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Article

PALEOCLIMATIC AND VEGETATION RECONSTRUCTION OF THE LAST 22,000 YEARS OF WESTERN SANTA CATARINA (BRAZIL) STUDIED BY POLLEN RECORDS

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ABSTRACT – This study reconstructs vegetation change in southern Brazil from a pollen record spanning the last 27,000 years. Five palynological phases were identified in a 154 cm core from the Floresta Nacional de Chapecó (Santa Catarina). Phase I (26,855–24,622 cal. BP) reflects colder-than-present conditions, with grasslands dominant and small patches of Araucaria Forest. Phase II (23,922–22,593 cal. BP) shows a further increase in grassland taxa, indicating a still-cold but more humid climate. Phase III (21,894–7,620 cal. BP) begins under cold conditions and then transitions to warmer conditions, particularly after 7,000 cal. BP. During Phase IV (6,595–2,355 cal BP), the Araucaria Forest expanded, followed by the spread of Seasonal Deciduous Forest; this interval corresponds to peak warmth and humidity in the sequence. Phase V (after 1500 BP) records forest retreat, especially toward the top of the core, likely associated with Euro-Brazilian colonization and the advance of the modern agricultural frontier.

Keywords: palynology, paleoenvironments, quaternary, Brazil, South America.

INTRODUCTION

Environmental reconstructions based on Quaternary palynology in Santa Catarina and Rio Grande do Sul have focused chiefly on the eastern sector of the southern Brazilian Plateau (*e.g.*, Bauermann, 2003; Behling, 1995, Behling *et al.*, 2004, 2005; Cancelli *et al.*, 2012; Kuhn *et al.*, 2017). By contrast, pollen records from western areas remain scarce, particularly for the Pleistocene and Holocene (*e.g.*, Evaldt *et al.*, 2014; Perin *et al.*, 2021), which motivates the present study. We analyze the composition and abundance of pollen and spores from a Quaternary sedimentary sequence in the Floresta Nacional de Chapecó (FLONA), western Santa Catarina (Figure 1). Unlike most sites in southern Brazil, FLONA is only marginally affected by the Atlantic atmospheric system, offering a valuable vantage point to reconstruct Pleistocene–Holocene vegetation dynamics in a region that remains underrepresented in the paleoenvironmental literature.

REGIONAL BACKGROUND

Previous palynological studies in eastern and central Santa Catarina have documented cold and dry conditions during the Late Pleistocene, with Campos vegetation persisting until the early Holocene, followed by gradual forest expansion—first of Atlantic taxa and later of Araucaria Forest (*e.g.*, Jeske-Pieruschka *et al.*, 2012; Behling, 1995; Behling & Oliveira, 2017; Oliveira *et al.*, 2006, 2008; Lima, 2010; Lima *et al.*, 2016). More recent analyses closer to the western sector, such as those from Caçador, Abelardo Luz, and Mondaí, reveal similar trends of fluctuating Campos and forest dominance under changing humidity and temperature regimes during the Quaternary (Graeff, 2023; Moraes, 2024; Moraes *et al.*, 2025 ; Borger *et al.*, 2023; Radaeski *et al.*, 2023).

Despite these advances, most records still come from eastern or central areas of Santa Catarina, while the western region remains poorly studied. Our analysis of the FLONA deposit directly addresses this gap, providing one of the first paleoenvironmental reconstructions for western Santa Catarina.

MATERIAL AND METHODS

Study area

The sample was collected at 27°05’56” S and 52°46’36” W, within Floresta Nacional de Chapecó (FLONA de Chapecó), a conservation park established in 1962 and currently managed by

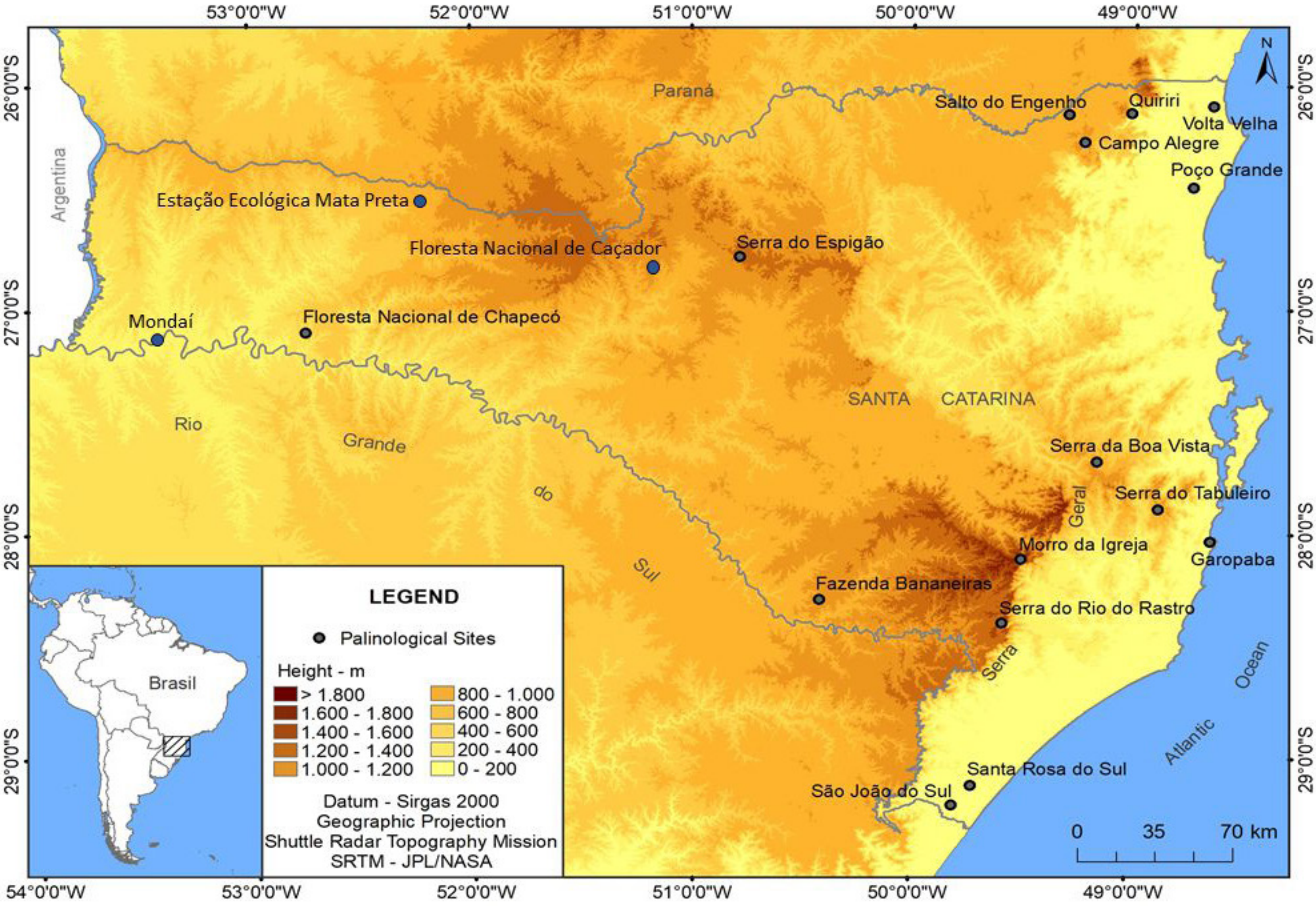

Figure 1. Locations of the sites mentioned in the text, including the FLONA site (Floresta Nacional de Chapecó - Chapecó National Forest).

