



## The last 25,000 years in the Eastern Plateau of Southern Brazil according to Alpes de São Francisco record

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### ABSTRACT

The palaeoenvironmental history has been studied based on palynology of a sedimentary profile from the Alpes de São Francisco bog (29°29'35''S, 50°37'18''W), São Francisco de Paula municipality, Rio Grande do Sul eastern Plateau, extreme Southern Brazil. The results indicate a regional cold and dry climate between 25,000 and 12,500 yr BP, interpreted from the grassland vegetation, forest taxa were present in refuges and the shallow local lake began to fill in. Climatic conditions became more aride after 16,000 yr BP, when grassland became rare. From 12,500 yr BP onwards, the climate began to change and at 11,000–9700 yr BP a warm and moist climate permitted the slight migration of pioneer arboreal taxa from refuges and locally a marsh formation. Between 9700 and 6500 yr BP a warm and dry climate resulted in reduction of grassland, confined the forest in refuges, dried out the marsh. The gradual increase of humidity between 6500 and 4000 yr BP allowed migration of forests from refuges and a bog developed. Between 4000 and 2000 yr BP *Araucaria* forest spread, indicating moister climate. The local bog expanded. From 2000 yr BP onwards, humid but warmer climate seems to result in a lower reproductive capacity of *Araucaria* forest taxa limiting its expansion. The bog reached the present-day in a decline condition. The results are compared to previous records from Southern Brazil highlands and some places from Argentina in order to better elucidate the climatic and vegetational history of these important South America areas during the late Quaternary.

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### 1. Introduction

The eastern undulated Plateau of Serra Geral in the Southernmost State of Brazil, Rio Grande do Sul, is an extensive mosaic of grassland, *Araucaria* forests and bogs (Rambo, 1956a; Hueck, 1972) at present heavily impacted by human activities (IBGE, 1982). This region is influenced by both, advection warmer climates from the northern areas of Brazil and by cold climate from Southern South America, making it a very sensitive area for the study of past regional changes. The proximity of the eastern Plateau (about 1000 m high) to the adjacent Coastal Plain results in elevated moisture, with precipitation between 1750 and 2500 mm, the highest amounts in South Brazil (IBGE, 1982; Nimer, 1989). There is no dry season and the high oceanic humidity spreads to the Plateau with gradual reduction until about 10 km distance inland. The annual average temperature is about 12–14 °C. The warmer month (January) has an average temperature of about 20 °C. July, the coldest month, registers an average temperature of ca. 6 °C (Nimer, 1989).

Studies from present-day vegetation provided important information about the eastern Plateau history of the last millennia. According to those studies the grassland is a probable relict of late Quaternary semi-arid climate unrelated to humid modern environment. Furthermore, *Araucaria* forest is still expanding because of the increase of moisture in the last millennia (Rambo, 1953; Veloso, 1962; Hueck, 1972; Klein, 1975). In recent years, some palynological studies have advanced the understanding of the last millennia palaeoenvironments in Rio Grande do Sul eastern Plateau (Roth and Lorscheitter, 1993; Behling et al., 2001, 2004; Behling and Pillar, 2007) and in other Southern Brazilian highlands (Behling, 1995, 1997, 1998, 2002). This paper adds new information to further elucidate the last 25,000 years of history of climate and vegetation of this region.

### 2. Study site

#### 2.1. Geographical setting

The site is situated in the locality of Alpes de São Francisco at 911 m elevation in the São Francisco de Paula municipality, southernmost highland region of Serra Geral, Southern Brazil (Rio Grande do Sul eastern Plateau). The site is formed by a bog

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(pH value 4.5) located in an elongated and sinuous basin of 880 m length and a maximum of 230 m width, surrounded by an *Araucaria* forest and grassland, near a canyon (29°29'35"S, 50°37'18"W), Fig. 1.

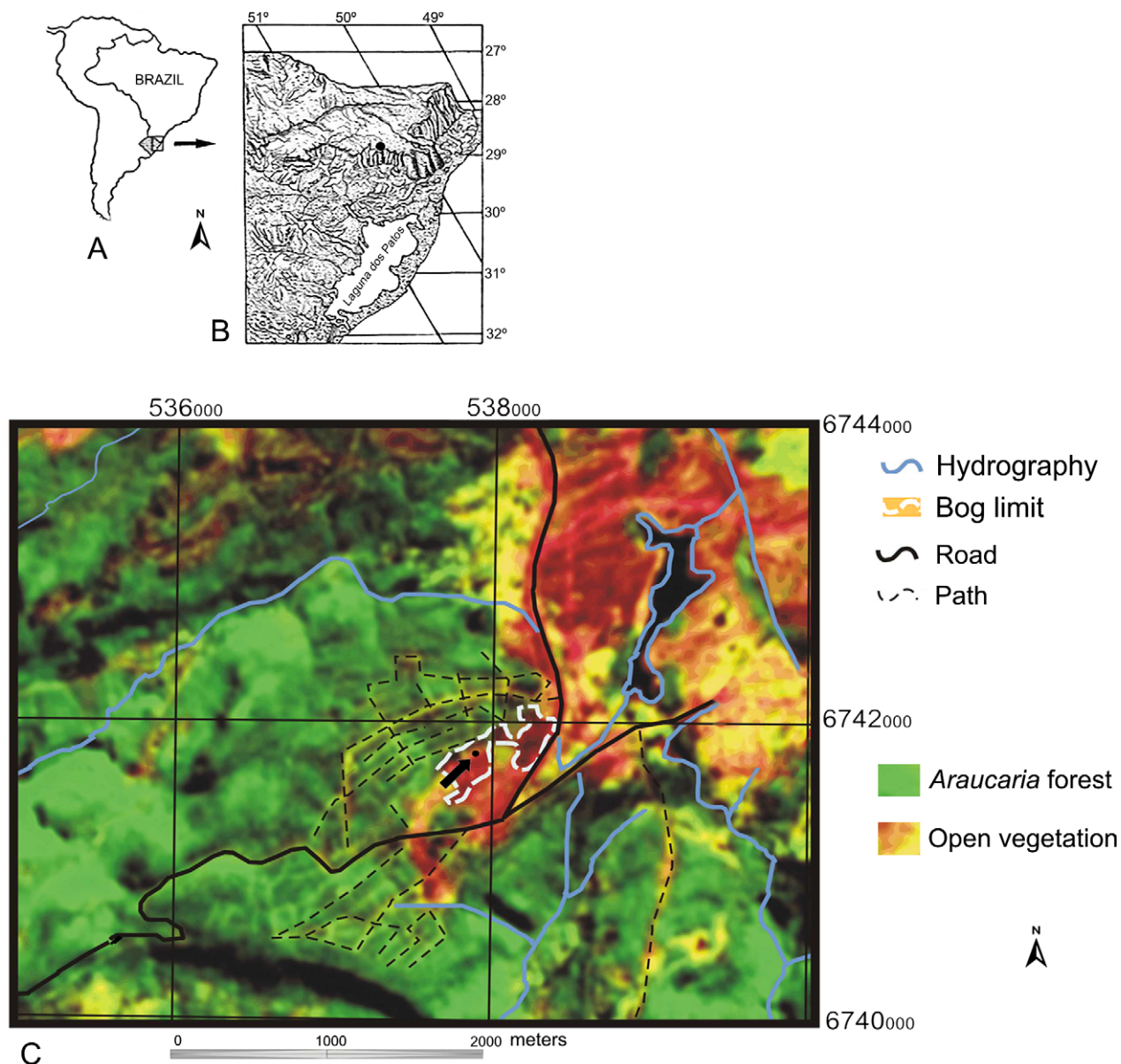
## 2.2. Flora

The main species of the bog are *Sphagnum cuspidatum* var. *recurvum* (P. Beauv.) Wilson, *Polytrichum juniperinum* Will. Ex Hedw., *Blechnum* cf. *imperiale* (Fée & Glaziou) H. Chr., *Eriocaulon gomphrenoides* R. Kunth, *Xyris teres* Nilsson and *Utricularia* spp., besides *Alstroemeria isabellina* Herb., *Blechnum cordatum* (Desv.) Hieron., *Hippeastrum santacatarina* (Traub) Dutilh, *Ludwigia* sp., *Lycopodiella alopecuroides* (L.) Cranfill, *Osmunda regalis* L., *Polygala linoides* Poir., *Siphocampylus* cf. *verticillatus* G. Don. and many plants of Cyperaceae. On one side of the bog *Araucaria* forest expands composed mainly by *Araucaria angustifolia* (Bertol.) Kuntze, *Dicksonia sellowiana* Hook., *Drimys brasiliensis* Miers, *Ilex paraguariensis* A. St.-Hil.,

