

VEGETATIONAL DYNAMICS IN THE LAST 40,000 YEARS IN MINEROTROPHIC PEAT BOG IN THE MATA PRETA ECOLOGICAL STATION, SUBTROPICAL PLATEAU WITH ARAUCARIAS – WESTERN SANTA CATARINA, BRAZIL

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ABSTRACT – This work presents the results obtained through a palynological analysis of a sedimentary core from a minerotrophic peat bog in the Mata Preta Ecological Station, Araucaria Subtropical Plateau in western Santa Catarina State, Brazil. The identification of palynomorphs and cluster analysis allowed the division of the core into three environmental phases and two subphases. The basal age of the core is 39,647 years BP, corresponding to the Middle Pleistocene, a period characterized by a cold and humid climate. Forest regeneration was observed after the Last Glacial Maximum (approximately 18,000 to 20,000 years BP). The vegetation is characterized by a grassland-forest mosaic, and the beginning of forest expansion in the center of the Araucaria Subtropical Plateau occurs earlier than that observed on its eastern edge. These results corroborate those of other studies already conducted in the Araucaria Subtropical Plateau.

Keywords: palynology, late Quaternary, paleoenvironment.

INTRODUCTION

Minerotrophic peat bogs are areas where accumulated plant materials are maintained by the influence of surface and subsurface waters, enriched in mineral nutrients (Franchi *et al.*, 2006). These sites are characterized by the high preservation of palynomorphs, including pollen grains, spores, and other biological materials, which are considered high-resolution proxies in paleoclimatic reconstruction studies (Salgado-Labouriau, 2007; Cui *et al.*, 2018). The high-resolution characteristic results from the vegetation cover being highly sensitive to environmental changes, especially those related to climate (Li *et al.*, 2019).

In Brazil, research on vegetation and climate variations based on Quaternary Palynology is relatively recent, having intensified

since the 1990s (Suguio, 2010; Oliveira *et al.*, 2006). These studies have focused mainly on the Amazon, in the Cerrado dominated areas, and in the southern region of Brazil. In the latter region, research was initially developed in the coastal plain of Rio Grande do Sul and on the eastern edge of the Subtropical Plateau with Araucaria, in the states of Santa Catarina and Rio Grande do Sul (Roth & Lorscheitter, 1990; Behling, 1995; Behling *et al.*, 2001, 2004; Jeske-Pieruschka *et al.*, 2010; Lima, 2010; Lima *et al.*, 2016). In these areas of southern Brazil, the analyzed cores indicated that vegetation was dominated by Campos, with a sparse distribution of Araucaria Forest in the valley bottoms, dating back to the Late Pleistocene (14,000 to 11,000 years BP). Specifically, in the Serra do Rio do Rastro and Morro da Igreja, the Campos vegetation was maintained until approximately 1,000 years BP. From that point on, the Araucaria



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Forest expanded, indicating an increasingly humid climate that persists to the present day (Behling, 1995).

Within the Subtropical Plateau with Araucarias in the Campos Gerais (PR) sector, at altitudes above 1,200 meters, Behling (1996) suggests that the area would have had a climate with temperatures 3 to 5 °C colder and drier than the current one during the Last Glacial Maximum (late Pleistocene). This environment would have favored a predominance of grassland vegetation, with scattered occurrences of Araucaria and Tropical Atlantic forests in the valley bottoms. From the early to middle Holocene, the area would have maintained a predominance of grassland in the higher sectors, with a relative expansion of Araucaria Forest in the valley bottoms, indicating a warmer and more humid climate compared to the Last Glacial Maximum. From the Middle Holocene onwards, the Araucaria Forest would have migrated to the upper sectors, favored by a more humid climate with a shorter dry season. These conditions culminate in the field-forest mosaic that has developed over the last 1,500 years BP, a condition also recorded in the highlands of the eastern border of Santa Catarina and in the coastal plain of Rio Grande do Sul.

In the interior of the State of Santa Catarina, core area of the Subtropical Plateau with Araucaria, palynological studies suggest that forest expansion began earlier than that observed in the eastern border and coastal plain sectors (Gadens-Marcon *et al.*, 2014; Lima *et al.*, 2016; Eidt, 2019; Perin *et al.*, 2021; Graeff, 2023; Piraquive-Bermúdez *et al.*, 2024). The same interpretation is supported by Bertoldo *et al.* (2014) in a core from the central sector of Serra da Fartura (Pato Branco, PR), located in the interior of the State of Paraná. Furthermore, these studies indicate that there was no replacement of the field by the forest in any of the cores analyzed, as verified in the eastern border of the Subtropical Plateau with Araucaria.

Paleoenvironmental studies using multi-proxies analysis (litho-, pedo-, allo- and chronostratigraphy; stable carbon isotope analysis; phytolithic indices; radiocarbon dating and Optically Stimulated Luminescence (OSL), developed on the Palmas-PR/Caçador-SC summit surface, eastern end of Serra da Fartura (Paisani *et al.*, 2008, 2013, 2014, 2017) also indicate an environment of humid and cold conditions at 45 thousand years BP, Last Interstadial, or MIS 3 (Rabassa & Ponce, 2013). Drier environmental conditions on this summit surface would have prevailed during the transition to the Last Glacial Maximum (MIS 2), persisting in the Late Holocene with a continuous dry environmental regime, punctuated by millennial climate fluctuations characterized by wetter conditions. This resulted in the replacement of the Campos Sujos vegetation by Campos Limpos in this segment of the Subtropical Plateau, characterized by Araucaria trees. From 2,600 years BP to the present day, the environment would become progressively more humid and colder, with the resumption of forest on the flanks of the bottoms of smaller 4th-order valleys and Campos Limpos vegetation on the slopes and tops of the relief (Paisani *et al.*, 2019).

From the above, there are still gaps regarding the environmental dynamics within the Subtropical Plateau with

Araucaria during the Late Quaternary, specifically concerning humidity conditions, which are responsible for the field/forest vegetation mosaic. In this sense, this work analyzes the vegetation dynamics over the last 40,000 years in minerotrophic peatlands at the Mata Preta Ecological Station (Mata Preta ESEC), Subtropical Plateau with Araucaria, western Santa Catarina (Brazil), core area of the Mixed Ombrophilous Forest, Mata Preta Ecological Station, located within the Subtropical Plateau with Araucaria, in dissected levels of the Serra da Fartura, on the border between the states of Paraná and Santa Catarina.

