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Late Quaternary *Araucaria* forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil

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Abstract

Late Quaternary vegetation, fire and climate dynamics have been studied based on high-resolution dated pollen and charcoal samples and multivariate data analysis. The samples were taken from a 212-cm-long sediment core of a bog in the Cambará do Sul region on the highlands of northeastern Rio Grande do Sul State, Brazil. The records, including seven AMS radiocarbon dates, span 42 840 ^{14}C years, for the first time extending the reconstruction of past environmental changes on the southern Brazilian highlands back to the Last Glacial Maximum (LGM) and pre-LGM times. The last 1100 years provide a decadal resolution. Initially the site was a permanent shallow lake which became seasonally dry after 26 900 ^{14}C yr BP. Seasonal climate with a long annual dry period prevailed until the late Holocene. The climate was somewhat wetter from 42 840 to 41 470 ^{14}C yr BP and from 41 470 to 26 900 ^{14}C yr BP than during the LGM and the late-Glacial period. Natural fires were rare, but became very frequent after 7400 cal BP, suggesting human occupation of the southernmost Brazilian highlands since that time. The records suggest that a species-rich Campos (grassland) vegetation existed in the area under a relatively dry and cold climate during glacial times under possibly as low as −10°C. The record also suggests that small populations of *Araucaria* were probably only present in refugia of deep and protected valleys and/or on wetter coastal slopes. Campos vegetation existed through the early and mid-Holocene until 4320 cal yr BP, after which *Araucaria* forest expanded into the network of gallery forests along the streams. By 1100 cal yr BP the *Araucaria* forest replaced the Campos vegetation reflecting the onset of the wettest period with no marked annual dry season. The marked expansion of the *Araucaria* forest coincided with the reduction in fire. Between AD 1520 and 1770 *Weinmannia* became a common taxa in the *Araucaria* forest, suggesting a shift to warmer climatic conditions on the highlands. This interval was synchronous with a cool phase within the Little Ice Age known from North Atlantic land records. After about AD 1780 human activities changed the original forest composition, first by introducing cattle into the forest and than by selective logging of

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Araucaria trees. Multivariate analysis of the pollen data shows compositional changes that follow a trajectory alternating undirectional, random phases and phases with directional, sometimes fast transitions. The results also show that compositional changes in the vegetation are slower during cool periods (LGM compared to pre-LGM) and faster in warm periods (Holocene).

Keywords: Late Quaternary; Last Glacial Maximum; Holocene; Little Ice Age; *Araucaria* forest; grassland (Campos); pollen; charcoal analysis; multivariate analysis; palaeoecology; palaeoclimatology; palaeofire; southern Brazil

1. Introduction

Earlier palaeoenvironmental studies from the *Araucaria* forest and Campos regions of the southern Brazilian highlands documented large-scale environmental changes during the late Quaternary. Paleoenvironmental data from Paraná (Serra Campos Gerais; cf. Behling, 1997), Santa Catarina (Serra do Rio Rastro, Morro da Igreja, Serra da Boa Vista; cf. Behling, 1993, 1995) and Rio Grande do Sul (Aparados da Serra; cf. Roth and Lorscheitter, 1993; São Francisco de Paula; cf. Behling et al., 2001) showed that extensive areas of Campos vegetation existed on the highlands throughout the late-Glacial and early to mid-Holocene times. The dominance of Campos vegetation was attributed to drier climates, cold and dry during the late-Glacial, and warm and dry during the early Holocene (Behling, 1997). An annual dry season lasting about three months was probably characteristic of the early and mid-Holocene period (Behling, 1997). About 3000 years BP expansion of the *Araucaria* forests started by migration from the gallery forests along the rivers, indicating a shift to a somewhat wetter climate. A marked expansion of *Araucaria* forests on the highlands, replacing Campos vegetation in Santa Catarina State, began about 1000 years ago, and in Paraná State (Serra Campos Gerais) about 1500 years ago. This is a period well within the late Holocene's very humid climate without a marked annual dry period. *Araucaria* forest apparently continues to expand today on the highlands under natural conditions (e.g. Klein, 1960, 1975; Rambo, 1956a,b, 1960).