*Podocarpus lambertii* Klotzsch ex Endl., *Myrsine lorentziana* (Mez) Arechav., besides *Acca sellowiana* (O. Berg) Burret and other Myrtales. Bromeliaceae, Orchidaceae and Hymenophyllaceae epiphytes are abundant in the forest. On the other side of the bog, grassland, composed mainly by Poaceae, Asteraceae and *Eryngium*, expands. Some grassland species have invaded the bog, such as *Briza calotricha* (Trin.) Hack., *Paspalum polyphyllum* Nees ex Trin., *Saccharum asperum* (Nees) Steud. and rare *A. angustifolia* plants.

## 3. Methods

The 286-cm-long sedimentary profile was collected in the deepest portion of the bog basin with a Hiller corer for palynological analysis and for  $^{14}\text{C}$  dating samples. The chemical pretreatment was performed using HCl, HF, KOH and acetolysis, after sieving through a 250  $\mu\text{m}$  mesh (Faegri and Iversen, 1989). *Lycopodium clavatum* L. tablets (Stockmarr, 1971) were added to calculate palynomorph concentration/cm $^3$ . The slides were mounted in



**Fig. 1.** South America map showing Rio Grande do Sul at southern Brazil (A), Alpes de São Francisco locality (●) at the eastern Plateau (B) and the location of the bog with sedimentary profile point (→ ● 29°29'35"S, 50°37'18"W) in a satellite image of Alpes de São Francisco (C).

glycerol-jelly. Taxonomic identification was based on the reference collection of the Palynology Laboratory, Botany Department of Federal University of Rio Grande do Sul. Unidentified palynomorphs were classified by morphology and/or number. The word “type” was used when a precise identification was impossible. A minimum number of 500 grains from regional taxa (grassland, forest and plants from indeterminate environments) and 100 exotic spores of *L. clavatum* L. were counted for each sample, excluding local taxa (aquatic plants, herbaceous marsh plants), fungi, exotic plants and other palynomorphs that were counted in parallel.

Palaeoenvironmental interpretation was based on all regional and local taxa, including fungal palynomorphs. For regional and local taxa the percentage of each taxon was calculated using the total pollen sum of the respective group. The percentages of algae, fungi, other palynomorphs and exotic pollen (not included in the pollen sum) were calculated as the following:

For algae: total of algae + local taxa.

For fungi: total of fungi + regional and local taxa.

For other palynomorphs: total of other palynomorphs + local taxa.

For exotic pollen: total of the exotic pollen + regional taxa.

Four <sup>14</sup>C dates provided by Beta Analytic Inc., Miami, Florida, USA were used to estimate ages. Tilia and Tilia Graph software

**Table 1**  
Radiocarbon dates for Alpes de São Francisco sedimentary profile.

Sample depth (cm)	Conventional ages ( <sup>14</sup> C yr BP) <sup>a</sup>	<sup>13</sup> C/ <sup>12</sup> C	Calendar age (yr BC) (cal yr BP) <sup>b</sup>	Lab. number
25	4140 ± 40	−25.1 o/oo	2880–2580	Beta 211188
63	6940 ± 40	−22.9 o/oo	5900–5730	Beta 248984
127	11830 ± 70	−25.0 o/oo	12130–11540	Beta 189287
273	24920 ± 180	−25.6 o/oo		Beta 194784

<sup>a</sup> C-13 adjusted.

<sup>b</sup> 2σ, 95% probability, beta analytic, Miami, Florida.

**Table 2**  
Palynomorphs found in the sedimentary profile counts of Alpes de São Francisco bog.

Grassland (regional)	<i>Agarista</i> D. Don ex G. Don, <i>Alternanthera</i> Forssk. 1, <i>Alternanthera</i> Forssk. 2, <i>Amaranthus</i> L. – Chenopodiaceae type, <i>Baccharis</i> L. type, Caryophyllaceae, <i>Cuphea carunculata</i> Koehne, Ericaceae type, <i>Gnaphalium</i> L. type, <i>Iresine</i> P. Browne type, Mutisieae 1, Mutisieae 2, Mutisieae 3, Mutisieae 4, <i>Plantago</i> L., Poaceae, <i>Polygonum</i> L., Scrophulariaceae type, <i>Verbena</i> L., <i>Vernonia</i> Schreb. type, <i>Vicia</i> L. type
Forest (regional)	<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg., <i>Allophylus edulis</i> (A. St.- Hil., Cambess. & Juss.) Radlk., Anacardiaceae, <i>Araucaria angustifolia</i> (Bertol.) Kuntze, <i>Bauhinia forficata</i> subsp. <i>pruinosa</i> (Vogel) Fortunato & Wunderlin, Bignoniaceae, <i>Celtis</i> L., <i>Chrysophyllum</i> L., Cyatheaceae, <i>Dicksonia sellowiana</i> Hook., <i>Drimys brasiliensis</i> Miers, <i>Evolvulus</i> L. type, <i>Huperzia</i> Bernh., <i>Hymenophyllum</i> Sm. type, <i>Ilex</i> L., Meliaceae type, <i>Microgramma vacciniifolia</i> (Langsd. & Fisch.) Copel. type, <i>Mimosa scabrella</i> Benth. type, <i>Myrsine</i> L., Myrtaceae, <i>Pleopeltis angusta</i> Humb. & Bonpl. ex Willd. type, <i>Podocarpus lambertii</i> Klotzsch ex Endl., <i>Polypodium</i> L. type, <i>Pteris</i> L., <i>Roupala</i> Aubl., Sapindaceae, <i>Trema micrantha</i> (L.) Blume, Urticales
Plants from indeterminate environment (regional)	<i>Cephalanthus</i> L., Cucurbitaceae, <i>Eryngium</i> L., Euphorbiaceae 1, Euphorbiaceae 2, <i>Galium</i> L. type, indeterminate monoletes, indeterminate pteridophytes, indeterminate tricolpates, indeterminate tricolporates, indeterminate triletes, Lamiaceae, Lamiaceae type, Liliaceae 1 type, Liliaceae 2 type, Malvaceae, Melastomataceae, <i>Mimosa</i> L., <i>Mimosa</i> ser. <i>Lepidotae</i> Benth. 1, <i>Mimosa</i> ser. <i>Lepidotae</i> Benth. 2, <i>Mimosa</i> ser. <i>Lepidotae</i> Benth. 3, Rosaceae 1, Rosaceae 2, Rubiaceae 1, Rubiaceae 2, Rubiaceae 3, tricolporate 1, tricolporate 2, triporate 1, <i>Valeriana</i> L.
Aquatic plants (local)	Alismataceae, <i>Botryococcus</i> Kützing, <i>Debarya</i> (De Bary) Wittrock, <i>Eichhornia</i> Kunth, <i>Isoëtes</i> L., <i>Mougeotia</i> C. A. Agardh, <i>Myriophyllum</i> L., <i>Pseudoschizaea rubina</i> Rossignol ex Christopher, <i>Spirogyra</i> Link, <i>Zygnema</i> C. A. Agardh
Herbaceous marsh plants (local)	<i>Aspiromitus punctatus</i> (L.) Schljakov, <i>Blechnum</i> cf. <i>imperiale</i> (Fée & Glaziou) H. Chr., <i>Blechnum</i> L. type, Cyperaceae, Eriocaulaceae, indeterminate bryophytes, <i>Ludwigia</i> L., <i>Lycopodiella alopecuroides</i> (L.) Cranfill, <i>Lycopodiella cernua</i> (L.) Pic. Serm. type, <i>Lycopodium clavatum</i> L. type, <i>Osmunda</i> L., <i>Phaeoceros laevis</i> (L.) Prosk., <i>Polygala</i> L., <i>Selaginella marginata</i> (Humb. & Bonpl. ex Willd.) Spring, <i>Sphagnum</i> L., <i>Typha</i> L., <i>Utricularia</i> L.
Fungi	<i>Athelia</i> Persoon type, <i>Bryophytomyces sphagni</i> (Navashin) Cif., <i>Gaeumannomyces</i> cf. <i>caricis</i> J. Walker type, <i>Gelasinospora adjuncta</i> Cain, <i>Glomus</i> Tus. & C. Tus., hyphae, indeterminate fungi, <i>Spirotremesporites multiplex</i> Dueñas type, spore 1, spore 2, spore 3, spore 4
Exotic plants	<i>Alnus</i> Mill., <i>Nothofagus</i> Blume
Other palynomorphs	Spermatophore of Copepoda, Palynomorph 1, Palynomorph 2, Palynomorph 3