PHYSIOGRAPHICAL ASPECTS

The Mata Preta ESEC corresponds to the conservation unit that safeguards the last remnants of Mixed Ombrophilous Forest (MOF) in the State of Santa Catarina. It is located in the central sector of the Subtropical Plateau with Araucaria (Ab'Saber, 1967; Paisani *et al.*, 2019), west of the State of Santa Catarina, bordering the State of Paraná, in the Uruguay River Basin. Regionally, this watershed relief between the basins of the Iguacú (PR) and Uruguay (SC) rivers is known as Serra da Fartura. This Conservation Unit is composed of three main MOF fragments, separated by the SC-467 highway and municipal roads, with a buffer zone reaching a small portion of the municipality of Clevelândia, in the State of Paraná (Figure 1). The totality of the fragments results in an area of 6,573.48 hectares (Prochnow, 2009). It is important to note that around the Mata Preta ESEC, there are crop/planting areas, marked in Figure 1 by pink lines. These areas produce soybeans and corn during the summer and wheat during the winter.

The core sample studied was collected in the fragment of the Mata Preta ESEC located to the east (Figure 1), with coordinates 26°29'0.33"S and 52°13'12.48"W, and altitude between 800 and 900 m (Figure 2). The area is composed of volcanic rocks of the Serra Geral Group, with a transition between outcrops of the Paranapanema and Chapecó formations (CPRM, 2014). Regionally, the relief of the area corresponds to the edge of an extensive plateau (Paisani *et al.*, 2014), which, locally, consists of several intermediate levels (Pontelli *et al.*, 2015), resulting in a relief with accentuated dissection. Specifically, the core collection sector corresponds to the lowest area in relation to the surrounding relief (Figure 2) and can be defined as a closed depression (Guerra & Guerra, 2009).

The current climate in the study area is influenced by several atmospheric systems operating in the State of Santa Catarina. In the spring and summer, intense heat and high humidity levels favor the formation of convective rains, resulting in significant rainfall volumes, which are more common in September and October under normal weather conditions. Generally, during these periods, the western part of the state experiences a high level of sunlight, resulting in maximum temperatures exceeding 30°C (Monteiro, 2001).

The autumn and winter months are characterized by reduced sunlight in the area and the successive arrival of cold fronts



Figure 1. Distribution of Mixed Ombrophilous Forest (MOF) fragments that make up the Mata Preta ESEC, western Santa Catarina, in the center of the Subtropical Plateau with Araucaria. Source: Prochnow (2009).

associated with polar air masses. In normal weather conditions, the months of June and July are more humid, while August is drier, corresponding to the lowest annual indexes. The combination of polar air mass dominance and high altitude favors the occurrence of frost in the region (Monteiro, 2001).

These annual climate characteristics correspond to the humid mesothermal type (Cfa), characterized by two well-defined seasons. Summers are hot and winters are cold, with average temperatures in the coldest month between 11.5 and 13 °C. The average annual temperature is 18 °C. Rainfall is well distributed, ranging from 1,790 to 2,280 mm/year, with the lowest rainfall recorded in August (Braga & Ghellre, 1999).

The vegetation formation found in the Mata Preta ESEC corresponds to the Mixed Ombrophilous Forest (MOF), a part of the Atlantic Forest Biome, also known as the Forest with Araucaria, due to the predominant presence of Araucaria *angustifolia*, the Brazilian pine or Paraná pine (Prochnow, 2009). The understory of the MOF is composed of varied and complex flora, with the presence of *Ocotea porosa* (imbuias), *Sloanea lasiocoma* (sapopema), *Ilex paraguariensis* (yerba mate), *Nectandra lanceolata* (yellow cinnamon), *Nectandra megapotamica* (black cinnamon), *Ocotea odorifera* (sassafras cinnamon), *Persea major* (pau-andrade), *Prunus sellowii* (wild peach tree), *Dicksonia sellowiana* (bugio tree xaxim or imperial fern) (Klein, 1978).

MATERIAL AND METHODS

The sediment core was obtained using a Russian-type collector in a peat bog area within the Mata Preta Ecological Station (**Mata Preta ESEC**), western Santa Catarina, Brazil. Six segments of 50 cm each and one segment of 20 cm were collected, totaling 320 cm in length. At this depth, an impediment level was found, which was not necessarily the base of the peat bog. The samples were stored in polyvinyl chloride tubes (**PVC**) that had been previously cut lengthwise, wrapped in plastic film, and placed in black plastic bags. In the laboratory, the sample segments were kept in a refrigerated environment at 4 °C.

To obtain the color, the core segments were unwrapped and exposed on a bench at the Geology Laboratory of the Universidade Federal da Fronteira Sul, Chapecó Campus. With the help of the Munsell Color Chart, the color variation was observed throughout the core, individualizing six (6) distinct volumes.

For the texture of the materials along the core, data from the wet granulometric treatment obtained in the research by Barros