Earlier palynological studies from highland sites relied on peat bog cores within the Campos area. In these records the *Araucaria* forest dynamics is muted. The present study analyzes a core from a peat bog from Cambará do Sul in the state of Rio Grande do Sul, Brazil, located within the *Araucaria* forest formation. It provides for the first time detailed insight into the long-term processes of *Araucaria* forest dynamics. Among the specific aspects affecting *Araucaria* forest dynamics are fires which have received little attention. The present paper reports on the last 42 840 ^{14}C years history of the *Araucaria* forest region.

2. Study area

2.1. Geographical setting

The study region is located on the southern Brazilian highlands, in the northeastern part of the Rio Grande do Sul State (Fig. 1). The studied bog (29°03′09″S, 50°06′04″W) is situated about 7 km east of the village of Cambará do Sul near the Aparados da Serra National Park, at a distance of 6–10 km from the steep escarpment of the Serra Geral mountains. The bog is located at 1040 m elevation in a small circular rocky basin of about 50 m in diameter.

2.2. Vegetation

The vegetation prior to post-Columbian settlement contained a mosaic of *Araucaria* forests and patches of Campos (grassland). Accounts of the floristic composition of highland vegetation are given by Hueck (1953, 1966), Klein (1978, 1979, 1984), Negrelle and Da Silva (1992), Rambo (1953, 1956a,b), Waechter et al. (1984), Por (1992), Boldrini (1997), and Rosario (2001). Regarding the geographic distribution, the subtrop-

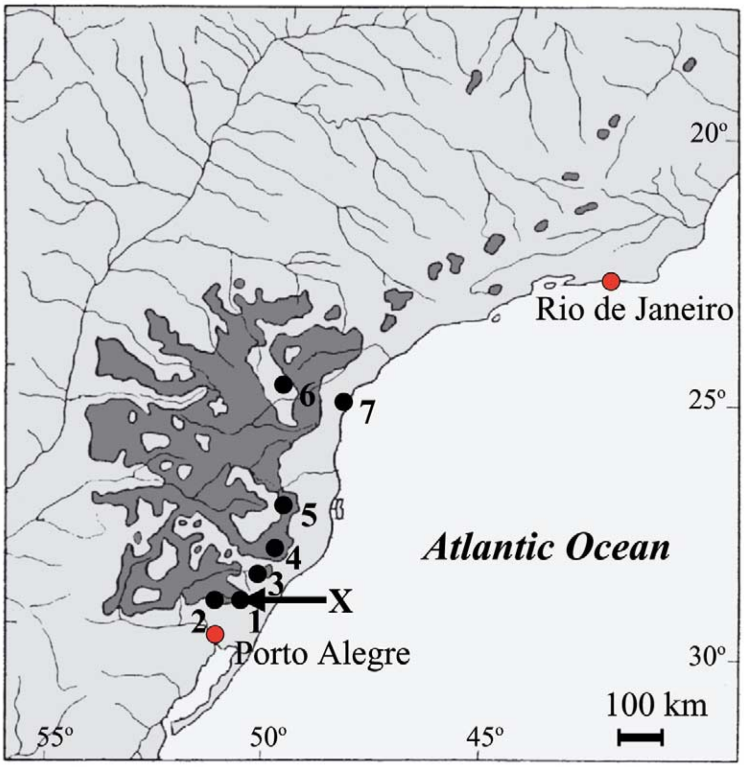

Fig. 1. Map showing the location of the study site (X) near Cambará do Sul and those of the other sites mentioned: (1) Aparados da Serra, (2) São Francisco de Paula, (3) Serra do Rio Rastro, (4) Morro da Igreja, (5) Serra da Boa Vista, (6) Serra Campos Gerais and Volta Velha (7).

ical *Araucaria angustifolia* forest occurs between latitudes 24° and 30°S, primarily at elevations between 500 and 1400 m in southern Brazil and in isolated islands between 18° and 24°S at elevations between 1400 and 1800 m in southeastern Brazil (Hueck, 1953; Rambo, 1956a,b) (Fig. 1). The primary tree species include *Araucaria angustifolia*, *Ilex paraguariensis*, *Mimosa scabrella*, and *Podocarpus lambertii*. Other trees of importance are species in the Myrtaceae (*Myrceugenia* spp., *Eugenia* spp., *Myrciaria* spp.) and Lauraceae (*Ocotea* spp., *Nectandra* spp.) families.