were used to construct the diagrams. Cluster analysis was performed by using CONISS (Grimm, 1987) proving the bases for zoning the diagram. Although the analysis included all palynomorphs, the percentage and concentration diagrams present only selected taxa. However, the group sum diagram includes all components of the group. To estimate past richness of the regional taxa rarefaction analysis of the samples was performed to obtain a standardized sample effort (*Excel for Windows* software), following Chi-square ( $\chi^2$ ) analysis with  $P < 0.001$  and presented in a graph.

#### 4. Results

The <sup>14</sup>C dates are listed in Table 1; all taxa counted are listed in Table 2; richness of regional taxa is plotted in Fig. 2; percentage diagrams and dendrogram in Fig. 3 and concentration diagrams in Fig. 4. Three zones were identified in the palynological diagrams based on taxa curves and cluster analysis (Fig. 3).

ZONE I (280–175 cm depth, 25,000–16,000 <sup>14</sup>C yr BP, nine samples) is composed of brown clayed-sands, compact at the base changing to brown-gray sandy-clays at the center towards the top (175 cm). The regional taxa richness declines towards the upper part of the zone and includes some of the lowest values of the record (Fig. 2). Grassland taxa dominate (79–92%) and forests taxa are present in low percentages (1–3%) (Fig. 3). Grassland taxa concentration is low at the base of the zone, increasing gradually towards the upper portion (Fig. 4). Poaceae (30–62%) are the main grassland component, followed by *Baccharis* type (8–53%), *Plantago* (8–15%) and *Vernonia* type (0.4–2%). In the upper portion of the zone Poaceae show a marked percentage decrease, before increasing at the top; *Baccharis* type shows opposite trend. *Amaranthus*-Chenopodiaceae type, Mutisieae 1, Mutisieae 2, Caryophyllaceae, *Vicia* type, *Cuphea carunculata*, Scrophulariaceae type, *Iresine* type, Mutisieae 3, Mutisieae 4, Ericaceae type, *Alternanthera* 1 and *Alternanthera* 2 are found in trace amounts (Figs. 3 and 4). Forest taxa are present with their lowest percentages and concentrations of the record (Figs. 3 and 4): Myrtaceae (0–0.4%), *P. lambertii* (0–0.4%) and *Huperzia* (0–0.4%), with rare amounts of *Myrsine*, *Alchor-*



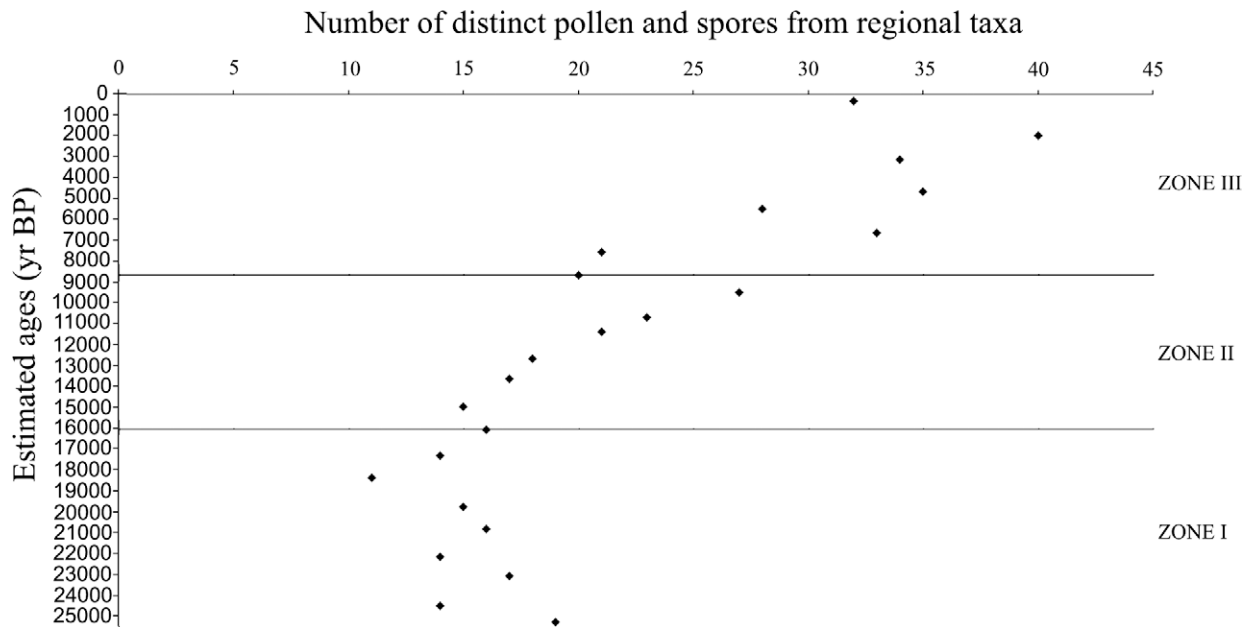


Fig. 2. Richness of the regional taxa in the samples of the palynological profile from Alpes de São Francisco bog.