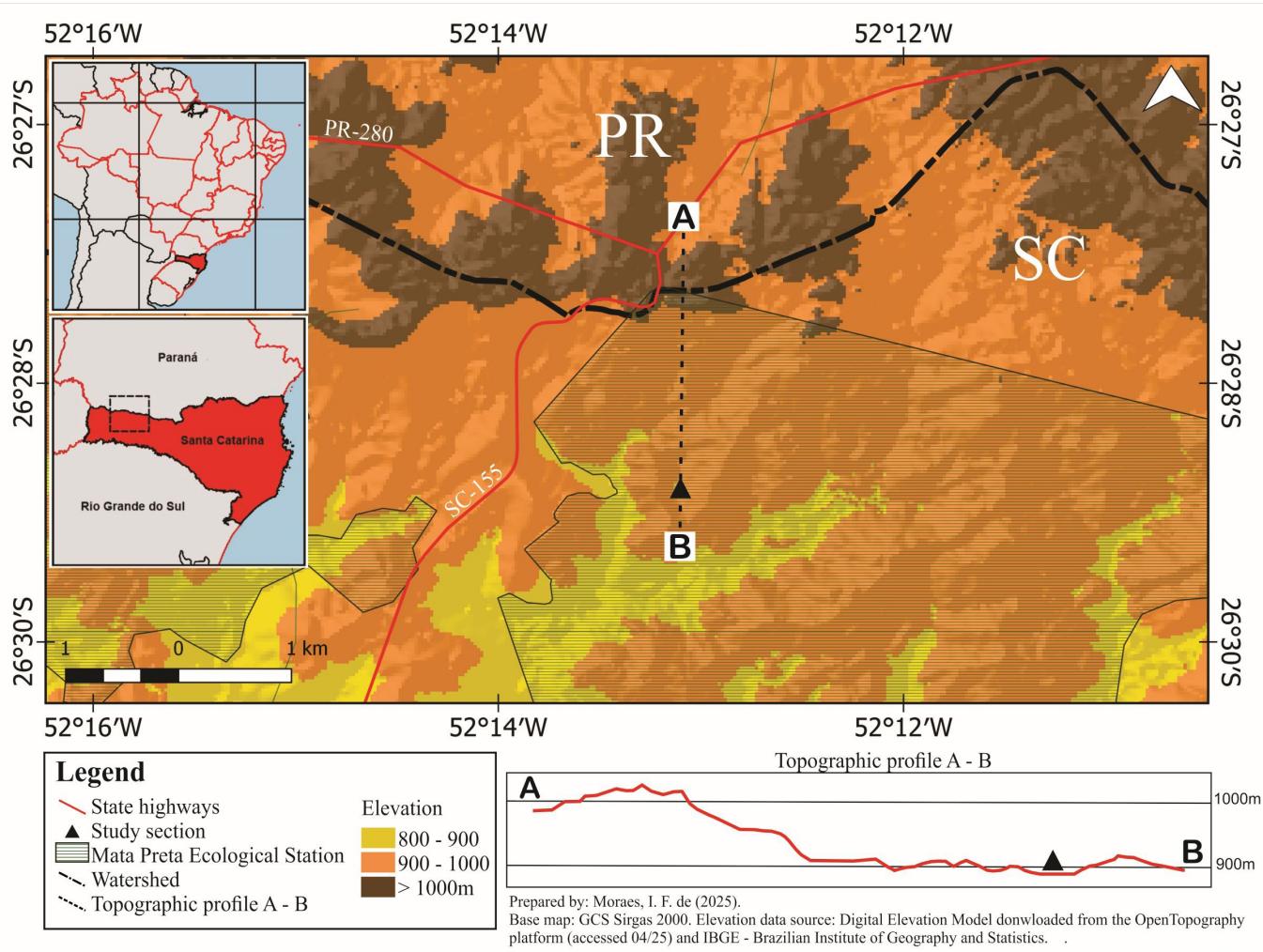


Figure 2. Location of the studied record, the study area and terrain morphology. Points A–B correspond to the “Topographic profile” Moraes, I.F. de (2025).

(2024) were used. In the pre-treatment to eliminate organic matter (OM), the author used a base of hydrogen peroxide and distilled water at a temperature of 105 °C, according to the protocol by Verdade (1954). After the elimination of the OM, the samples were subjected to the wet separation technique to obtain granulometric fractions from a CALGON-type deflocculant solution. The fine fractions were obtained by pipetting and the coarse fractions by sieving. To determine the textural class, the author utilized the Flemming (2000) diagram, which provides a hydrodynamic classification of the materials.

Chemical processing was performed on 41 subsamples of 1 cm³, obtained at intervals of every 8 cm. Chemical processing followed the standard for Quaternary Palynology (Faegri & Iversen, 1975; Salgado-Labouriau, 2007), which consists of: (i) adding a *Lycopodium clavatum* tablet (nº of spores/cm³ of 18,583 ± 762) to the samples. The introduction of *Lycopodium clavatum* is necessary for calculations of palynomorph concentration and influx; however, this data will not be used

in this study; they will be used in future studies; (ii) treatment with 10% hydrochloric acid (HCl) to remove carbonates; (iii) use of potassium hydroxide (KOH), 10% solution, to disperse humic acids and organic matter; (iv) use of glacial acetic acid (CH₃COOH) for dehydration; (v) removal of the internal contents of the palynomorphs through acetolysis, from a mixture of nine parts of acetic anhydride (CH₃CO)₂O and one part of sulfuric acid (H₂SO₄). All steps were interspersed with washing using distilled water and centrifugation. Filtration was performed with a 150 µm mesh using distilled water. This step was carried out at the Bromatology Laboratory of the Universidade Federal da Fronteira Sul, located on the Chapecó Campus.

After chemical processing, five slides were mounted on glycerin gelatin for each subsample, totaling 405 slides. For quantitative analysis, at least 200 pollen grains were counted, with spores counted separately. Taxonomic identification of palynomorphs was performed to the lowest possible hierarchical level using a biological optical microscope. Pollen taxa were

grouped according to their habitat (Souza & Lorenzi, 2008; JBRJ, 2024).

A palynological percentage diagram was prepared using *TILIA* 3.0.3 software. To determine the paleoenvironmental phases, a cluster analysis was performed using *CONISS* software. This step was carried out at the Geology Laboratory of the Universidade Federal da Fronteira Sul, Chapecó Campus, as well as at the Optical Microscopy Laboratory – Center for Paleoenvironmental Studies (NEPA), of the Universidade Estadual do Oeste do Paraná, Francisco Beltrão Campus.

The radiocarbon age determination was obtained from three 20-g samples of dry material. The treatment was conducted at the Center for Applied Isotope Studies at the University of Georgia (USA), utilizing the ^{14}C -AMS method. For paleoenvironmental interpretation purposes, an age-depth model was constructed using the Bacon package (Blaauw *et al.*, 2019) for R 4.3.2, and ages were calibrated using the SHCal20 curve (Hogg *et al.*, 2020).

RESULTS

Description of sedimentary core

The color and texture parameters allowed the identification of 6 layers along the worked core (Table 1). Layer 01, from 320 to 300 cm, exhibits a very dark gray color (7.5YR13/1) when wet and has a slightly silty clay texture.

The sediments in layer 02, from 300 to 250 cm, are black (7.5YR2.5/1, wet), with humidity. The texture varies greatly in this layer: slightly silty clay between 290–300 cm; silty clay (280–290 cm); slightly clayey silt (270–280 cm); clayey silt (260–270 cm), and returning to silty clay between 250–260 cm.

Layer 03, from 250 to 200 cm, displays a dark gray color (7.5YR4/1, wet) when wet, with reddish-yellow mottling (7.5YR6/8, wet). During this interval, the texture is silty clay between 250–240 cm, changing to clayey silt (240–220 cm) and then to slightly silty clay (220–200 cm).

Layer 04, from 200 to 150 cm, presents a gray coloration (7.5YR5/1, moist) with humidity and presence of reddish-yellow mottling (7.5YR6/8, moist). The texture varied from slightly silty clay (200–190 cm) to silty clay from 190 to 150 cm in depth.

In layer 05, between 150 and 50 cm deep, very dark gray material (7.5YR3/1, wet) is observed when wet, with no apparent fibrous organic material and clear contact with the next layer. The texture varies between silty clay (150–130 cm); clayey silt (130–90 cm); silty clay (90–80 cm) and clayey silt (80–50 cm).

The material in layer 06, corresponding to the first 50 cm of depth, is black in color (7.5YR2.5/1, moist) with moisture and the presence of roots. The texture changes from slightly clayey silt (50–40 cm) to clayey silt from 40 cm to the surface.

