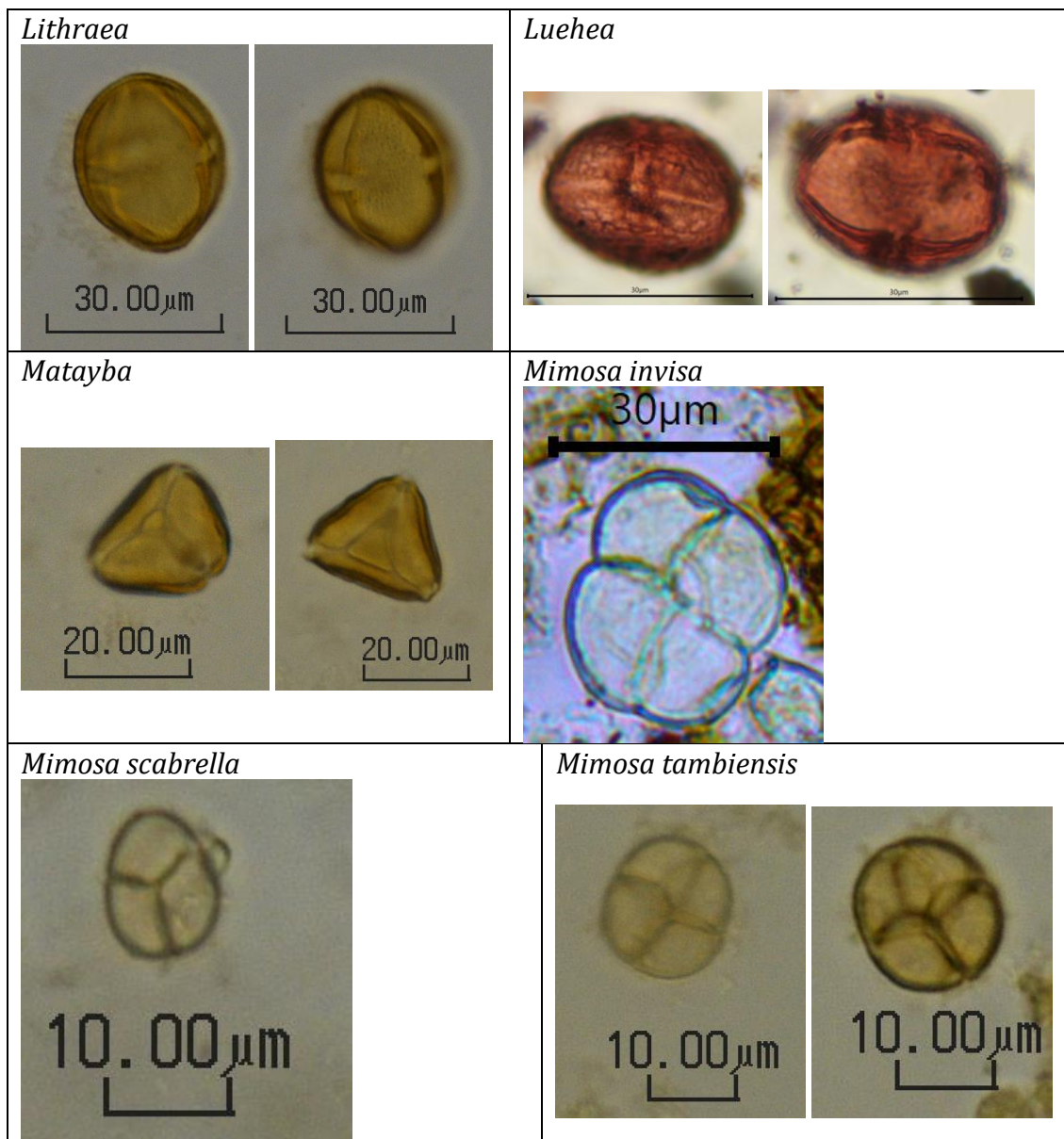
Angiospermae, Monocotyledoneae

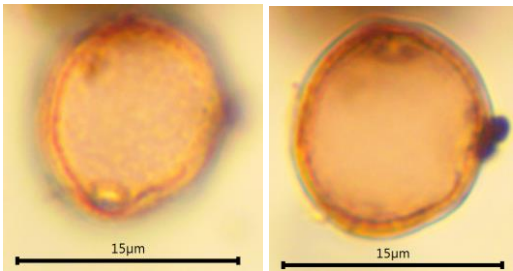
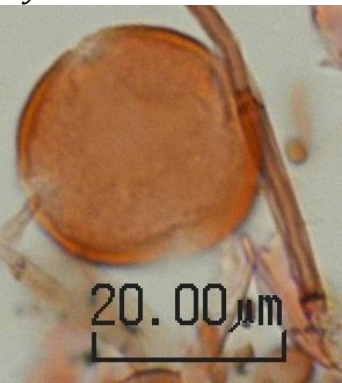
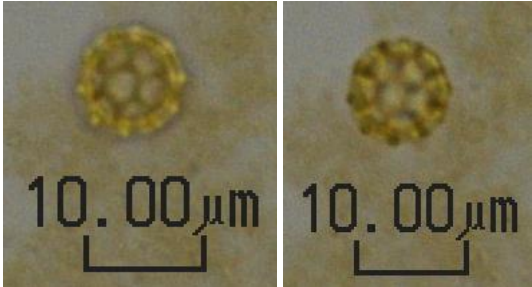