the Instituto Chico Mendes de Conservação da Biodiversidade (Figure 2). FLONA is located on a floodplain in the Tigre River basin, 11 km north of the Uruguay River. The sampling site is at an altitude of 600 m above sea level (masl). The environment corresponds to the ecotone between the Upper Paraná Atlantic Forest, characteristic of the Uruguay Valley and landscapes below 600 masl, and the Araucaria Forest, which dominates areas above this elevation. The climate is subtropical, with average

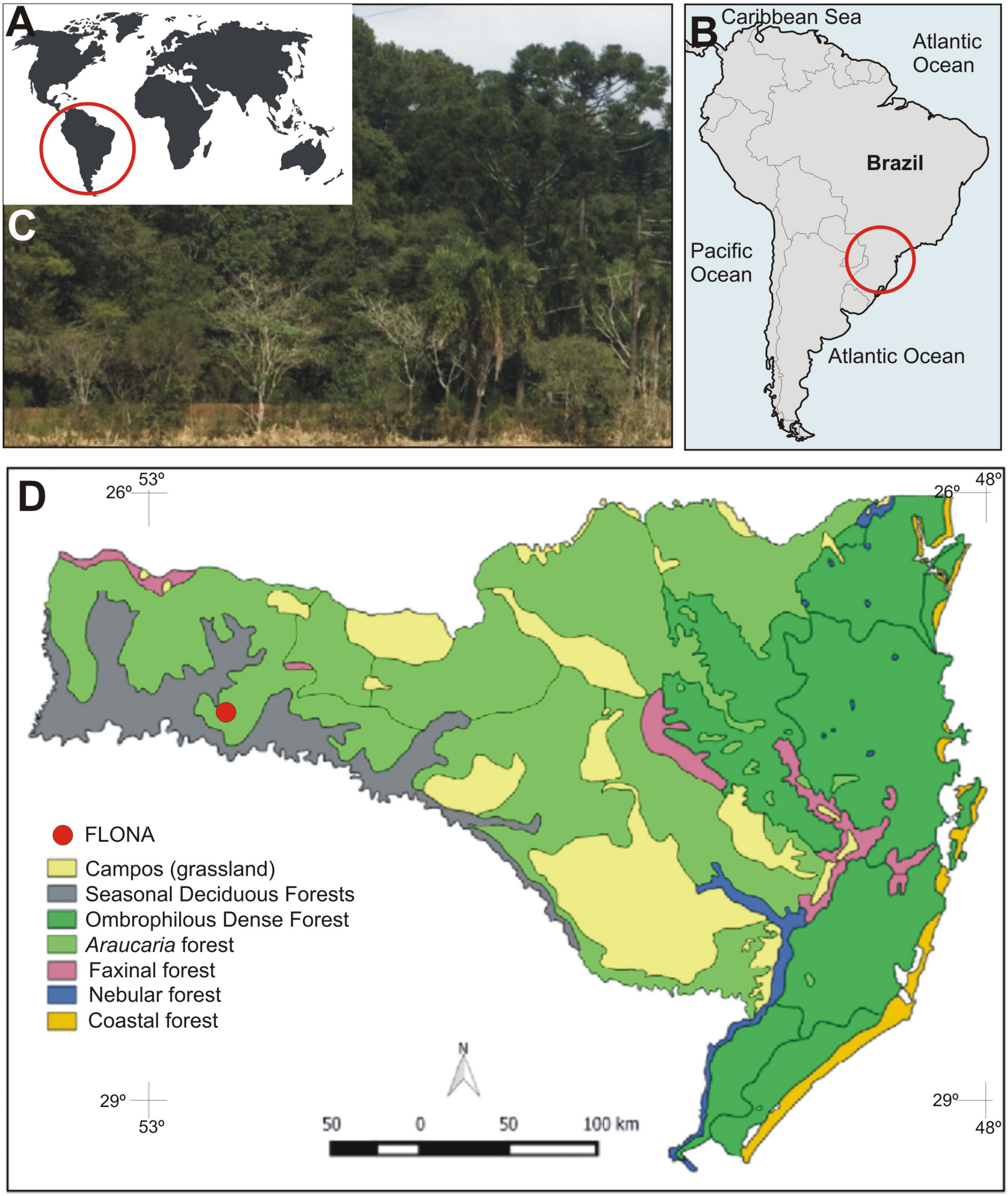

Figure 2. A, South America (red circle); **B**, location of Santa Catarina State within South America; **C**, Araucaria Forest vegetation in FLONA; **D**, vegetation map of Santa Catarina according to Klein (1978).

temperatures exceeding 22°C during the warmest months, rainy summers, and infrequent frosts. Annual precipitation averages 2,000 mm.

The park's geomorphology is diverse: on one side, deep V-shaped valleys characterize the landscape, where the typical flora belongs to the Upper Paraná Forest ecoregion. On the other hand, the terrain transitions to higher altitudes dominated by the Chapecó Plateau, where Araucaria Forest prevails (Peluso Júnior, 1986). Thus, FLONA represents a transition zone between two ecoregions: Araucaria Forest and Seasonal Deciduous Forest (Figure 2).

In the Araucaria Forest of southern Brazil, predominant species include *Araucaria angustifolia*, *Ilex paraguariensis*, *Drimys brasiliensis*, *Podocarpus lambertii*, *Dicksonia sellowiana*, *Lamanonia ternata*, and species of the Lauraceae and Myrtaceae families, genera such as *Ocotea*, *Nectandra*, *Myrcia*, *Myrceugenia* and *Eugenia* (Boldrini *et al*., 2009; Oliveira, 2009).