From the calibration of the ages (Table 2) it was identified that the base of the core, not being the base of the peat bog, dates back to 39,647 years BP. The second sample dated back to 32,259 years BP, and the third sample is up to 20,203 years BP.

Description of the palynological diagram

Of the 41 samples analyzed throughout the core, 15 did not reach the minimum value of 200 palynomorphs, being interpreted as sterile, which resulted in two pollen hiatuses. During the first hiatus, eight samples were devoid of any palynomorphs, whereas during the second hiatus, seven samples contained a maximum of 50 palynomorphs. A total of 78 types of palynomorphs were identified.

Table 1. Color and textural classification of individual layers in the peat bog. *Textural classification according to Flemming (2000). All samples analyzed by Barros (2024) were classified in the “mud” textural group, which has a maximum of 5% sand.

Layer	Depth (Cm)	Color	Textural Classification*
VI	0–50	black (7.5YR2.5/1, wet)	slightly clayey silt to clayey silt
V	50–150	very dark gray (7.5YR 3/1, wet)	clayey silt to silty clay
IV	150–200	gray (7.5YR4/1, wet) with reddish yellow mottling (7.5YR6/8, wet)	silty clay to slightly silty clay
III	200–250	dark gray (7.5YR4/1, wet) with yellow mottling reddish (7.5YR6/8, wet)	clayey silt to slightly silty clay
II	250–300	black (7.5YR2.5/1, wet)	clayey silt to slightly silty clay
I	300–320	very dark gray (7.5YR13/1, wet)	slightly silty clay

Table 2. Radiocarbon ages and calibrated ages. *Ages were calibrated using the Bacon package (Blaauw *et al.*, 2019) and the SHCal20 curve (Hogg *et al.*, 2020).

Laboratory code	Depth (cm)	Material	Age 14C (years BP)	Calibrated 14C Age (years BP)*
70987	150	Sediment	$16,760 \pm 40$	20,203
70988	248	Sediment	$28,240 \pm 80$	32,259
70990	320	Sediment	$34,530 \pm 130$	39,647

The cluster analysis enabled the identification of three environmental phases, designated as AL-I, AL-II, and AL-III (Figure 3). The AL-I phase corresponds to 11 material samples, analyzed between 320 cm and 136 cm in depth, with ages ranging from 39,637 years BP to 18,483 years BP. This phase allows the identification of two subphases: AL-Ia and AL-Ib.

The Subphase AL-Ia corresponds to nine samples analyzed in the interval between 320 cm and 256 cm in depth. In this

phase, the grassland taxa exhibit greater variability, ranging from 72.8% to 89.4% (Figure 3). The taxonomic groups with the greatest representation are Poaceae (38.5%–61.6%), *Baccharis* (7.2%–24.4%) and, secondarily, Asteraceae (1%–5%), *Plantago* (0.3%–4%), *Senecio* (0.7%–6%), Cyperaceae (0.3%–4.3%), *Eryngium* (0.3%–1.6%) and Fabaceae (0.3%–1.7%) (Figure 4). The forest is present in this subphase, varying from 10.6% to 27.2%. It is represented by the families Euphorbiaceae (2.4%–

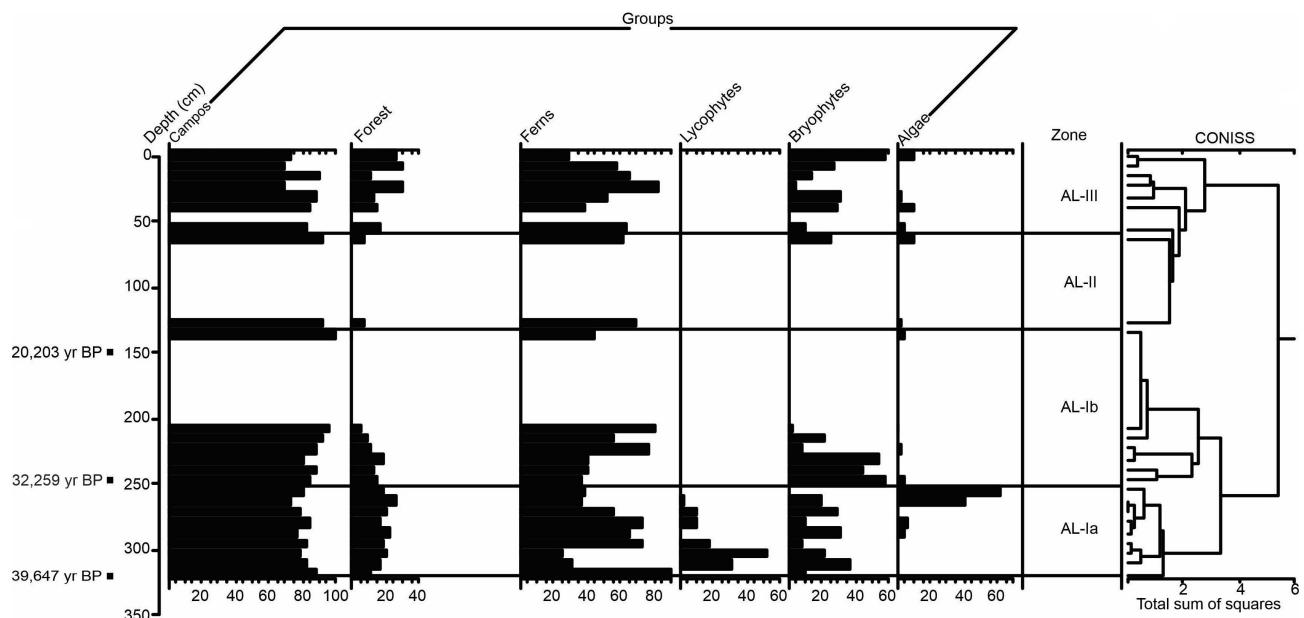


Figure 3. Diagram of the groups and types of vegetation found in the studied core.