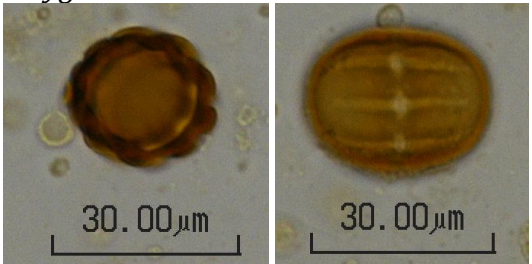
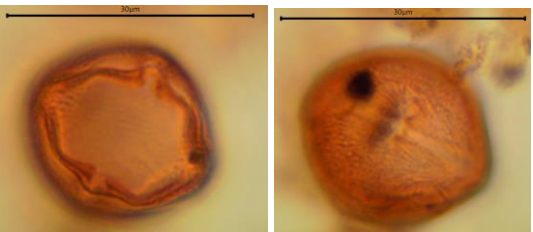
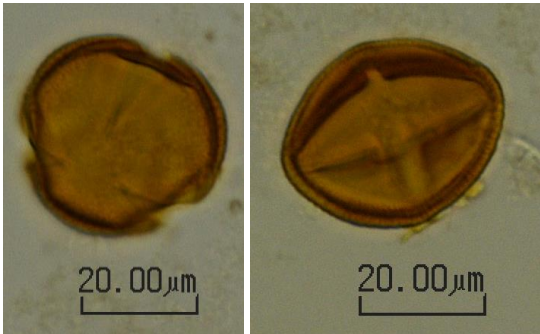
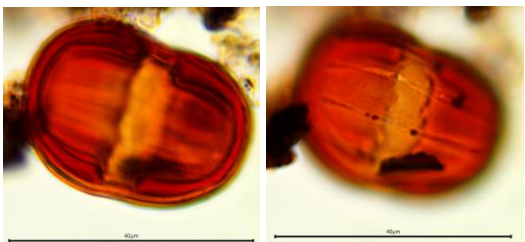