On the other hand, species characteristic of the Seasonal Deciduous Forest include *Cabralea canjerana*, *Nectandra megapotamica*, *Heliocarpus popayanensis*, *Apuleia leiocarpa*, *Maclura tinctoria*, *Cedrela fissilis*, *Cordia trichotoma*, *Cordia ecalyculata*, *Cordia americana*, *Aloysia virgata*, *Solanum mauritianum*, *Syagrus romanzoffiana*, *Actinostemon concolor*, *Sorocea bonplandii*, *Piper* sp., *Inga marginata*, *Lonchocarpus* sp., *Parapiptadenia rigida*, *Balfourodendron riedelianum*, *Pilocarpus pennatifolius*, *Guarea macrophylla*, and *Ocotea puberula* (Rio Grande do Sul, 2005; Oliveira, 2009; Vibrans *et al*., 2012).

In some areas, the vegetation forms a mosaic of Araucaria Forest and grasslands (Boldrini *et al*., 2009; Oliveira, 2009). *Campos* (grasslands) are composed of species from the Poaceae, Fabaceae and Asteraceae families (Boldrini *et al*., 2009).

Processing and analysis of the sediment core

The core was extracted from the floodplain of a low-order stream (1st-order channel) that drains an area of native forest and serves as a tributary to the Tigre River basin. This small, low-energy watercourse flows through shallow slopes, resulting in the slow deposition of fine sediments, primarily clay. During rainfall events, suspended material is transported downstream, occasionally overflowing the main channel and depositing sediment along the edges, where it settles and forms flat, homogeneous sedimentary layers over time. Radiocarbon dates obtained from the analyzed sequence indicate a slow and consistent rate of sediment deposition (see next section).

The sediment core was collected using a Peat Sampler (Russian Corer) from the surface down to the basal level, which is likely composed of gravel, resulting in a 154 cm-long column. For palynological analysis, subsamples were taken at 8 cm intervals, totaling 20 samples. In each subsample, 300 pollen grains were counted and identified, while spores were counted separately. Subsamples were processed following the standard acetolysis methodology described by Erdtman (1952). This procedure involves alternating acid treatments, centrifugation, and heating in a water bath to remove internal contents and clear the exine (outer wall) of the palynomorphs. Originally developed for modern material, acetolysis is now widely used for processing pollen and sediments with high organic content (Salgado-Labouriau, 2007, p. 257). All laboratory procedures were conducted at the Laboratory of Toxicology at Unochapecó.

Identification was carried out by comparing fossil material with modern equivalents, using reference collections from the Laboratory of Palynology at Universidade Luterana do Brasil (Campus Canoas) and the Laboratory of Surface Geodynamics at Universidade Federal de Santa Catarina/Universidade Federal da Fronteira Sul (Campus Chapecó).

The Neotropical Fossil Pollen Key software (Department of Geosciences, University of Bremen, Germany), which includes a database compatible with palynomorphs from southern Brazil, was employed to facilitate identification by matching morphological characteristics and enabling taxonomic classification at the family, genus, and species levels. Specialized catalogs and the Pollen Catalog Network (RCPol, 2026) were also consulted.

Palynomorphs were classified according to their evolutionary order, following Bicudo & Menezes (2005) for algae, Vitt (1984) for bryophytes, Kramer & Green (1990) for pteridophytes, and APG IV (2016) for gymnosperms and angiosperms. After counting and identifying the palynomorphs in each subsample, a percentage-based palynological chart was generated using Tilia and Tilia Graph software (version 3.0.3). Cluster analysis was also performed to support the interpretation of environmental phases, using CONISS software (Grimm, 1987). The analyzed core presented in this study is curated at the Universidade Comunitária da Região de Chapecó (Santa Catarina State, Brazil).

Four radiocarbon (AMS) dates were obtained from organic content (gyttja) in sediments from different depths in the sequence. Pollen types were categorized into Araucaria Forest and Seasonal Deciduous Forest, following Flora e Funga do Brasil (2022).

We established the core chronology with a piecewise linear age–depth model (LM) based on calibrated radiocarbon ages (cal BP). Independent linear segments were fit between consecutive dated depths; interpolation was confined to their intervals, and extrapolation was limited to the core ends using the first/last segment and flagged as higher uncertainty. Uncertainty was derived from each date's HPD 95% and propagated via bootstrap resampling (n = 4000) to produce 68% and 95% confidence intervals. This segmented approach captures changes in accumulation rates and avoids the bias of a single constant-rate fit.

RESULTS

Stratigraphy and chronology

The sediment core consists of black clayey silt with a predominantly fine texture, showing a slight increase in grain size with depth. The base of the core, at a depth of 154 cm, was dated to 22,690 ± 80 ^{14}C years BP (Beta-500013), 27,235–26,476 cal

BP. The dates and their corresponding calibrations are included in Table 1. Together with the modern reference point, these four radiocarbon dates define an approximate chronological framework for the core, captured by a piecewise linear age–depth model (Table 2; Figure 3).

Pollen diagrams

Based on the palynological results, a Constrained Incremental Sum of Squares (CONISS) analysis was performed, identifying five main environmental phases, from FLN-I at the base of the sequence to FLN-V at the top (Figures 4–8 and Table 3).

FLN I. Four samples from 154 to 130 cm depth (26,855–24,622 cal. BP).

This phase is characterized by a predominance of grassland species (80.3–88.8%) and a lower proportion of arboreal species (11.2–19.7%) (Figures 4 and 5). Within the group Ferns, Aquatic Plants, Lycophytes, and Bryophytes, fern spores account for up to 92.3% (Figure 7), while lycophytes, bryophytes, and pollen grains from aquatic plants are scarce or nearly absent during this stage (up to 9.7%).

Identified grassland taxa include the botanical families Poaceae (46.1–50.8%), Asteraceae (12.7–18.2%), Cyperaceae (3.0–6.9%), and the genus *Croton* (3.0–8.8%). The Poaceae-dominated pollen spectrum indicates a lack of arboreal (forest) taxa and suggests a predominance of Poaceae C_3 herbaceous and C_4 species. By the end of this phase, the presence of the family Ericaceae is minimal (<2%; 0.0–1.7%) (Figure 8).

Among forest taxa, the genera *Mimosa* (3.0–6.6%) and *Peperomia* (0.0–2.8%) are identified, along with the families Piperaceae (0.0–2.3%) and Fabaceae (0.3–2.4%), the subfamily Mimosoideae (0.0–8.8%), and *Ilex paraguariensis* (0.3–3.1%). Fern species are also evident, including *Blechnum imperiale* (up to 7.7%) and *Microgramma* sp. (up to 5.9%) (Figures 3–6).

FLN II. Three samples from 122 to 106 cm depth (23,922–22593 cal. BP).