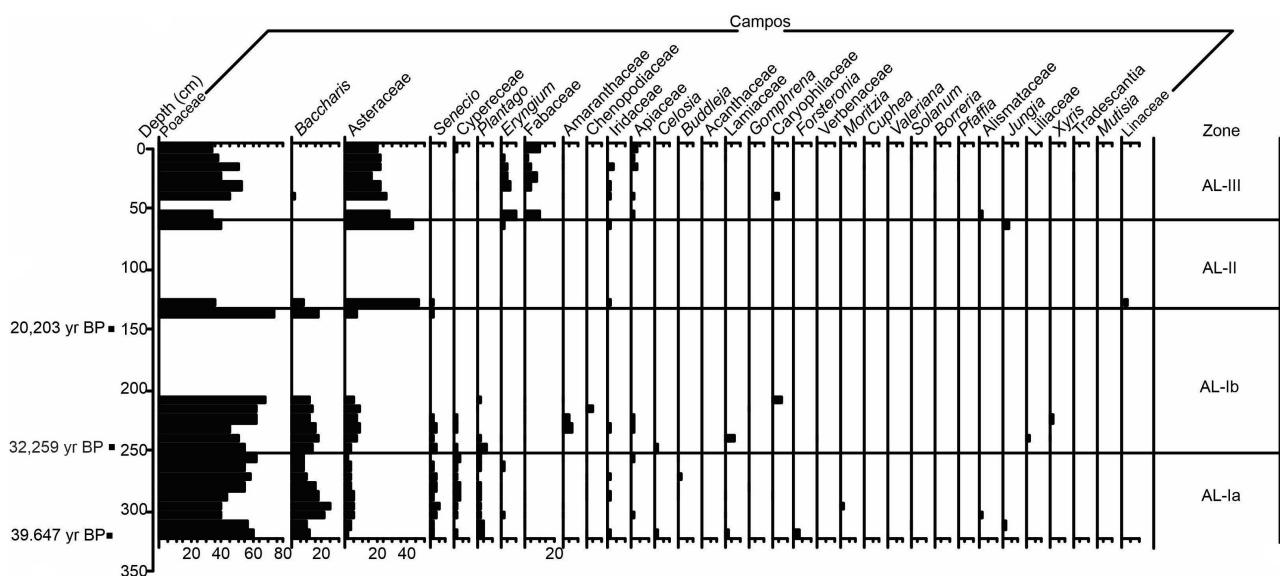


Figure 4. Pollen percentage diagram of Campos vegetation.

7.6%), Piperaceae (1%–3.3%), Myrtaceae (1%–5.1%), by the genera *Sebastiania* (1.7%–4.9%), *Podocarpus* (0.3%–2.3%), by the family Ericaceae (0.3%–2.3%), *Mimosa* (0.3%–2%) and by the species *Mimosa scabrella* (0.3%–2.6%). Although less expressive, it is possible to observe the presence of *Araucaria angustifolia* (0.3%–1%), *Ilex paraguariensis* (0.3%), and *Croton* (0.3%–1%) (Figure 5). In this subphase, a pollen grain of the *Alnus* type was found in the 280 cm sample. The Lycophytes present in this subphase are represented exclusively by the genus *Isoetes* (52.2%–2.6%). Ferns of the genera *Blechnum imperiale* (3.2%–50%), *Asplenium* (17.9%–19.4%), and *Osmunda* (3.4%–13.3%) have important representation. Bryophytes are represented only by the genus *Sphagnum* (37.5%–9.1%). The algae, on the other hand, are represented by *Zygnema* (3.4%–61.3%) (Figure 6).

In the AL-Ib subphase, with a range of 256 cm to 136 cm, seven samples were analyzed, with a predominance of grassland taxa, with a minimum variation of 85.2% to 99.7% (Figure 3). Pollen grains from the Poaceae family (55.4%–74%), Asteraceae family (3.4%–9.2%), *Baccharis* genus (12.4%–16.8%), *Senecio* (1%–3.7%), *Plantago* (1.5%–6.7%), Cyperaceae (1%–1.3%), Fabaceae (0.7%–1.5%), Amaranthaceae (1%–5.9%). Pollen grains of the *Eryngium* type appear in this phase at 240 cm with 0.7% (Figure 4). The forest in this subphase appears with a variation of 0.3% to 18.8%. Forest pollen grains are mainly represented by the families Euphorbiaceae (0.3%–2%), Piperaceae (0.7%–1.9%), Myrtaceae (0.7%–3.3%), Ericaceae (0.7%–4%),

by the genus *Podocarpus* (0.5%–5.1%), *Vernonia* (0.3%–0.7%), *Weinmannia* (0.3%), *Araucaria angustifolia* (0.3%–0.5%) and *Ilex paraguariensis* (0.5%–4%) (Figure 5). It was also possible to observe important percentages of ferns of the type *Blechnum imperiale* (1.9%–15%), *Osmunda* (1.9%–8.7%), *Asplenium* (2.2%–30%), *Lycopodium* (1.9%–10.6%). Bryophytes of the type *Sphagnum* range from 9.1% to 58.7%. Algae are represented by the types *Zygnema* (3%–5%) and *Pseudoschizaea* (5%) (Figure 6). At the top of this subphase, between 200 and 144 cm, there is an absence of palynomorphs, which characterizes this interval in the core as a pollen hiatus.

The sediments from the 136 cm to 64 cm depth interval individualize the AL-II phase, corresponding to the period between 18,483 years BP and 9,639 years BP (Figure 3). In this phase, two samples were analyzed, whose grassland taxa did not show significant variation concerning the previous interval, with percentages ranging from 92.3% to 92.7%. The grasslands are represented by the Asteraceae family (42.8%–46.5%), which has the highest rate, followed by the Poaceae family (35.5%–39.5%), Iridaceae (1%–1.3%), Linaceae (0.7%), Fabaceae (1.7%), *Eryngium* genus (0.7%–2.7%), *Senecio* (1%), *Baccharis* (7%), *Jungia* (4%) (Figure 4). The Forest undergoes no variation in this phase, with a slight change observed from 7.3% to 7.7%. The forest taxa with the highest percentages are the genus *Piper* (6.6%), the Euphorbiaceae (2.7%), and Urticaceae (2.3%) families. The species *Mimosa scabrella* and the family Myrtaceae appear at a frequency of 0.3%. The genus *Celtis*, the