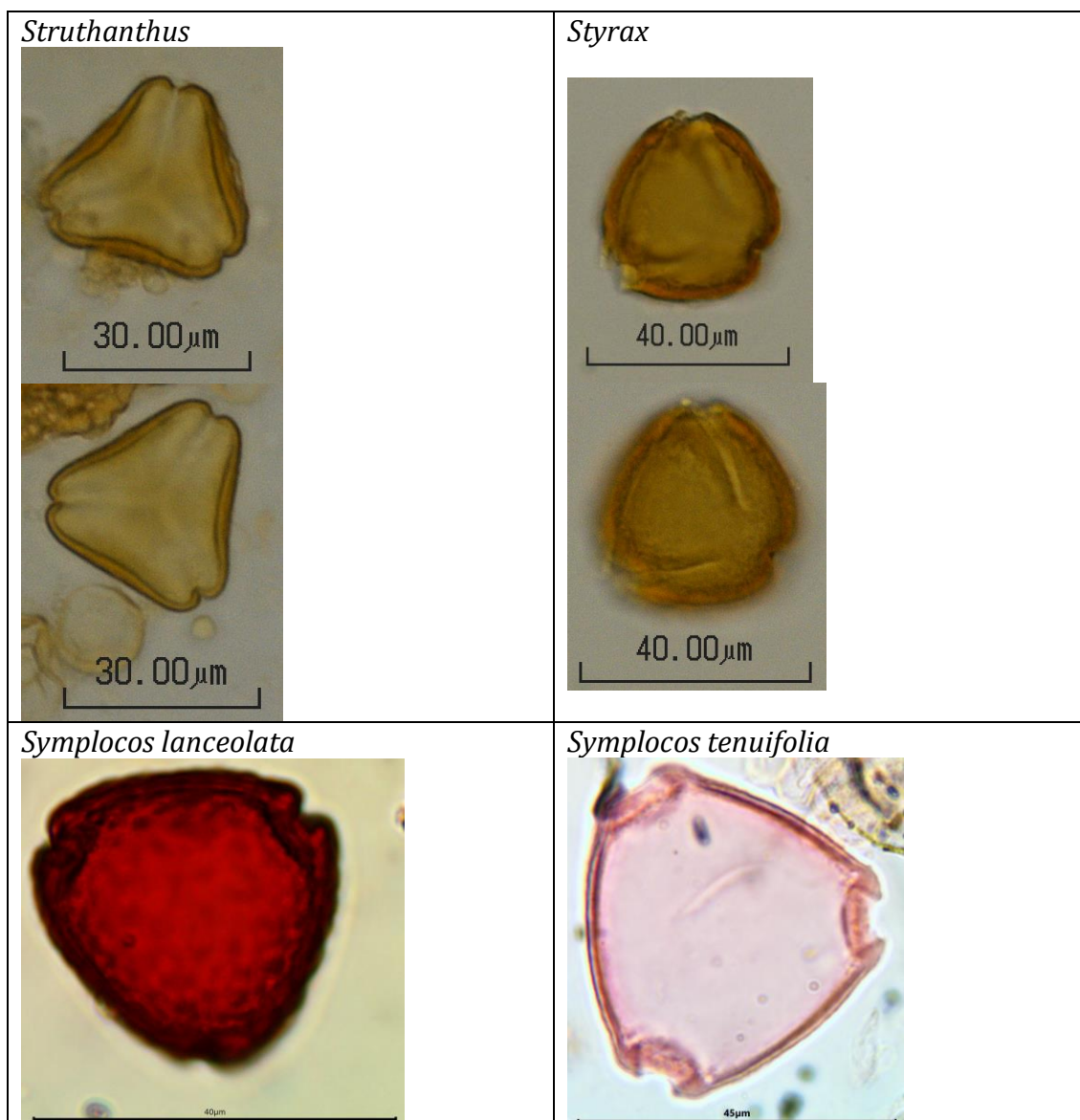
Angiospermae, Dicotyledoneae





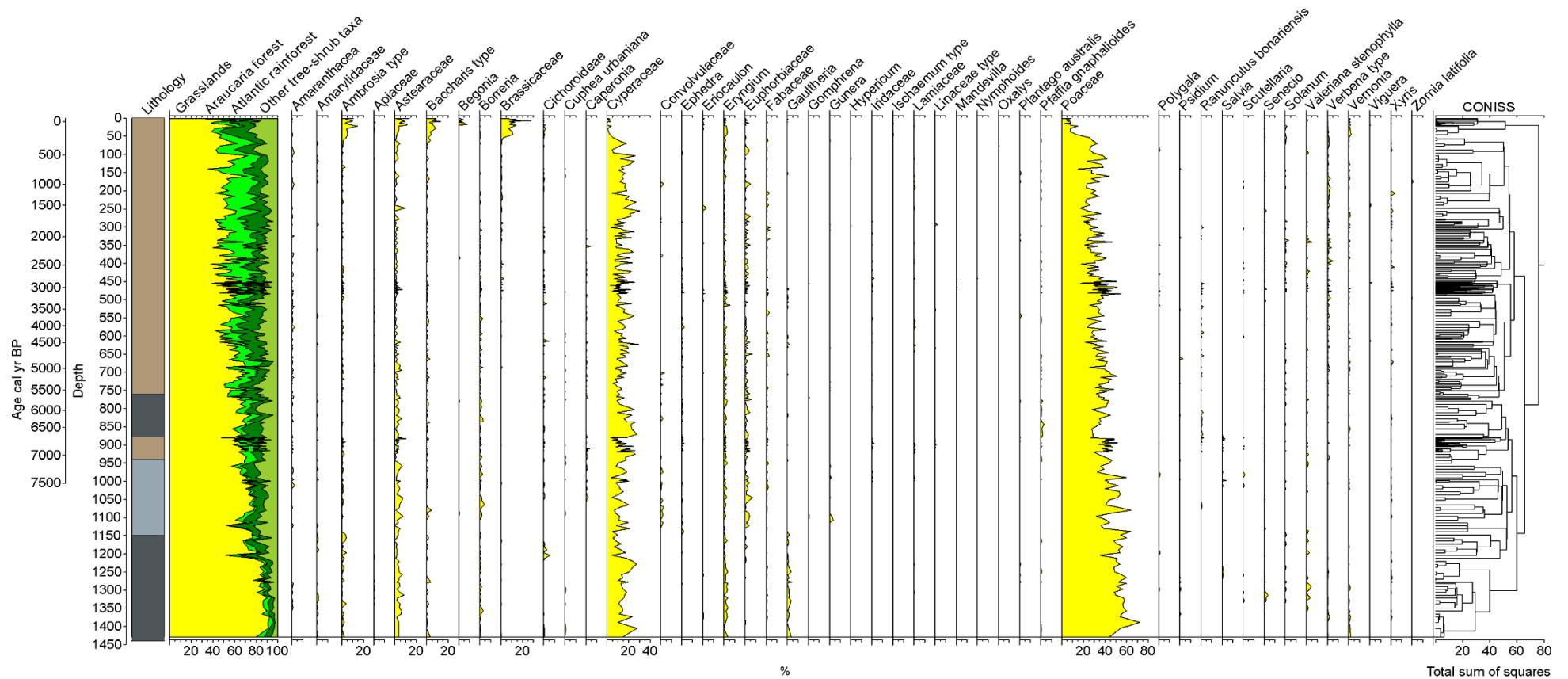


<p>Moraceae/Urticaceae</p> 	<p><i>Myrsine</i></p> 
<p><i>Pfaffia gnaphalioides</i></p> 	