Forest species constitute less than 13.6%, showing a slight decrease compared to the previous phase, while grassland species dominate (86.4–87.7%), which indicates a predominance of Campos Aquatic plants (up to 35.3%) are also recognized. The grassland environment remains predominant, represented by the families Poaceae (50.2–55.5%), Asteraceae (10.0–15.9%), Cyperaceae (2.7–6.7%) and Ericaceae (1.0–4.4%). Poaceae pollen grains of forest species remain without representation as well as pollen from species exclusive C_3 and Poaceae herbaceous of grasslands have a high pollen percentage. Forest species are represented by pollen grains of the genera *Peperomia* (2.4–6.7%) and *Mimosa* (up to 0.7%), the families Fabaceae (0.7–3.1%), Piperaceae (up to 3.4%), and Myrtaceae (up to 0.3%), and the subfamily Mimosoideae (1.0–2.4%). Fern spores are represented by the species *Blechnum imperiale* (up to 4.3%) and genera *Microgramma* (up to 4.3%). Bryophyte spores were not identified. Pollen grains from aquatic plants are evidenced by the genera *Sagittaria* (up to 29.4%) and *Echinodorus* (up to 10.3%) (Figures 3–6).

FLN III. Seven samples, from 98 cm to 49 cm depth (21,894–7,620 cal. BP).

Grassland taxa (72.4–89.6%) begin to decline as tree species advance (10.4–27.6%). The Campos environment is characterized by the presence of Poaceae (24.5–54.2%), Asteraceae (4.3–12.1%), Cyperaceae (7.6–31%), and Begoniaceae (up to

Table 1. Radiocarbon dates of the FLONA core.

Depht (cm)	Laboratory #	^{14}C BP	±1s	Upper Bound Cal. BP	Lower Bound Cal. BP	Median
154	Beta-500013	22690	80	27235	26476	26855,5
96	Beta-566013	17860	50	21882	21412	21647
68	Uciams-252951	9220	30	10490	10243	10366,5
43	Beta-521538	5950	30	6848	6655	6751,5
0	Surface	0	0	0	0	0

Table 2. Equations of the age–depth model.

Depth_start_cm	Depth_end_cm	age_start_cal_bp	Age_end_cal_bp	Slope_age_per_cm (cal BP per cm)	Intercept (cal BP)	Equation (age_cal_BP = a + b*depth_cm)
0	43	0	6752	157,023256	0	age_cal_BP = 0.00 + 157.023256 * depth_cm
43	68	6752	10367	144,6	534,2	age_cal_BP = 534.20 + 144.600000 * depth_cm
68	96	10367	21648	402,892857	-17029,71	age_cal_BP = -17029.71 + 402.892857 * depth_cm
96	154	21648	26721	87,465517	13251,31	age_cal_BP = 13251.31 + 87.465517 * depth_cm

In the equation, the symbol * denotes multiplication.

Table 3. Pollen types from the Araucaria Forest and Seasonal Deciduous Forest found in the FLONA core samples.

Araucaria forest	Seasonal Deciduous Forest	Araucaria forest/Seasonal Deciduous Forest
Ilex paraguariensis	Urticaceae/Moraceae	*Mimos*a sp.
Araucaria angustifolia	Arecaceae	Piperaceae
Heliconia sp.	Trigoniaceae	Fabaceae
Zingiberaceae	Cannabaceae	Mimosoideae
Oleaceae	Cunoniaceae	Myrtaceae
Podocarpus sp.	Costaceae	Rubiaceae
Gunneraceae	Rhamnaceae	Bignoniaceae
Faramea sp.	Sapotaceae	*Allophylus* sp.
Berberis sp.	*Sebastiania* sp.	Sapindaceae
Abutilon sp.		Lauraceae
Gentianaceae	*Tetrorchidium rubrivenium*	Phytolaccaceae
Marcgraviaceae	*Matayba* sp.	Annonaceae
Myristicaceae		Anacardiaceae
Ranunculaceae		Celastraceae
Matayba sp.		*Bauhini*a sp.
Thymelaeaceae		Malpighiaceae
Myrsinaceae		Melastomataceae
		Meliaceae
		Menispermaceae
		Orchidaceae
		Proteaceae
		Phyllanthaceae
		Tripodanthus acutifolius
		Roupala sp.
		Symplocaceae
		Salicaceae
		Peperomia sp.
		Celtis sp.

22.3%). Poaceae herbaceous of grasslands are well represented in the early phase but decline abruptly in the final phase, increasing Poaceae arboreal of forest (Bambuseae) to 67%. C_3-exclusive Poaceae also increases in pollen percentage toward the end of this phase. Tree species are recognized by pollen grains from the families Piperaceae (up to 11.4%), Fabaceae (up to 1.7%), and Myrtaceae (up to 1%), as well as *Ilex paraguariensis* (up to 8.6%). It is worth noting that there are two peaks in forest taxa. The first occurs at 90 cm depth (~19,230 BP; dominated by Piperaceae), and the second at 58 cm depth (~8,921 BP; primarily *Ilex paraguariensis*). Ferns are represented by spores from the families Anemiaceae (up to 4.3%) and Aspleniaceae (up to 12.5%), as well as by the species *Blechnum imperiale* (6.1–48.8%), genera *Microgramma* (up to 14.9%), and *Osmunda* (12.5–43.6%). Bryophyte spores begin to be recorded at this stage, represented by the families Bartramiaceae (up to 5%) and Notothyladaceae (up to 6.3%), and the species *Phaeoceros laevis* (up to 2.5%). Aquatic plant species are also recorded, such as genera *Myriophyllum* (upto 2.6%) at the end of this phase (Figures 4–7).

FLN IV. Four samples, from 42 to 15 cm depth (6,595–2,355 cal. BP).

At the beginning of this phase, and even slightly earlier, an increase in forest taxa is observed, reaching its highest representation at the end of the stage, with forest species accounting for up to 44.2%. Campos taxa declined from 72.1% at the start of this phase to 55.8%. Grassland pollen is attributed to the families Poaceae (19.1–31.9%), Asteraceae (1.8–8.7%), Cyperaceae (2.5–11.4%), Euphorbiaceae (0.3–5.6%), Apocynaceae (up to 5.3%), Convolvulaceae (up to 3.2%), and Malvaceae (up to 2.7%), as well as the genera *Valeriana* (up to 3.9%) and *Oxalis* (1.3–9.5%). A high percentage (73%) of arboreal forest Poaceae (Bambuseae) and C_3 species is recorded during this phase, while the frequency of herbaceous Poaceae pollen from the Campos environment remains low.