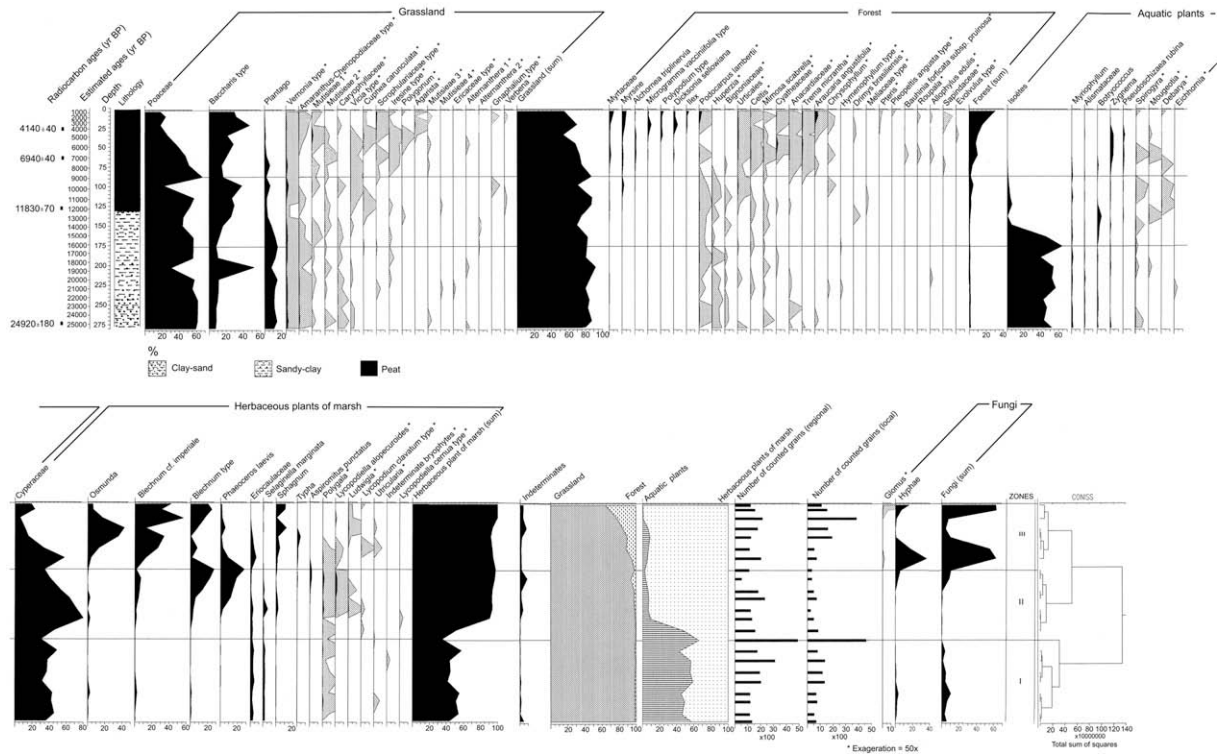
*nea triplinervia*, *Microgramma vacciniifolia* type, *D. sellowiana*, Bignoniaceae, Urticales, *Celtis*, *Mimosa scabrella*, Cyatheaceae, Anacardiaceae, *Trema micrantha*, *A. angustifolia*, *Chrysophyllum*, *Hymenophyllum* type and *Allophylus edulis*. Other plants from indeterminate environment (not shown in diagrams) are *Eryngium* (5–13%), indeterminate tricolporates (0.4–2%) and Liliaceae 2 type (0.3–2%), besides *Galium* type, indeterminate monoletes and triletes, indeterminate tricolpates, Lamiaceae, Liliaceae 1 type, Malvaceae, Melastomataceae, *Mimosa*, *Mimosa* ser. *Lepidotae* 1, *Mimosa* ser. *Lepidotae* 2, Rosaceae 1, Rosaceae 2, Rubiaceae 2, Rubiaceae 3, tricolporate 1, tricolporate 2 and *Valeriana*.

This zone is characterized by abundant local taxa in the percentage diagrams including aquatic plants (43–66%) and herbaceous marsh plants (34–57%) (Fig. 3). The concentration values of these indicators increase towards the top (Fig. 4). *Isoëtes* (39–64% and high concentration) is the main aquatic indicator, more abundant at the top of the zone. Other aquatic taxa occur with lower percentage and concentration: *Myriophyllum*, Alismataceae, *Botryococcus*, *Zygnema*, *Pseudoschizaea rubina*, *Spirogyra*, *Mougeotia* and *Eichhornia* (Figs. 3 and 4). The herbaceous marsh plants, less represented than the aquatic ones, show a gradual concentration increase towards the top of the zone (Fig. 4). Cyperaceae are dominant (30–49%, with high concentration, Figs. 3 and 4). With marked lower percentage are Eriocaulaceae (2–5%) and *Selaginella marginata* (0.4–2%). *Osmunda*, *Blechnum* cf. *imperiale*, *Blechnum* type, *Phaeoceros laevis*, *Sphagnum*, *Polygala*, *Utricularia* and indeterminate bryophytes are in trace amounts (Fig. 3). Fungal spores show low percentages (0.2–11%), hyphae (0.4–3%) and very low concentrations (Figs. 3 and 4). Indeterminate fungi (0.1–6%), rare *Athelia* type, *Bryophytomyces sphagni*, *Spirotremesporites multiplex* type, spore 1 and spore 2 occur (not shown in diagrams). Trace amounts of the exotic *Alnus* pollen, from the Andes were found (not shown in diagrams).

ZONE II (175–85 cm depth, 16,000–8600 <sup>14</sup>C yr BP, seven samples) is composed of brown-gray to light gray clay sediment at the base and black organic-rich peat at the upper half becoming sandy and liquid at the top of the zone. The richness of regional taxa increases markedly from the base to the upper part of the zone (Fig. 2). Grassland taxa (70–88%) dominate the regional component (like in the previous zone, Fig. 3) but their concentration is

markedly lower in the bottom of the zone, with a pronounced increase in the center (the highest of the profile), and declining to the top of the zone (Fig. 4). Poaceae (22–67%) and *Baccharis* type (12–39%) are dominant. Poaceae reach the highest percentages of the record at the top of this zone. *Baccharis* type increases gradually along this section, with lower percentage at the top of the zone (Fig. 3). Poaceae and *Baccharis* type concentrations are higher in the central portion of the zone and decline markedly above (Fig. 4). The percentages of *Plantago* (2–12%) decrease gradually in the zone. Other taxa with low amounts are *Vernonia* type, *Amaranthus*–Chenopodiaceae type, Mutisieae 1, Mutisieae 2, Caryophyllaceae, *Vicia* type, *C. carunculata*, Scrophulariaceae type, *Iresine* type, *Polygonum*, Mutisieae 4, *Alternanthera* 2, *Gnaphalium* type and *Verbena* (Fig. 3). In contrast to the grassland group, the forest components (1–7%) are poorly represented in this zone. Their percentages increase to the top (Fig. 3), but concentration is higher in the center of the zone (Fig. 4). Such as with grassland indicators, this increase is followed by a marked decline, with low concentrations towards the end of the zone (Fig. 4). The main components are Myrtaceae (0.1–0.6%), *Myrsine* (0.2–3%), *Ilex* (0–0.3%) and *P. lambertii* (0.1–0.3%) (Figs. 3 and 4). Other forest taxa with low amounts are *A. triplinervia*, *M. vacciniifolia* type, *Polypodium* type, *D. sellowiana*, *Huperzia*, Bignoniaceae, Urticales, *Celtis*, *M. scabrella*, Cyatheaceae, Anacardiaceae, *T. micrantha*, *Chrysophyllum*, *D. brasiliensis* and Meliaceae type (Figs. 3 and 4). Plants from indeterminate environment (not shown in diagrams) are markedly lower compared to other groups but somewhat higher represented in the center of this zone. *Eryngium* (4–23%) is the main component. Other taxa of this group, occurring in low amounts, are *Valeriana* (0.4–3%) and indeterminate tricolporate (0.7–6%). Rare amounts of Euphorbiaceae 1, *Galium* type, indeterminate monoletes and triletes, indeterminate tricolpates, Lamiaceae, Liliaceae 1 type, Liliaceae 2 type, Malvaceae, Melastomataceae, *Mimosa*, *Mimosa* ser. *Lepidotae* 1, Rubiaceae 1, tricolporate 2 and triporate 1 are found in this zone.