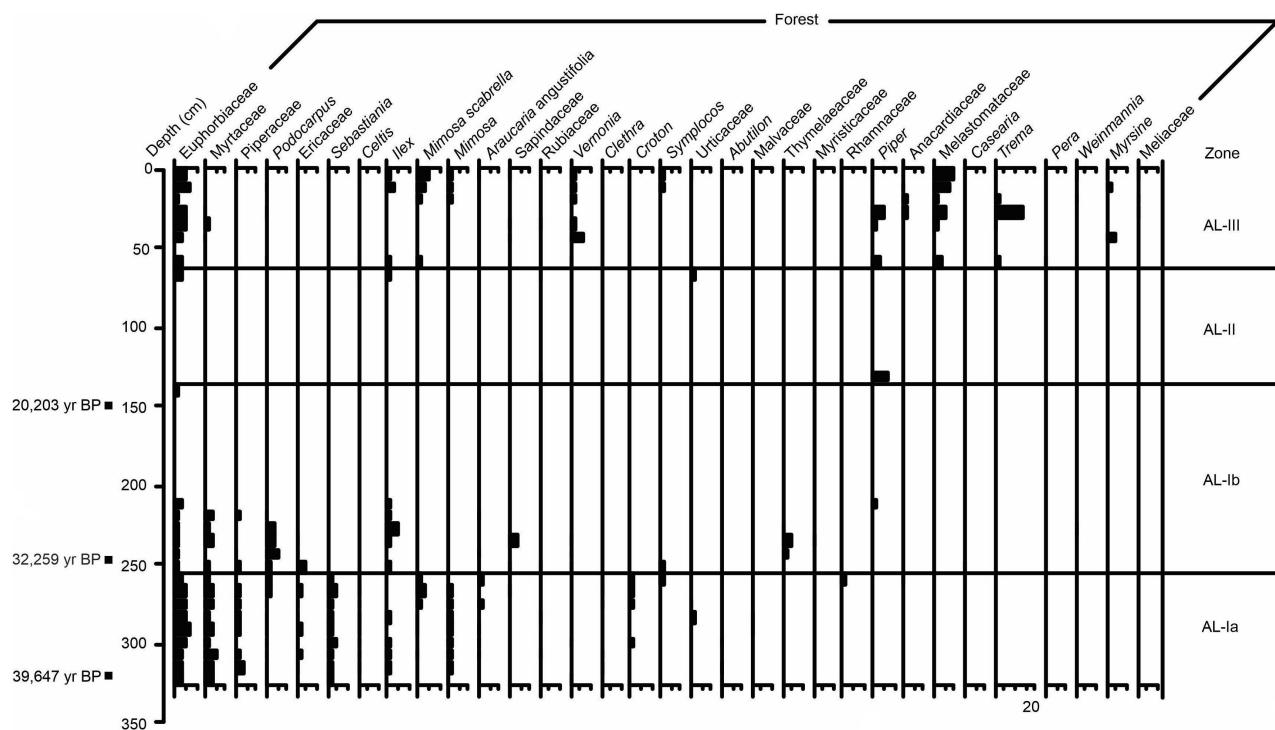


Figure 5. Pollen percentage diagram of Floresta vegetation.

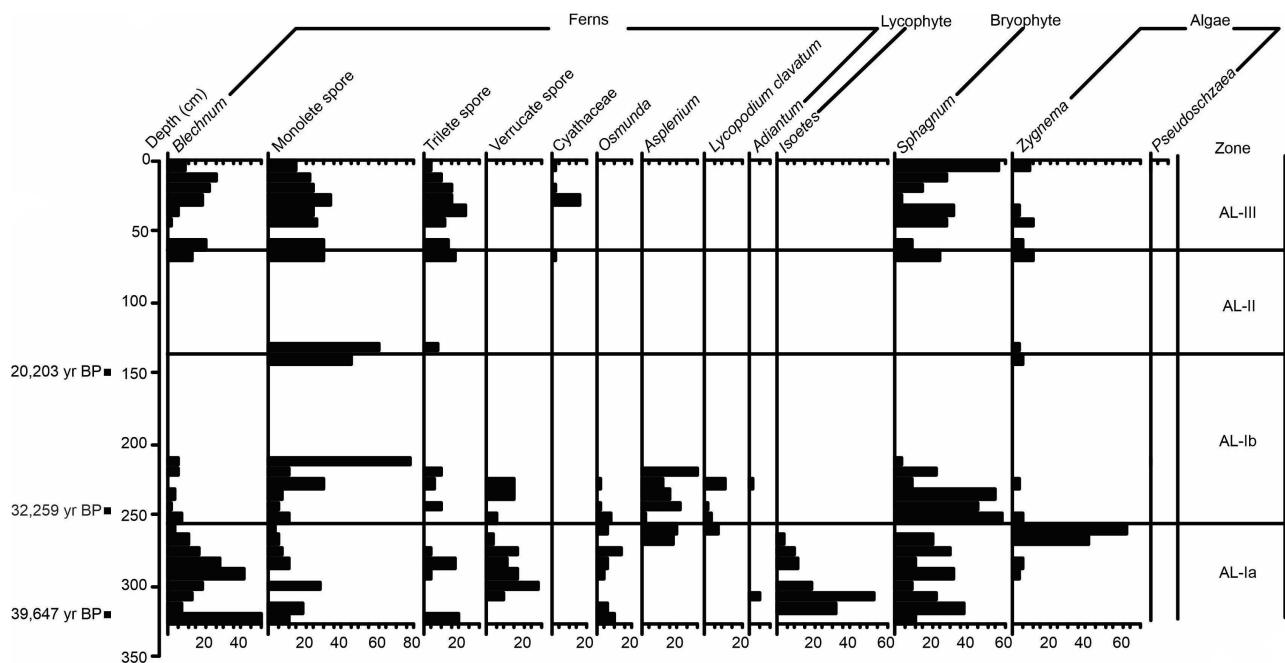


Figure 6. Percentage diagram of plant and algae spores observed in the studied core.

species *Ilex paraguariensis*, and the family Rubiaceae appear with 0.7% each (Figure 5). Ferns of the type *Blechnum imperiale* (12.4%) and Cyatheaceae (2.2%) are found in this environmental phase, as well as Bryophytes of the type of *Sphagnum* (24.7%) and algae *Zygnema* with variation of 2.8% to 10.1% (Figure 6).

In phase AL-III, seven samples were analyzed, representative of surface sediments, spanning from 64 cm to 0 cm, and corresponding to the period of the last 9,639 years BP (Figure 3). Fields with variation of 69.8% to 89.6% were recorded. The highest percentages were found in the families Poaceae (32.8%–52.3%), Asteraceae (17.5%–27.3%), *Baccharis* (2.5%), *Eryngium* (1%–9.6%), Fabaceae (3.1%–10.4%), Apiaceae (0.5%–2.3%), Iridaceae (1.7%–2.1%), *Solanum* (0.7%), *Pfaffia* (0.3%–0.9%) (Figure 4). The forest in this environmental phase has a variation of 10.4% to 30.4%, being represented by the family Euphorbiaceae (1.1%–7.5%), Melastomataceae (1.1%–8.7%), by the genera *Podocarpus* (0.3%–1%), *Mimosa* (0.7%–1.1%), by the species *Mimosa scabrella* (0.7%–4.3%), *Vernonia* (1%–7.1%), *Piper* (0.7%–3%), *Symplocos* (0.9%–1.7%) being the latter found in the first two samples, *Myrsine* (0.3%–3.9%), *Trema micrantha* (0.3%–13.3%), *Ilex paraguariensis* (0.5%–2.5%) (Figure 5). A pollen grain of *Araucaria angustifolia* was found. Spores of ferns of the *Blechnum imperiale* type (1.4%–25.9%) and Cyatheaceae (2.4%–16.7%) obtained an important percentage, as well as Bryophytes of the *Sphagnum* type (3.7%–58.4%). Algae of the *Zygnema* type (2.8%–10.8%) and *Pseudoschizaea* (0.8%) were also found in this phase (Figure 6).