Forest species are characterized by pollen grains of *Araucaria angustifolia* (1.0–6.3%), which appears for the first time in the

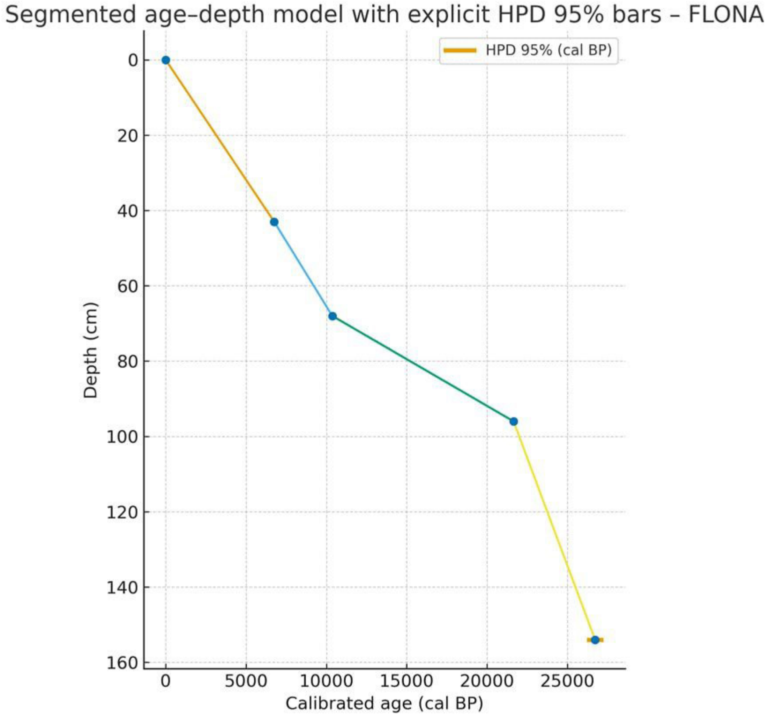

Figure 3. Depth and chronology of the sedimentary column analyzed in this study.

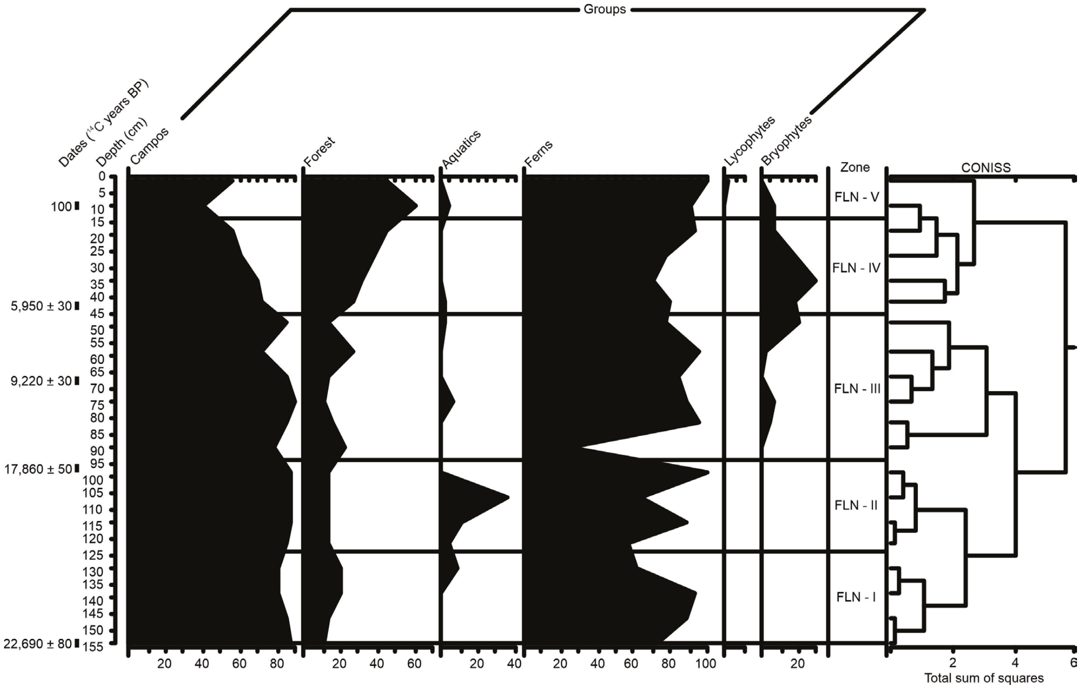

Figure 4. Summary percentage palynological diagram of FLONA de Chapecó and radiocarbon dates.

palynological record, accompanied by the families Arecaceae (0.7–5.6%), Myrtaceae (0.3–1.7%), Piperaceae (5.6–7.7%), Zingiberaceae (up to 3.3%), and Lauraceae (0.3–1.3%), as well as the genera *Heliconia* (2.3–6.0%) and specie *Ilex paraguariensis* (4.2–7.6%).

Pteridophytes are represented by spores of the species *Blechnum imperiale* (31.3–56.1%) and genera *Microgramma* (16.2–28.1%), as well as the family Cyatheaceae (1.3–12.5%). Bryophytes are predominantly represented by spores of *Phaeoceros laevis* (up to 23.8%). Aquatic plants are indicated

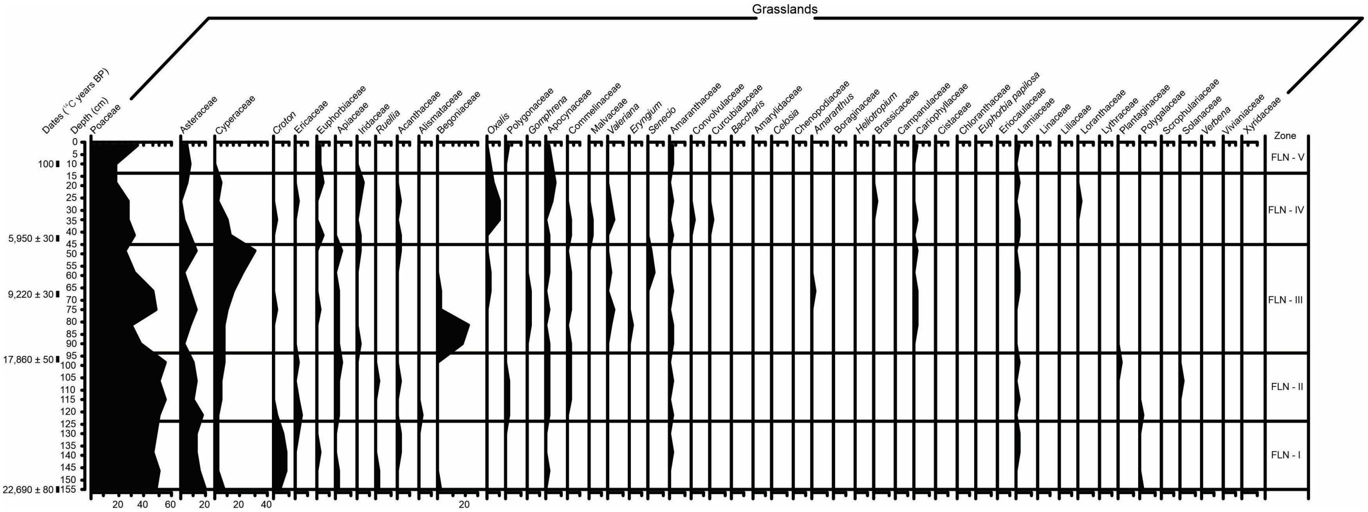

Figure 5. Percentage summary palynological diagram of FLONA de Chapecó – Grasslands.