*Isoëtes* (0.4–64%) is the main aquatic component in the lower portion of the zone, but decreases towards the top, with a slight increase in the central portion, presenting very low percentages and concentrations in the rest of this zone (Figs. 3 and 4). *Botryococcus* is present in very low percentages (0–5%), with a slight increase in

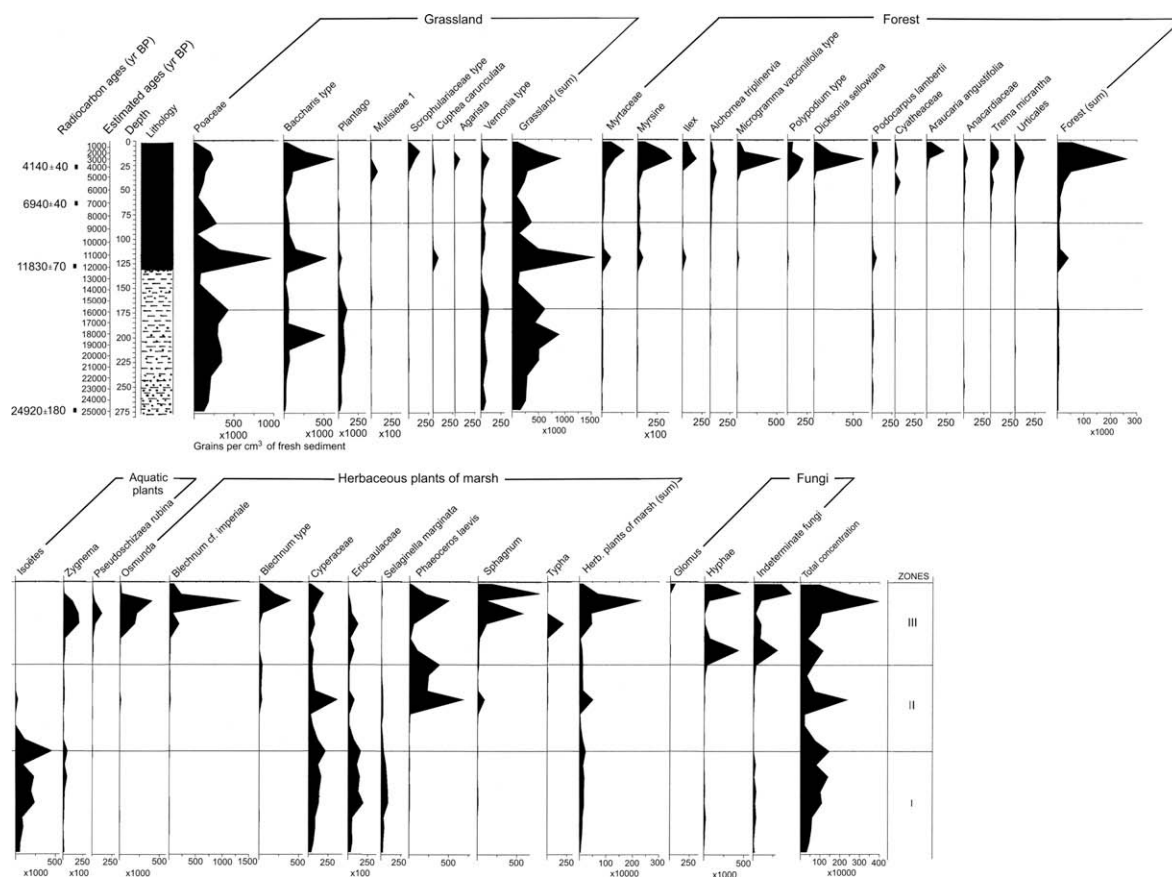


**Fig. 3.** Palynological percentage diagrams for the sedimentary profile from Alpes de São Francisco bog, including chronology, depth, lithology, indicators of grassland, forest, aquatic plants, herbaceous marsh plants, composite diagrams, number of counted grains, fungi, zones and dendrogram.

the central portion. Other rare aquatic indicators in this zone are *Myriophyllum*, *Alismataceae*, *Zygnema*, *P. rubina*, *Spirogyra*, *Mougeotia* and *Debarya* (Figs. 3 and 4). In contrast to the previous zone, there is a marked increase of the herbaceous marsh plants (34–97%) coinciding with a decrease in the aquatic component (Fig. 3). Some herbaceous marsh plants are present in higher concentrations at the center of the zone (Fig. 4). Cyperaceae (35–80%) increase compared to the previous zone and are the main component of the marsh group, with the highest frequencies of the profile in this zone. Cyperaceae concentration is the highest of the profile in the central portion, with a pronounced decline in the upper portion. In contrast, there is an increase in the percentages of *Blechnum* cf. *imperiale* (0.2–7%), *Blechnum* type (0.2–27%) and *P. laevis* (0–28%) in the upper portion of this zone. *Osmunda* (0–3%), *Eriocaulaceae* (0.8–3%), *S. marginata* (0.2–5%) and *Sphagnum* (0–2%) are better represented at the central portion of the zone (Figs. 3 and 4). Other taxa in low amounts are *Typha*, *Aspiromitus punctatus*, *Polygala*, *L. alopecuroides*, *Ludwigia*, *L. clavatum* type and *Lycopodiella cernua* type (Fig. 3). The percentages of fungi are lower than in the previous zone (0.1–11%), increasing in the upper portion of the zone (Fig. 3). The main components are hyphae (0–6%) and indeterminate fungi (0–5%). Present with very low percentages are *Athelia* type, *Gaeumannomyces* cf. *caricis* type, *Gelasinospora adjuncta*, spore 1 and spore 2 (not shown in diagrams). Trace amounts of *Alnus* and *Nothofagus* from the Andes are found (not shown in diagrams).

**ZONE III** (85–0 cm depth, 8600 <sup>14</sup>C yr BP – present-day, eight samples) is composed of brown friable peat, with abundant plant remains. The richness of regional taxa increases markedly in this zone and reaches its highest values of the record in the upper portion, decreasing at the top (Fig. 2). The grassland dominates the regional taxa in terms of percentage (54–87%), decreasing towards the top (Fig. 3). They show a high increase in concentration at

the upper portion of the zone and a marked decrease at the top like in percentage; the primary components are mainly Poaceae (18–67%) and *Baccharis* type (15–49%) (Figs. 3 and 4). *Plantago* gradually decreases along the zone (Fig. 3) showing very low concentrations. Other taxa present in low amounts are *Vernonia* type, *Amaranthus-Chenopodiaceae* type, *Mutisieae* 1, *Mutisieae* 2, *Caryophyllaceae*, *Vicia* type, *C. carunculata*, *Scrophulariaceae* type, *Iresine* type, *Polygonum*, *Agarista*, *Mutisieae* 3, *Gnaphalium* type and *Verbena* (Fig. 3). The forest components have higher percentages (3–32%) compared to the previous zones, gradually increasing to the top, where its highest percentage of the profile occurs (Fig. 3). However, its concentration increases markedly to the upper portion of the zone with a marked decrease to the top (Fig. 4). The main forest components are *Myrtaceae* (0.1–5%), *Myrsine* (0.5–5%), *A. triplinervia* (0.2–2%), *M. vacciniifolia* type (0–4%), *Polypodium* type (0–4%), *D. sellowiana* (0–5%), *Ilex* (0–3%), *P. lambertii* (0–3%) and *A. angustifolia* (0–3%). Other forest taxa, with lower amounts, are *Huperzia*, *Bignoniaceae*, *Urticales*, *Celtis*, *M. scabrella*, *Cyathea*, *Anacardiaceae*, *T. micrantha*, *Chrysophyllum*, *D. brasiliensis*, *Pteris*, *Pleopeltis angusta* type, *Bauhinia forficata* subsp. *pruinosa*, *Roupala*, *A. edulis*, *Sapindaceae* and *Evolvulus* type (Figs. 3 and 4). There is a gradual increase of forest from the bottom to the upper portion of the zone in composite diagram (Fig. 3). The percentage of the main plants from indeterminate environments (not shown in diagrams) is higher in the upper portion of the zone, decreasing to the top, including *Eryngium* (0.4–11%), indeterminate pteridophytes (0–6%) and indeterminate tricolporates (1–6%). Present with very low percentages are *Cephalanthus*, *Cucurbitaceae*, *Galium* type, indeterminate monoletes and triletes, indeterminate tricolporates, *Lamiaceae*, *Lamiaceae* type, *Liliaceae* 1 type, *Liliaceae* 2 type, *Malvaceae*, *Melastomataceae*, *Mimosa*, *Mimosa* ser. *Lepidotae* 2, *Mimosa* ser. *Lepidotae* 3, *Rosaceae* 2, *Rubiaceae* 1, *tricolporate* 2 and *Valeriana*.