<p><i>Phrygilanthus acutifolius</i></p> 
<p><i>Polygala</i></p> 	<p><i>Schinus</i></p> 
<p><i>Sebastiania brassiliensis</i></p> 	<p><i>Securidaca</i></p> 



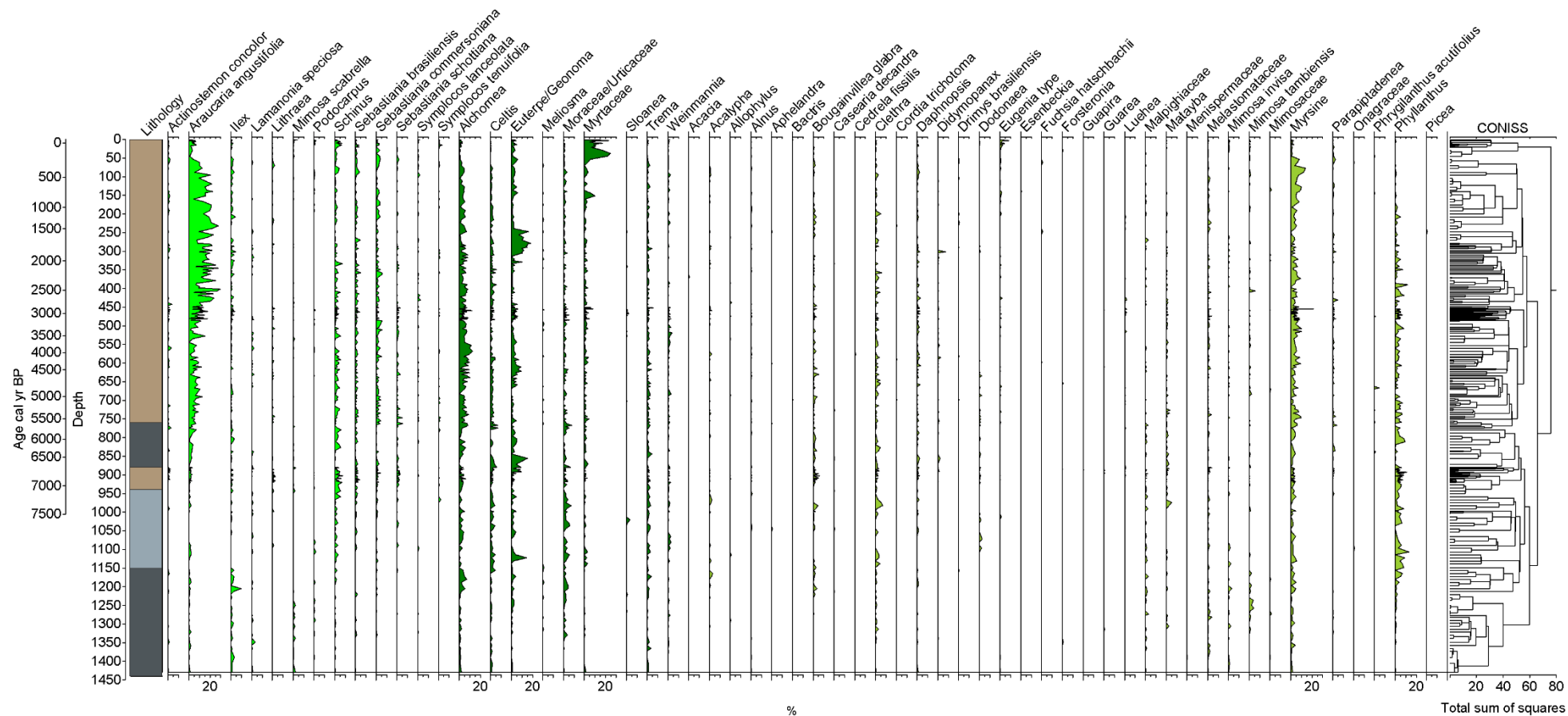