DISCUSSION

Characterization of the color and texture of materials

Observing the granulometric data (Table 1), we can verify that the material from the Mata Preta ESEC core has a certain amount of sand. However, it does not allow the individualization of the sandy texture. From this set of fractions, the peatland where the collection was carried out is characterized as a minerotrophic peatland (Franchi *et al.*, 2006). In other words, those peatlands that are influenced by both surface and groundwater. Furthermore, analyzing the ages obtained by radiocarbon dating, this minerotrophic peatland has been developing for at least 40 thousand years BP.

Forest expansion and retraction during the Middle Pleistocene – 39,647 yr BP to 18,483 yr BP

Data obtained from the Mata Preta ESEC evidence indicate that during this period, the landscape was predominantly composed of grassland vegetation, characterized as Humid Field. This is due to the presence of taxa such as *Plantago*, Cyperaceae, and *Eryngium*, suggesting a regionally cold and humid environment (Behling, 1995). Cyperaceae is a family that prefers to inhabit marshy and swampy terrains (Joly, 2002). According to Irgang (1973), most species of the genus *Eryngium* are found in humid environments. However, the palynological record shows the presence of a forest that, despite being dominated by the Euphorbiaceae family, is characterized as a Mixed Ombrophilous Forest (MOF), or Forest with Araucaria.

The taxa that characterize this forest are present in all phases: *Podocarpus*, *Mimosa*, *Mimosa scabrella*, *Ilex paraguariensis*, and *Araucaria angustifolia*, although these appear in small percentages. The presence of *Araucaria angustifolia* demonstrates a high amount of humidity, while the presence of *Podocarpus* suggests cold climate conditions (Oliveira *et al.*, 2006). *Mimosa scabrella* is a pioneering forest taxon exclusive to the Mixed Ombrophilous Forest (Burkart, 1979; Sobral & Jarenkow, 2006).

The appearance of ferns of the types *Blechnum imperiale* and *Osmunda* corroborates the humidity demonstrated by the presence of the forest. Presence of *Isoetes*, an aquatic plant that grows submerged (Fuchs-Eckert, 1986), suggesting the existence of an ephemeral lake, as described by Behling *et al.* (2004), in addition to algae of the types *Zygnema* and *Pseudoschizaea*. Both provide evidence of the existence of a local water table. *Sphagnum* mosses, which are present throughout the entire extension of samples from this period, demonstrate the presence of peat bogs over the last 40,000 years BP (Joly, 2002).

Moisture during the Middle Pleistocene, evident in this palynological diagram, was also identified in materials from the surface of the Palmas/Caçador summit (Paisani *et al.*, 2019), as well as in the Cambará do Sul region (Behling *et al.*, 2004) and in the São Bento do Sul Plateau (Oliveira *et al.*, 2008). However, the forest described in the Cambará do Sul region by Behling *et al.* (2004) is less biodiverse than that described in this study. In this sense, the forest that developed in this sector, a Subtropical Plateau with Araucaria, resembles that described by Oliveira *et al.* (2008) on the São Bento do Sul Plateau.

During the Middle Pleistocene, forest expansion occurred due to temperature changes, from colder to warmer, which favored the development of MOF, while fields retreated. The Middle Pleistocene falls within MIS 3, defined in the humid tropical and subtropical areas of the planet as a hot and humid period (Thomas *et al.*, 2001). However, this temperature change does not last long, since forest retreat is recorded at the end of this phase. Despite the decrease in *Isoetes* spores towards the top of this phase, which suggests the filling of the ephemeral lake, as occurred in Cambará do Sul (Behling *et al.*, 2004), the constant presence of *Sphagnum* and *Zygnema* suggests that humidity prevailed.

Unlike other studies carried out in the Subtropical Plateau with Araucaria during the Middle Pleistocene (Paisani *et al.*, 2019; Behling *et al.*, 2004), where a change or trend towards a drier environment was observed, the sector where Mata Preta ESEC is currently located presented sufficient humidity, throughout the analyzed period, to maintain the MOF, even presenting the occurrence of local water sheets, as indicated by the high *Isoetes* indices.

During this phase, a gray sedimentary layer with reddish-yellow mottling is observed. Gray-colored materials indicate the action of a hydromorphic environment, which is typically developed in areas with poor drainage (Kämpf & Curi, 2012). Reddish-yellow mottling indicates the presence of secondary iron oxide (Cornell & Schwertmann, 1996), suggesting that the hydromorphic process was not complete. These characteristics

of partial hydromorphism were likely acquired in the source area of these sediments, in the hillslope position. The hillslope origin of these gray, mottled materials, similar to those found on hillslopes and therefore drier, would explain the palynological hiatus observed at this depth. This is because palynomorphs do not resist oxidizing environments (Bauermann *et al.*, 2002).

Late Pleistocene Campos expansion – 18,483 years BP to 9,639 years BP

Between the end of the Pleistocene and the beginning of the Holocene, the fields covered the Subtropical Plateau with Araucaria trees, including the Mata Preta ESEC location, in a nearly generalized manner. These fields are composed of shrubs and herbs, with predominant families including Asteraceae and Poaceae. However, the growth of the genus *Eryngium* and the family Fabaceae was observed. The genera *Baccharis* and *Senecio* appeared at the beginning of this phase, suggesting an environment with colder temperatures (Behling, 1995). The forest in this phase, compared to that of the previous phase, is smaller and less biodiverse, consisting of *Piper*, Euphorbiaceae, and Urticaceae. There was a low occurrence of the genera *Mimosa scabrella* and *Ilex paraguariensis*, taxa found in the Mixed Ombrophilous Forest. At the end of this phase, a significant concentration of *Sphagnum* was observed, suggesting the permanence of the peat bog. Bertoldo *et al.* (2014) also demonstrate the occurrence of MOF at the end of the Pleistocene in a core analyzed in the Pato Branco region, approximately 100 km west of Mata Preta ESEC.

This period is described by Iriondo (1999) as a phase of dry and cold climate, as attested by the palynological record of Mata Preta ESEC. However, the presence of *Blechnum imperiale* and *Sphagnum* spores suggests the permanence of the peat bog. Graeff (2023) describes the existence of a possible ephemeral lake for this period, indicated by the presence of *Isoetes*. The high humidity in the Subtropical Plateau with Araucaria can be corroborated by Gadens-Marcon *et al.* (2014), who found an increase in precipitation between 9,542- and 9,238-years BP in Ametista do Sul, RS. Graeff (2023) also highlights humidity conditions during this period. Paisani *et al.* (2019) identify climatic oscillations on the Palmas/Caçador summit surface from the end of the Pleistocene to the late Holocene. According to these authors, a continuous climate regime with dry characteristics prevailed during the period, accompanied by climatic fluctuations towards more humid conditions. A cold and humid climate during the late Pleistocene and early Holocene, with a predominance of grassland vegetation, is also observed in Caçador (Graeff, 2023), Chapecó (Eidt, 2019), and Serra do Espigão (Lima *et al.*, 2016).