**Fig. 4.** Palynological concentration diagrams for the sedimentary profile from Alpes de São Francisco bog, including chronology, depth, lithology, the main indicators of grassland, forest, aquatic plants, herbaceous marsh plants, fungi, total concentration and zones (taxa with a minimum of 5000 grains/cm<sup>3</sup> of fresh sediment in at least one sample).

The aquatic plants are present in very low percentages (0.5–9%) and low concentrations in the zone, with marked decrease close to the top (Figs. 3 and 4). *Isoetes* occurs only in very low percentages (0–0.3%) at the bottom of the zone. Other rare aquatic components are *Zygnema* (0.1–4%) and *P. rubina* (0–2%), including traces of *Myriophyllum*, *Alismataceae*, *Botryococcus*, *Spirogyra*, *Mougeotia* and *Debaria* (Figs. 3 and 4). The herbaceous marsh plants dominate the local group in concentration, the highest of the whole profile in the upper portion of the zone, diminishing to the top (Fig. 4). Like in the previous zone, they dominate the local group in percentage in the entire zone (91–100%) (Fig. 3). The group includes *Osmunda* (0.9–43%), *Blechnum cf. imperiale* (2–57%), *Blechnum type* (0.5–27%) and *Sphagnum* (0.5–12%), almost all of them are higher values in the upper portion of the zone, decreasing in concentration towards the top, like *P. laevis* (Figs. 3 and 4). Cyperaceae are present with high percentages (6–58%) in the beginning of the zone, diminishing in the upper portion (Fig. 3), but their concentration increases towards the top (Fig. 4). Other taxa with very low amounts are Eriocaulaceae, *S. marginata*, *Typha*, *A. punctatus*, *Polygala*, *L. alopecuroides*, *Ludwigia*, *L. clavatum type* and *Utricularia* (Fig. 3). The herbaceous marsh plants widely dominate the aquatic components in the composite diagram (Fig. 3). Fungi show the highest percentages (5–64%) and the highest concentrations of the profile in this zone, mainly at the bottom and (or) at the top of the zone (Figs. 3 and 4). Hyphae (0.1–37%), indeterminate fungi (2–34%) and spore 2 (0.1–17%) occur. Present with lower percentages are *Glomus* (Fig. 3), besides *Athelia type*, *B. sphagni*, *Gaeumannomyces cf. caricis type*, *G. adjuncta*, spore 1, spore 3 and spore 4 (not shown in diagrams). There are trace amounts of *Alnus* and *Nothofagus* (not shown in diagrams).

## 5. Palaeoenvironmental interpretation

### 5.1. 25,000–16,000 <sup>14</sup>C yr BP (ZONE I)

At 25,000 yr BP (Table 3) the last glacial maximum (LGM) was dominated by treeless grassland suggesting a dry regional climate. The abundance of *Isoetes* indicates presence of a shallow local lake with herbaceous plants growing at the marsh margin (high values of Cyperaceae). Richness of regional taxa was low in this phase (Fig. 2). It is possible that the forest indicators, Myrtaceae and *P. lambertii*, better represented in this phase (but with very low percentage and concentration), represented a shrubby vegetation. Myrtaceae taxa may occur as shrubs or psammophytic shrubs in the modern grassland (Prieto, 2000; Sobral, 2003). *P. lambertii*, a pioneer species, may occur in the present-day in grassland and brushwood (Backes and Irgang, 2002). The low percentage and concentration of these two taxa also could suggest distant refuges, where the microclimate permitted the survival of the forest in a generally unfavorable environment. Refuges in eastern Plateau are possible as gallery forests along the streams or forests close to the margin of canyons.

For eastern Plateau of Southern Brazil, only Behling et al. (2004), Behling and Pillar (2007), in Camará do Sul, show comparable results, with the same general palaeoenvironment interpretation.

Between 22,000 and 16,000 yr BP our data from Alpes de São Francisco show slightly denser vegetation compared to the previous phase based on higher concentration of aquatic taxa, herbaceous marsh plants, grassland taxa especially Poaceae and *Baccharis type* and plants from indeterminate environment. The



aeolian influence seems lower in this phase due to the lower content of sand in the sediment.

### 5.2. 16,000–8600 <sup>14</sup>C yr BP (ZONE II)

From 16,000 yr BP onwards, a depauperate regional and local vegetation suggest generally cold and drier climate. Data show that between 14,000 and 12,500 yr BP this LGM tendency became even more accentuated given very low concentration of aquatic taxa, herbaceous marsh plants, grassland taxa and of various indeterminate environment taxa, fungi and total concentration; also arboreal indicators became extremely rare. Richness of regional taxa was lower (Fig. 2), suggesting a cold and semi-arid conditions. The depauperate grassland seems to have dominated the regional landscape while forest taxa were restricted to refuges (Fig. 4).

This semi-arid scenario between 16,000 and 12,500 yr BP may be comparable to the results of Roth and Lorscheitter (1993) and Behling et al. (2004) from Cambará do Sul (Rio Grande do Sul eastern Plateau) and Rio Grande do Sul Coastal Plain and adjacent areas (Lorscheitter and Romero, 1985; Lorscheitter, 1992, 2003; Leal and Lorscheitter, 2007) and from 22,000 yrs. BP onwards with Rio Grande do Sul western region (Bombin, 1976; Behling et al., 2005). For Serra Geral of Santa Catarina (14,000–10,000 yr BP, Behling, 1995) and for Serra Campos Gerais region, Paraná (12,500 yr BP, Behling, 1997), data show the dominance of subtropical grassland; the *Araucaria* forest would have been preserved only in deep valleys, suggesting a cold and dry climate, also supported by Behling (1998). Other data suggest extensive areas of subtropical grassland in Southern and Southeastern Brazil during the LGM, with small areas of valley and gallery forests, under much lower temperatures than the present and dry conditions, with intense aeolian sediment transport (Ab'Saber, 1977; Behling, 1998, 2002; Lichte and Behling, 1999). In Argentina (Buenos Aires province), south of Rio Grande do Sul, LGM is also characterized by cold and dry or sub-humid-dry or semi-arid climates, with grassland and shrubby dry steppe (Quattrochio and Borromei, 1998; Prieto, 2000). The same dry phase is related to other regions of South America, like Bariloche (Markgraf, 1984) and the south of Tierra del Fuego (Quattrochio and Borromei, 1998).

In Rio Grande do Sul strong dry winds occurred from the southwest throughout the year (Bombin, 1976). The maximum marine regression in the LGM in Rio Grande do Sul is referred to 18,000 yr BP (Villwock and Tomazelli, 1998), with the coastal line as low as the modern isobath of –110 m (Kowsmann et al., 1977). This far more extensive distance to the ocean probably resulted in a profound decrease of moisture over the adjacent Coastal Plain and the Southern Brazilian Plateau. The cold ocean currents reached the coast of Southern Brazil and only from east–west in the Rio Grande do Sul Plateau (Serra Geral) a high mountain barrier promoted some orographic rain in its medium and upper areas (Ab'Saber, 1977).

Between 12,500 and 9700 yr BP the climate became different (Table 3). The evidence indicates a marked environmental change ca. 11,000–9700 yr BP, with expansion of regional and local vegetation (an increase mainly in concentration of herbaceous marsh plants, grassland and forest taxa, some components of plants from indeterminate environment, as well as the total pollen concentration, Fig. 4) showing the beginning of the Holocene. The sediments become markedly richer in organic matter after ca.12,000 yr BP. The results suggest a change to warm and moist climates. The local marsh formation can be seen by the increase in Cyperaceae, herbaceous taxa and small amounts of *Sphagnum*. Higher moisture levels probably accumulated water in some portions of the local marsh, and *Isoetes* reappeared in low frequencies. The richness of regional taxa markedly increased in this phase (Fig. 2). In contrast to the dry phase of the LGM, the increased moisture promoted expansion of grassland. Pioneer forest taxa slightly spread from refuges.