APPENDIX 6

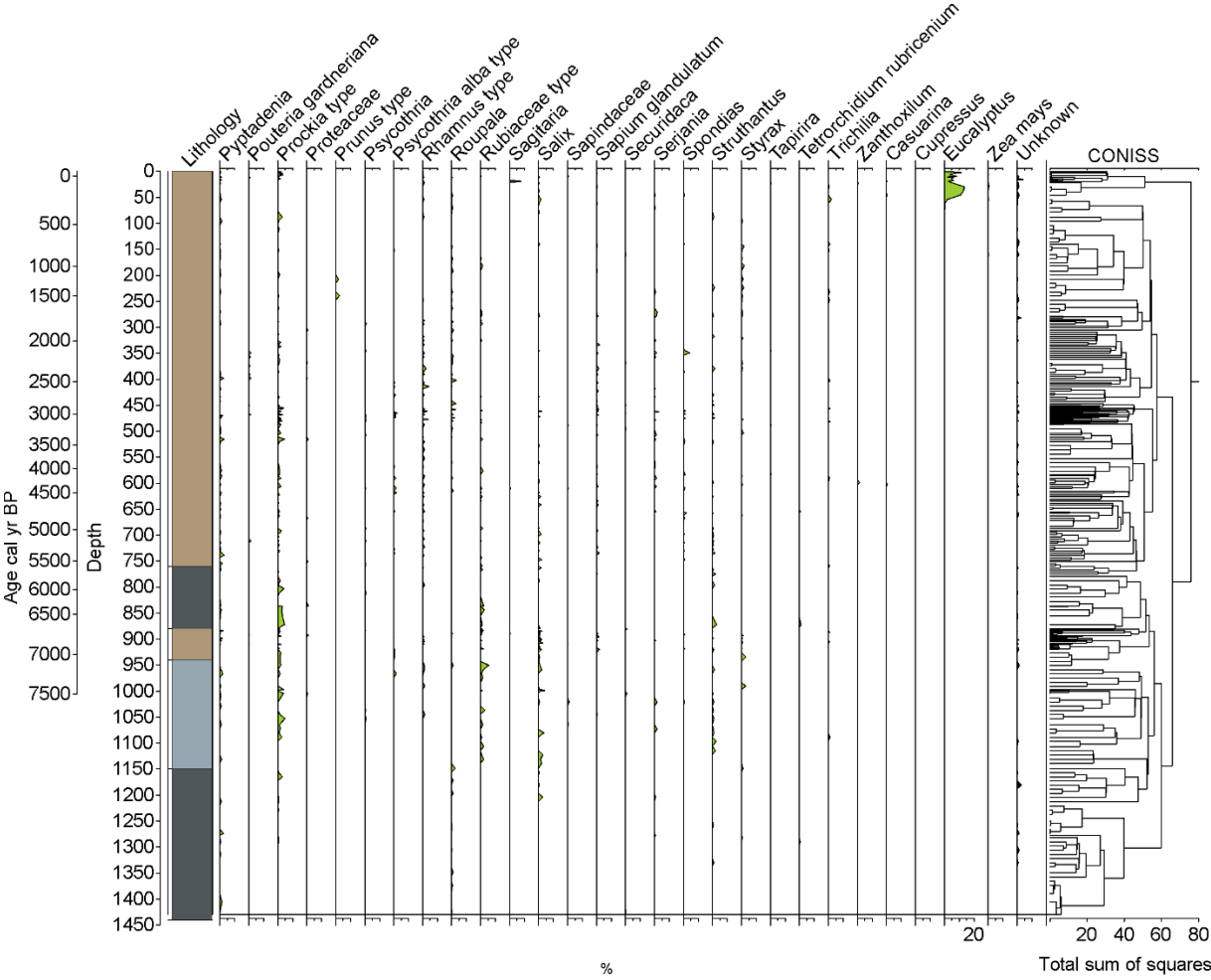
Appendix 6. High resolution full pollen diagram of Lagoa Dourada record 1 out 3.



2 out 3

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APPENDIX 7

Appendix 7. Results of charcoal analysis from the entire core Lagoa Dourada. Grey bands represent depths in which samples have not been analysed.