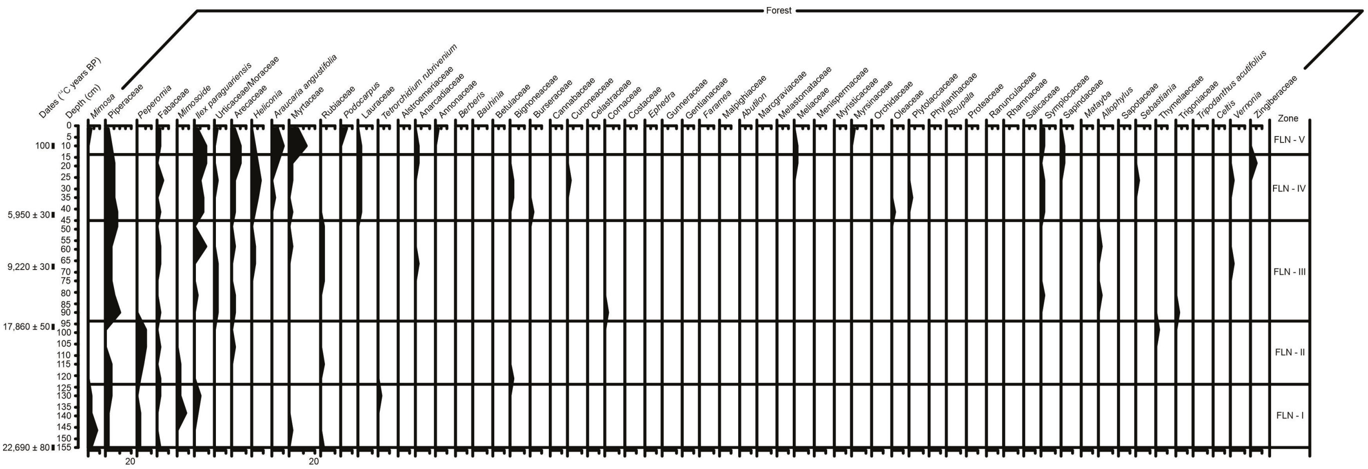

Figure 6. Percentage summary palynological diagram of FLONA de Chapecó – Forest.

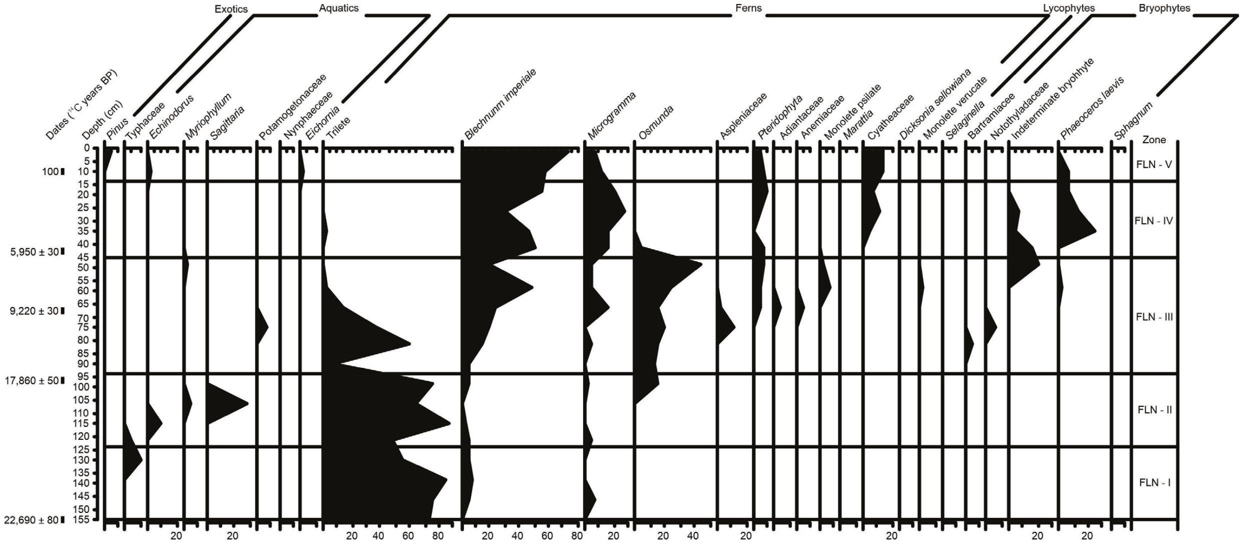

Figure 7. Percentage summary palynological diagram of FLONA de Chapecó – Exotics, Aquatics, Ferns Lycophytes and Bryophites.