The same environmental change at the beginning of the Holocene is registered in records from Cambará do Sul (Roth and Lorscheitter, 1993), indicating markedly warmer and moister climates than in the previous phase. The accentuated moisture in this phase was also reported from the Coastal Plain and adjacent areas in Rio Grande do Sul (Lorscheitter, 1992, 2003; Leal and Lorscheitter, 2007). According to these references, the pollen concentration of individual taxa increased markedly at the beginning of the Holocene, showing a rapid climatic change, not as clearly seen in percentage diagrams. Indications of regional rainfall increase in highlands of Santa Catarina (Serra da Boa Vista, Behling, 1995), have been suggested based on the expansion of Atlantic rain forest and *Araucaria* forest. In the Paraná region (Serra Campos Gerais, Behling, 1997) the beginning of the Holocene is marked by expansion of grassland in the highlands and the expansion of Atlantic rain forest in the valleys, suggesting a humid climate, as the result of increase of the annual rainfall. However, according to Behling (1997), seasonal dry phases must have occurred to explain the lack of expansion of *Araucaria* forest in highlands of Southern Brazil between the beginning and the middle of the Holocene, different from the results of the same author in Serra da Boa Vista (Behling, 1995).

Evidence of temperature and moisture increase at the beginning of the Holocene was indicated to southwestern of Provincia de Buenos Aires (Quattrochio and Borromei, 1998). The change from dry steppe to humid grassland and the sudden evolution to the marsh environments at the beginning of the Holocene suggest environmental changes with sub-humid to humid climate in the Pampa plains in the eastern Argentina (Prieto, 2000). The humidity increase in this phase was detected to Argentina Pampa northeast (Prieto et al., 2004).

However, many records from Southern Brazil show contrasting climate patterns, ranging from seasonal climate with a long dry annual period lasting until the late Holocene (Cambará do Sul, Rio Grande do Sul, Behling et al., 2004); warm and dry climates until 5000 yr BP, when gallery forest expansion began (São Francisco

**Table 3**  
Survey of climatic and vegetational changes in the eastern Plateau of Rio Grande do Sul, Southern Brazil, according to Alpes de São Francisco palynological profile.

Chronology (yr BP)	Climate	Local environment	Regional landscape
2000–present-day	Warmer and humid	Decline of the bog	Mosaic of <i>Araucaria</i> forest with more difficult expansion over the declined grassland
4000–2000	Warm, more pluviosity and humidity	Bog expansion	Expansion of <i>Araucaria</i> forest over the grassland
6500–4000	Warm with humidity increase	Development of the bog	Migration of the forests from refuges
9700–6500	Warm and dry	Drying marsh	Scarce grassland, forests in refuges
12,500–9700	Warm and moist	Marsh formation	Expanded grassland, slight spread of pioneer arboreal plants from refuges
25,000–12,500	Cold and dry to semi-arid	Shallow lake in a filling up process	Grassland, forests in refuges

de Assis, Rio Grande do Sul, Behling et al., 2005); dry annual season longer in the South and Southeast of Brazil (Behling, 1998); hot and dry climate between 10,000 and 2900 yr BP (Morro da Igreja and Serra do Rio do Rastro, Santa Catarina), but with Atlantic rain forest expansion at the same phase (Serra da Boa Vista), Behling (1995).

The diagrams of Behling et al. (2004) show the rapid increase of *Blechnum* cf. *imperiale* spores ca. 10,000 yr BP, and an accumulation of dark sediments rich in the organic matter, which the authors recognize to reflect a bog environment, that is more related to a humid climate. On the other hand, presence of *P. laevis*, characteristic of humid soils (Menéndez, 1962), was interpreted to originate from the dry soils around the bog, suggesting warm and dry climates (and not warm and humid climates) at the beginning of the Holocene. In the diagrams of Behling et al. (2005), the high total pollen concentration at ca. 10,000 yr BP suggests warm and humid climates and not warm and dry climates. However, the absence of pollen concentration of each taxa does not permit a better comparison.

Then, the results of Alpes de São Francisco are according to the information from distinct southeastern areas of the South America in relation to the increase of temperature and humidity at the beginning of the Holocene. Then, it would be interesting to re-evaluate the results that infer warm and dry climates during this phase in South Brazil. In a similar way, Ybert et al. (2001) suggest a re-interpretation of the results of Morro da Igreja and Serra do Rio do Rastro, showing that the expansion of the Atlantic rain forest about 10,000 yr BP was related to temperature and moisture increase. More information of new records at additional sites, including pollen concentration diagrams, is necessary to clarify this question.

After the moisture increase at the beginning of the Holocene, the environmental conditions suggested a moisture decrease from ca. 9700 yr BP onwards, resulting in a warm and dry climate (Table 3). The data show markedly decreased local and regional vegetation (low concentration of the aquatic taxa, herbaceous marsh plants, grassland and forest taxa, as well as the total concentration, Fig. 4, and the decrease of plants from indeterminate environment, not shown in diagrams). The lower water-table certainly resulted in the drying of the marsh, now surrounded by impoverished grassland. The richness of the regional taxa diminishes (Fig. 2). The forests were confined in the refuges (composite diagram of grassland × forest, Fig. 3).

### 5.3. 8600 <sup>14</sup>C yr BP–present-day (ZONE III)

The dry phase reached 8600 yr BP and it continued until about 6500 yr BP (Figs. 3 and 4). Some increase of temperature can be interpreted from the data during this phase (based on higher fungal frequencies at ca. 7500 yr BP, Figs. 3 and 4).

The same result of a decrease in grassland indicators was inferred from records at Cambará do Sul (Roth and Lorscheitter, 1993), but without a precise chronology. Dry phase, between 7500 and 4000 yr BP was indicated at São Francisco de Paula (Rio Grande do Sul eastern Plateau) by Behling et al. (2001) related to poor pollen preservation in sediments. Other records in high areas from Southern Brazil (Behling, 1995, 1997; Behling et al., 2004) and for western areas of Rio Grande do Sul (Behling et al., 2005) also show this dry climate, but with distinct chronologies. Evidence show a dry climate between 7000 and 5000 yr BP at the lower northeast slope of Serra Geral in Rio Grande do Sul (Leal and Lorscheitter, 2007). The lack of palynological records showing humid conditions at the coast between 8000 and 4000 yr BP is due to the Holocene marine transgression (Lorscheitter, 2003).

The results of Alpes de São Francisco show clear evidence of the dry phase (9700–6500 yr BP) (Table 3). Other distinct chronologies of this phase in the highlands of Southern Brazil are probably due

to the variable micro-regional conditions. In addition new dates are needed to better define the chronology of this dry phase.

Between 6500 and 4000 yr BP data show the progressive return of the regional moisture over the eastern Plateau (Table 3). This condition is more accentuated between 5000 and 4000 yr BP, when local and regional taxa were already abundant (higher concentration of aquatic taxa, herbaceous marsh plants, grassland, forest taxa, the total concentration, Fig. 4, and plants from indeterminate environment).

The richness of the regional taxa increased (Fig. 2). The forest expanded regionally mainly between 5000 and 4000 yr BP, probably migrating from refuges (forest sum and composite diagram of grassland × forest and increase of Myrtaceae, *Myrsine*, *A. triplinervia*, *M. vacciniifolia*, *Polypodium* type, *D. sellowiana*, *T. micrantha* and Urticales, Figs. 3 and 4), but *A. angustifolia* was rare (Figs. 3 and 4). During this humid phase local herbaceous marsh plants expanded (high concentrations of *Osmunda*, *Blechnum* cf. *imperiale* and *Sphagnum*, Fig. 4), as well as algae (the highest concentrations of *Zygnema* and *P. rubina*, Fig. 4). The increase of *Sphagnum* between 5000 and 4000 yr BP indicates transformation of a marsh to a bog.