During this phase, a gap was observed between the analyzed samples, which corresponds to the depths classified as sterile. However, a trend was observed that resembled fertile samples, with field dominance in the landscape. These were composed of herbs and shrubs, characterized mainly by the Poaceae and Asteraceae families, with a significant presence of *Baccharis*, grassland taxa associated with colder temperatures (Behling, 1995). During this gap, the forest showed a tendency to expand

and was composed of Euphorbiaceae, Piperaceae and *Araucaria angustifolia*, which may be dispersed throughout the landscape or even grouped in small refuges. The presence of ferns, represented by monolete and trilete spores, as well as *Blechnum imperiale* spores, and the presence of algae of the *Zygnema* and *Pseudoschizaea* types, suggest a humid environment throughout this period. Furthermore, the presence of *Sphagnum*, albeit in lower concentration, indicates the permanence of the peat bog, which has been recorded since 39,647 years BP.

Resumption of forest expansion from the lower Holocene – 9,639 years BP to the modern period

This period is marked by a new advance of the Mixed Ombrophilous Forest (MOF), from the base to the top, with significant expansion of the forest. This expansion is observed in conjunction with a considerable increase in Euphorbiaceae. In addition to this taxon, this forest is composed of the family Melastomataceae, the genera *Mimosa*, *Vernonia*, *Podocarpus* and *Symplocos*, and the species *Mimosa scabrella* and *Ilex paraguariensis*. During this period, a pollen grain of *Araucaria angustifolia* was found, evidencing the existence of the MOF in this phase. Despite the significant presence of fields, which suggests a cold climate, this new expansion of the MOF indicates a more humid environment. This evidence corroborates the results of Paisani *et al.* (2019) in the Palmas/Caçador summit region, where a cold and humid climate is also identified during this period.

Despite the cold climate, suggested by the predominance of fields, which has been declining towards the top of the core, the environment is conducive to the expansion of the MOF, due to the permanence of humidity. During the Middle Holocene, Piraquive-Bermúdez *et al.* (2024) highlight the transformation of vegetation composition in Lagoa Dourada, where the tree cover becomes denser. During this period of increased humidity, Eidt (2019) in the Floresta Nacional de Chapecó (FLONA) also observes the expansion of forest areas. Graeff (2023) identifies the expansion of the forest during the late Middle Holocene and early Late Holocene, with higher percentages in the Caçador region. All corroborate the data obtained at Mata Preta ESEC, showing that this is a regional occurrence.

Ferns of the Cyatheaceae and *Blechnum imperiale* types are still present. *Sphagnum* mosses indicate that the peat bog is still present, as they are commonly found in acidic soils, such as marshes and swamps (Joly, 2002). Algae of the *Zygnema* and *Pseudoschizaea* types are noted on the surface.

The expansion of the Mixed Ombrophilous Forest in Abelardo Luz began around 10,343 years BP. Ewald (2015), based on phytolith analysis, demonstrates that around 6,000 years BP the forest expanded over fields, but the author suggests a change from a dry to a more humid climate. Humidity was present throughout the entire period analyzed in the Mata Preta ESEC region, corroborating the results of Gadens-Marcon *et al.* (2014), who identified humidity oscillation during this period (6,810 years BP to the present), demonstrating a change in the precipitation pattern in the Ametista do Sul region, upper Uruguay (RS). Bertoldo *et al.* (2014) also observed the expansion

of the MOF around 13,000 years BP. In other regions of the Subtropical Plateau, including those with Araucaria and the eastern edge of this Plateau, this expansion began in the lower Holocene, approximately 4,200 years BP (Behling *et al.*, 2001, 2004; Gadens-Marcon *et al.*, 2014; Graeff, 2023).

During the late Holocene, Graeff (2023) identifies a slight decrease in the MOF and the Wet Fields and relates this change in the landscape to human action. However, during this period, an increase in the Araucaria Forest is observed in Mata Preta ESEC, ranging from 20% to 30%.

CONCLUSIONS

The palynological record analyzed documents the history of vegetation in the Mata Preta ESEC area over the last 40,000 years. The paleoenvironmental history told here is mainly similar to that of the São Bento do Sul Plateau (Oliveira *et al.*, 2008). These areas, together with the data obtained by Paisani *et al.* (2019), suggest that the region had a middle Pleistocene climate characterized by cold and humid conditions. It was possible to identify the regeneration of forest vegetation after the Last Glacial Maximum. This study also corroborates the data of Oliveira *et al.* (2006), Bertoldo *et al.* (2014), and Eidt (2019), which suggest that forest expansion began earlier in the interior of the Subtropical Plateau, featuring Araucaria trees, compared to studies carried out on the edge of this plateau. The field-forest mosaic, which has characterized the vegetation of the interior of the Subtropical Plateau with Araucaria trees, is also present in the Mata Preta ESEC records. Furthermore, peat bogs have been present in this area for at least 40,000 years BP.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article.

ACKNOWLEDGEMENTS

The authors would like to thank Antônio de Almeida Correia Junior, environmental analyst at the ICMBio Palmas NGI, and Fábio de Almeida Abreu, head of the ICMBio Palmas NGI. They would also like to thank Jefferson Radaeski for his help during the field trip. They would also like to thank Gustavo Bloemer, laboratory technician at the Universidade Federal da Fronteira Sul.

FUNDING

The authors would like to thank the National Council for Scientific and Technological Development (CNPq), process 406215/2023-5, for financial support for the research; the Coordination for the Improvement of Higher Education Personnel (CAPES), for the Social Demand scholarship granted; the Graduate Program in Geography - Unioeste/FB, for granting

AUXPE resources for the field survey; and the Chico Mendes Institute for Biodiversity Conservation (ICMBio) for support during the field survey.

AUTHOR CONTRIBUTIONS

Isis Fumagalli de Moraes: writing – original draft; editing; visualization; methodology; investigation; formal analysis; software; resources; data curation. Marga Eliz Pontelli: writing – review; formal analysis; data curation; conceptualization. Gisele Leite de Lima Primam: writing – review; formal analysis; data curation; conceptualization. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Received: 29 September 2024. Accepted: 23 June 2025.

Associated editor: Marcelo de Araújo Carvalho
Editor-in-chief: Matias do Nascimento Ritter