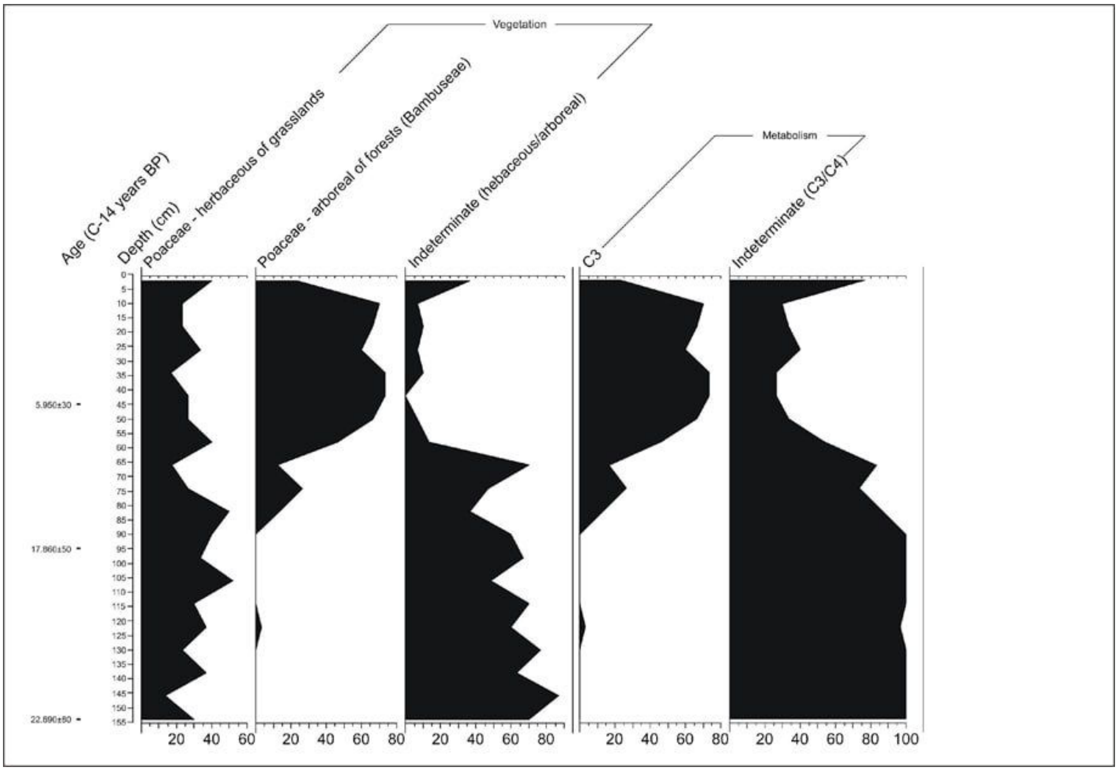

Figure 8. Poaceae pollen percentage diagram from FLONA showing the changes in Poaceae species (herbaceous grassland, arboreal forests (Bambuseae), C3 and C3/C4) during Late Pleistocene and Holocene.

by pollen grains from the family Nymphaeaceae (up to 0.3%) (Figures 4–7).

FLN V. Two samples, from 10 to 2 cm depth, 1,570 cal BP–Present time.

Grassland taxa increase compared to the previous period, reaching a peak (56%) at the top of the sedimentary column, indicating the current plant cover. These taxa are well-represented by the families Poaceae (17.7–33.8%) and Asteraceae (6.9–5.3%) (Figure 5). The first part of this phase has a high pollen percentage of Poaceae pollen from species of arboreal of forests, but this pollen percentage decreases drastically in the final phase. Also is evident a low pollen percentage of species of Poaceae of exclusive C_3 metabolism. Conversely, forest species (up to 60.3%) show a higher percentage at the base of this phase and progressively decrease toward the top. These are represented by the families Myrtaceae (13.8–6%), Piperaceae (3.2–2.3%), and Fabaceae (2.3–2%), as well as the genera *Podocarpus* (up to 4.6%), *Mimosa* (up to 2.3%), species *Araucaria angustifolia* (9.2–4.6%), and *Ilex paraguariensis* (9.5–2.3%). Pollen grains from the genus *Pinus* (up to 5.6%) are also recorded near the top of the sequence, indicating the introduction of exotic species through anthropic action (Figure 6).

Ferns are represented by spores from the species *Blechnum imperiale* (56.5–73.9%) and genera *Microgramma* (7.6–11.6%), as well as the family Cyatheaceae (13–14.5%). Bryophyte spores are represented by the species *Phaeoceros laevis* (up to 5.8%). Aquatic plants are not significantly represented during this period (Figures 4–7).

Although the constrained cluster analysis (CONISS), groups the uppermost samples within the same higher-order cluster as Zone IV, providing limited statistical support for a fully independent Zone V, we retain Zone V because it is defined by the first occurrence and persistent presence/increase of exotic (non-native) taxa, which marks an ecologically meaningful, likely anthropogenic, shift. In other words, the boundary is supported by a biostratigraphic criterion (appearance of diagnostic indicator taxa), even if the dissimilarity separating IV and V is small. Notably, the dendrogram still shows a branching that separates the top assemblages from Zone IV (albeit at low linkage distance), consistent with a discrete change. To acknowledge the modest clustering support while highlighting the exotic-taxa signal, Zone V can alternatively be presented or considered as an interpretative subzone (*e.g.*, FLN-IVa) rather than collapsed entirely into Zone IV.

The expansion of Araucaria Forest and Seasonal Deciduous Forest

Pollen types from the Araucaria Forest (17 pollen types), Seasonal Deciduous Forest (11 pollen types), and species shared by both forests (28 pollen types) were identified in the samples (Table 3). In FLN I, the small forest component (11.2–19.7%) was likely composed of taxa from the Araucaria Forest, such as *Ilex paraguariensis*, *Mimosa* sp., Mimosoideae, *Peperomia* sp., Piperaceae, and Fabaceae. Pollen types from the Seasonal Deciduous Forest are absent in this phase. FLN II is similar to FLN I in terms of the dominance of Araucaria Forest species, but towards the end of this phase, a few pollen types from the Seasonal Deciduous Forest (Rhamnaceae and Trigoniaceae) appear. In FLN III, the Araucaria Forest continues to expand, with species such as *Ilex paraguariensis*, genus *Heliconia* sp., families Piperaceae, Ranunculaceae, and Thymelaeaceae, while pollen types from the Seasonal Deciduous Forest also increase (*e.g.*, Urticaceae/Moraceae, Arecaceae, Burseraceae, and Rhamnaceae).

FLN IV is characterized by the greatest forest expansion in the sequence, primarily of the Araucaria Forest (*Araucaria angustifolia*, *Ilex paraguariensis*, *Heliconia* sp., Zingiberaceae, Oleaceae, *Berberis* sp., Myristicaceae, and Ranunculaceae). The Seasonal Deciduous Forest also expanded, with species such as Arecaceae, Urticaceae, Moraceae, Trigoniaceae, Cunoniaceae, and *Sebastiania* sp. Finally, in FLN V, both the Araucaria Forest and the Seasonal Deciduous Forest show a decline due to anthropic activity at the end of the sequence.

DISCUSSION

The FLN I phase is characterized by a predominance of grassland taxa, indicative of a colder climate than today, as supported by the presence of Ericaceae and Verbena (*e.g.*, Souza & Lorenzi, 2019). However, the presence of taxa such as *Ilex paraguariensis*, the genus *Mimosa*, and the families Fabaceae, Piperaceae, and Myrtaceae suggests the existence of Araucaria Forest patches, associated with relatively humid conditions. This facilitated the maintenance of a Campos (grassland)–forest mosaic.

At the end of this phase, an increase in moisture is evidenced by the presence of the Typhaceae family, which includes aquatic plants found in shallow water, although in low concentrations. Studies conducted in both the highlands and lowlands of southern Brazil also indicate a predominance of Campos (grasslands) at the end of the Pleistocene (Bauermann, 2003; Behling *et al.*, 2004, 2005; Ledru *et al.*, 2005, 2009; Spalding & Lorscheitter, 2015), including the interior lowlands of the South American continent (Behling *et al.*, 2005; Prieto, 2000).