Data from Alpes de São Francisco are comparable with Cambará do Sul results, that show the same evidence of moisture increase (Roth and Lorscheitter, 1993).

The higher moisture after 5000 yr BP is seen also in other registers from South Brazil (20°S or higher), which had been interpreted to suggest *El Niño* type events resulting in higher precipitation and more stable moisture conditions (Martin et al., 1991; Ybert et al., 2001). About 5000 and 4000 yr BP maximum marine transgression occurred over the adjacent Coastal Plain of Rio Grande do Sul highlands (Kowsmann et al., 1977; Villwock and Tomazelli, 1998), affecting the coastal vegetation (Lorscheitter, 2003). On the other hand, the greater proximity of the ocean certainly resulted in a general increase of moisture on the eastern Plateau.

During 4000–2000 yr BP the vegetation is expanding (Table 3). At ca. 3000–2000 yr BP, precipitation seems to have increased even more. During this phase, the highest regional taxa richness of the last 25,000 years occurred (Fig. 2). The grassland expanded (higher concentration, Fig. 4). However, *Baccharis* type (the major grassland indicator at ca. 3000 yr BP, Figs. 3 and 4), could also be related to shrub taxa, representing an intermediary successional stage between grassland and forest. The forest expanded (the highest concentrations in the profile ca 3000–2000 yr BP, Fig. 4), only now with increase of characteristic taxa of *Araucaria* forest (*A. angustifolia*, *D. sellowiana*, *D. brasiliensis*, *Ilex* and *P. lambertii*, Figs. 3 and 4). Probably the high altitude environments maintained temperatures sufficiently low to favor the *Araucaria* forest expansion.

High amounts of *Sphagnum* indicate the expansion of ombrotrophic bog (highest *Sphagnum* concentration ca. 2000 yr BP, Fig. 4). Aquatic plants were rare in the local flora (composite diagram of aquatic taxa × herbaceous marsh plants, Fig. 3).

From 2000 yr BP to present (Table 3), the percentage diagrams show increase in forest indicators (Fig. 3), although concentration decreased (Fig. 4), suggesting that the *Araucaria* forest and grasslands declined in this interval. *A. angustifolia* was present with about the same low percentages values in last 2000 years but decreased markedly in concentration to the present, like *D. sellowiana*, *Ilex* and other forest taxa (Fig. 4). The richness of the regional taxa diminished after 2000 yr BP (Fig. 2). Herbaceous marsh plants decreased after around 2000 yr BP, especially in terms of concentration (Fig. 4); *Sphagnum* decreased markedly, probably out-competed by other marsh taxa and Poaceae invasion. At present, *Sphagnum* is almost completely replaced by Poaceae in many areas of Alpes de São Francisco bogs.

The general decrease of regional and local vegetation during the last 2000 years is probably not related to drier climates, but per-



haps to temperature increase, aggravated by regional human impact, like fire and clearing including *A. angustifolia*, *D. sellowiana* and extensive *Pinus* plantations. The presence of *Glomus* during the last 2000 years suggests temperature increase, humid soils and mycorrhizal activities (Figs. 3 and 4). Research of present-day physiological aspects of *A. angustifolia* from Santa Catarina (Southern Brazil) and Misiones (Argentina), show a substantial reduction in the number of microsporangia in the microsporophylls and of microsporophylls in the male cones when the regional average temperature is higher during the month of their formation, resulting in a lower seed production (Marta Caccavari, personal communication). The same could possibly be affecting also other taxa of the *Araucaria* forest on the eastern Plateau of Southern Brazil, in response to a temperature increase during the last 2000 years. At present this temperature increase is detected in the ecotone zones of *Araucaria* forest with adjacent tropical forest, especially in the west, resulting in a slow invasion of the more competitive tropical taxa into the *Araucaria* forest (Reitz and Klein, 1966). In contrast to the limited dispersibility of the heavy seeds of *A. angustifolia*, the tropical species with small and light seeds can disperse more easily and are adapted to various levels of luminosity (Backes, 1988). Expansion of *A. angustifolia* into grasslands (Reitz and Klein, 1966) would also be more difficult under a temperature increase. In contrast, this temperature increase and higher moisture certainly would have favored the adjacent Coastal Plain Atlantic rain forest, having expanded as a whole since 3000 yr BP (Lorscheitter, 2003).

In spite of living in humid environment, *A. angustifolia* needs some drier periods to induce its reproductive cycle (Backes, 1988). More or less continuous moisture occurs at the extreme southern Plateau of the South of Brazil (Rio Grande do Sul eastern Plateau) but during some months lower temperatures affect the hydrologic balance of plants, promoting the physiologic dry that is important to *A. angustifolia* reproductive cycle in this region. *A. angustifolia* is able to withstand intensive low temperatures, with a minimum average equal or lower to 10 °C, a periodic seasonal temperature fluctuation of about 12 °C; both factors limitary to the advance of tropical forests taxa (Backes, 1988). Thus, the increase in annual average temperatures can alter significantly *A. angustifolia* reproductive cycle, which promotes the expansion of the tropical adjacent forest.

The marked decrease of grassland in concentration after 3000 yr BP (Fig. 4) can be related to the partial loss in the reproductive capacity, in this case, due to the temperature increase and (or) to higher regional precipitation. After Rambo (1956b) the modern grasslands discordant with modern moisture conditions in Southern Brazil eastern Plateau are considered a relict of a drier geologic past. This unfavorable condition of the grassland can be accentuated by human local activities.

At São Francisco de Paula (Behling et al., 2001) the records suggesting increase in moisture occurred only after 4000 yr BP, and the *Araucaria* forest expansion occurred during the last millennium and the *A. angustifolia* during the last 850 years. At Cambará do Sul other results (Behling et al., 2004) show *Araucaria* forest migration at 4320 cal yr BP and expansion replacing grassland at 1100 cal yr BP, interpreted to represent increase of moisture, without accentuated annual dry seasons. In the other records from the Southern Brazil highlands (Santa Catarina and Paraná Serra Geral), this humid phase is registered from 2900 yr BP onwards (Behling, 1995, 1997).

Therefore, the results from Alpes de São Francisco are according to the other highland areas from South Brazil related to a moisture increase from ca. 5000 yr BP onwards. The different ages of the beginning of this humid phase and expansion of *Araucaria* forest are certainly due to micro-regional geographic differences. It is important to emphasize that all palynological results of Southern

Brazilian highlands based in percentage diagrams indicating only the expansion of *Araucaria* forest after 5000 yr BP. In the same way, the percentage diagrams of distinct taxa in Alpes de São Francisco show expansion of *Araucaria* forest until present-day in this phase, but the concentration diagrams indicate a general marked decrease in Rio Grande do Sul Plateau vegetation after 2000 yr BP.

## 6. Conclusions

The results of Alpes de São Francisco provide new information about the palaeoenvironments in the Southern Brazilian highlands indicating a cold and dry climate during the LGM, an increase of temperature and humidity at the beginning of the Holocene, a dry phase at Mid Holocene times, increase in moisture from ca. 6500 yr BP onwards and the possible increase of temperature at the last 2000 years.

The lack of a large expansion of *Araucaria* forest at the eastern Plateau in the beginning of the Holocene was perhaps due to the short time involved, different from the length of time of the moist phase during the late Holocene. On the other hand, different ages for the Mid Holocene dry phases need new investigations to resolve the climate patterns.

In contrast to percentage diagrams, concentration diagrams show clearly the humid climate at the beginning of the Holocene and, for the first time in the region, the marked decline of the *Araucaria* forest expansion from 2000 yr BP onwards, possibly due to the temperature increase. Therefore, the concentration diagrams are a relevant tool to the palaeoenvironment study in Southern Brazilian highlands and it would be important to include them in the future analysis.

The results show *Araucaria* forest moisture dependence and the great problem of the global warming on this ecosystem survival. Urgent conservation programs are necessary to minimize global climatic events and human impact to preserve this so unique highland vegetation.

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