During the FLN II phase, the significant decrease in forest taxa, along with the increase in the Ericaceae family and the aquatic genus *Echinodorus*, suggests a climate that was even colder and more humid than in the previous phase. High humidity levels during this period have also been observed in the lowlands of Uruguay (Mourelle *et al.*, 2017), where evidence of riparian woodland development during glacial times has been documented, as well as isolated trees and shrubs in the lowlands of western Rio Grande do Sul (Behling *et al.*, 2005).

During the FLN III phase, no major changes are observed in the local palynological record. However, some climatic oscillations can be noted, such as the expansion and contraction of Campos (grassland vegetation) and certain forest taxa (*e.g.*, *Ilex paraguariensis*), as well as the presence of *Gomphrena*, a genus common in warmer environments (Trinta *et al.*, 1997). The first peak of *Ilex paraguariensis* and other forest taxa occurs near the Early–Middle Holocene transition (~9,000 BP), reflecting increased temperature and humidity; this is especially evident in the overall rise of forest cover from ~7,000 BP onward, which marks the transition to the next phase. Bryophytes, represented by the Notothyladaceae and Bartramiaceae families, appear in the record for the first time, also signaling an increase in moisture. The rise in the percentage of pteridophyte spores, primarily from the Aspleniaceae family and the genera *Blechnum* and *Osmunda*, corresponds to fluctuating periods of increased humidity (Tryon & Tryon, 1982).

Notably, certain periods show alternating patterns, with aquatic species peaking at specific intervals, while a decline in forest taxa suggests episodes of lower average temperatures with high humidity, as well as brief warming events. A similar warming trend during the Early Holocene has been observed in the highlands of Santa Catarina (*e.g.*, Behling & Oliveira, 2017).

The vegetation taxa present in the early stage of this phase suggest a predominantly cold climate, yet with sufficient humidity to sustain wetland environments, as evidenced by the presence of the genus *Eryngium* (cf. Souza & Lorenzi, 2019). The onset of this phase may be correlated with the end of the Last Glacial Maximum, which occurred around 18,000 BP (Suguio, 1999), followed by a subsequent climatic improvement starting around 10,000–8,000 BP.

FLONA Phase IV marks a period of significant climate change (after 7000 BP). Forests advanced, possibly expanding from valley bottoms and isolated patches (Figure 4). Grassland taxa decreased, while bryophytes such as *Phaeoceros laevis*, a wetland species characteristic of permanently moist environments, increased, indicating sustained humidity (Menéndez, 1987). The species *Ilex paraguariensis* and families Myrtaceae and Lauraceae show a significant increase in the palynological record. The predominance of *Microgramma* sp. further supports the evidence of a forested environment. Additionally, the Lauraceae family and the genus *Cyathea*, which requires shade for full development, were identified. *Araucaria angustifolia* first appears at ~35 cm depth (~5,500 BP), after which its abundance increases, extending its range and becoming progressively more dominant. The palynological composition as a whole indicates an ecotone between Araucaria Forest (today largely above ~600 masl) and the Upper Paraná Forest (predominantly below this elevation), consistent with rising temperature and humidity approaching modern conditions characterized by high rainfall and brief or absent dry periods (Bauermann *et al.*, 2009).

The climatic amelioration near 7,000 BP aligns with signals from the upper Uruguay River lowlands adjacent to FLONA, where Araucaria Forest reaches ~20% of palynomorphs at ~7,500 BP, followed by an expansion of Deciduous Forest (Loponte *et al.*, 2024). After 7,000 BP, Figure 4 shows a gradual expansion of Araucaria Forest throughout the Late Holocene in FLONA area.

The final phase, FLN V, likely represents the centuries leading up to European colonization (< 500 BP) and the entire historical period in western Santa Catarina, when the region was populated by European immigrants. The sudden decline in forest taxa and the expansion of grassland species appear to be linked to extensive deforestation associated with the so-called economic wood cycle (Belani, 1991; Bavaresco, 2017; Salini, 2018).

This modern-era deforestation has also been observed by Behling *et al*. (2016) in the Caçapava do Sul region, by Secchi (2017) in the Arvorezinha region, and by Behling *et al*. (2004) in the Cambará do Sul region. Evidence of human impact during the historical period is further supported by the presence of *Pinus* sp. at the top of the sedimentary core, introduced to the area around 1900 CE to restore wood resources that had been virtually depleted in the previous economic cycle. Pollen grains of *Pinus* sp. have also been found in pollen records from the southern highlands and lowlands, dating to the last ~150 years BP (Behling, 1995, Behling, 1995, Behling *et al*., 2005, 2007; Lima, 2010; Behling & Oliveira, 2017; Jeske-Pieruschka *et al*., 2012; Radaeski *et al*., 2023). In western Santa Catarina, the planting of *Pinus* sp., encouraged by the federal government, began in the 1960s (Moretto, 2016). Following this period, the appearance of *Podocarpus* sp. and *Dicksonia sellowiana* in the palynological record marks the establishment of the current natural forest.

CONCLUSIONS

The pollen record from the FLONA region documents vegetation dynamics over the last 27,000 BP in a western sector of southern Brazil, where palynological studies remain scarce. The results indicate fluctuations in temperature and humidity toward the end of the Pleistocene, with the Last Glacial Maximum peaking around 20,000–18,000 BP. Notably, even at the close of the Pleistocene, small, isolated forest patches persisted, fluctuating with climatic shifts. During the Holocene, Araucaria Forest began to expand ca. 9,000 BP and increased progressively after 7,000 BP. This trajectory accords with evidence for rising temperature and humidity in the adjacent Uruguay River valley (Loponte *et al*., 2024) and with the expansion of Araucaria along the margin of the southern plateau; by contrast, in the Atlantic-influenced region this expansion occurred later (*e.g*., Behling, 1995; Jeske-Pieruschka *et al*., 2012; Lima, 2010; Oliveira *et al*., 2008). The early expansion at FLONA was followed by the spread of Seasonal Deciduous Forest, whereas the final retreat of both formations likely reflects intensive colonization over the past two centuries and the advance of the modern agricultural frontier.

DATA AVAILABILITY STATEMENT

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

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AUTHOR CONTRIBUTIONS

Ivan Luís Kirchner Eidt: writing – original draft, editing, visualization, investigation, formal analysis, software, resources, data curation. Mirian Carbonera: writing – review, data curation, conceptualization, resources. Gisele Leite de Lima Primam: editing, visualization, investigation, formal analysis, software, data curation. Jefferson Nunes Radaeski: investigation, formal analysis, data curation. Soraia Girardi Bauermann: formal analysis, data curation. Guilherme Luiz Girardi: data curation. Cristina Gouvêa Redin: data curation. Daniel Loponte: writing – original draft, editing, visualization, formal analysis, data curation. 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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