The Campos vegetation is highly diverse and characterized by non-arboreal species mainly in the Poaceae, Cyperaceae, Asteraceae, Apiaceae, Rubiaceae, Fabaceae, and Eriocaulaceae families. Other important taxa in this formation include representatives of the genera *Polygala*, *Xyris* and *Plantago*. The tall grasses dominate (*Andropogon* spp., *Aristida* spp., *Schizachyrium* spp.), mixed with shrubs such as *Baccharis* spp., *Vernonia* spp. (Asteraceae) and *Eryngium horridum* (Apiaceae).

Tropical Atlantic rain forest occurs in southern Brazil as a 100–200-km-broad belt in the coastal lowlands near the border between the states of Santa Catarina and Rio Grande do Sul, and on the slopes of the Serra Campos Gerais mountains at elevations up to 1000 m. Some rain forest species extend their range into the valleys of Serra Campos Gerais. The Atlantic rain forest is highly diverse in trees, shrubs, climbers, tree ferns and epiphytes. The dominant trees are in the Euphorbiaceae (*Alchornea*), Arecaceae (*Euterpe*), Myrtaceae, Moraceae, Bignoniaceae, Lauraceae, and Sapotaceae families (Hueck, 1966; IBGE, 1993).

Along the upper coastal mountains of the Serra Geral a zonal dense cloud forest expands, composed of medium high trees and shrubs including *Weinmannia humilis*, *Siphoneugena reitzii*, *Myrceugenia euosma*, *Drimys brasiliensis*, *Ilex microdonta*, *Berberis kleinii*, and *Gunnera manicata*.

The modern vegetation is strongly affected by the logging of the *Araucaria angustifolia* forests and different agricultural land-use practices. Large-scale aforestation by *Pinus* is seen on the highlands in the last few decades.

The study site is surrounded by a little disturbed *Araucaria* forest in the vicinity of the Aparados da Serra National Park. The local vegetation of the peat bog is a mosaic of different herbs, a few small shrubs and *Sphagnum* and *Polytrichum* moss patches.

2.3. Climate

The atmospheric circulation of southern Brazil is dominated by the South Atlantic anticyclone, a semi-permanent high pressure system which transports moist tropical air masses over the continent from easterly and northeasterly directions during the whole year. Disturbances to this pattern are related to polar cold fronts, which when meeting the tropical air masses, produce strong rainfall in southern Brazil (Nimer, 1989; Hastenrath, 1991). Higher rainfall in southern Brazil is also related to El Niño events (Martin et al., 1993; McGlone et al., 1992; Ratisbona, 1976).

The climate of the Cambará do Sul region is defined as warm temperate (subtropical) and humid without marked dry periods (Nimer, 1989). The southern highlands form an orographic barrier for southeasterly winds. As a consequence, rainfall is high. The study area is located in a zone with an average annual rainfall of over 2000 mm, one of the highest in southern Brazil. São Francisco de Paula, 60 km southwest of the study region, records a mean annual precipitation of 2456 mm. The mean annual temperature is 14.5°C. The lowest recorded temperature during the last 100 years is −6.5°C (Nimer, 1989).

3. Materials and methods

3.1. Sampling

The bog was cored in its deepest part using a Russian corer. Sections of 50 cm length were extruded on-site, wrapped in plastic film and aluminum foil and stored under refrigeration (+4°C) in the laboratory prior to sub-sampling. Seven 1-cm-thick bulk samples were submitted for AMS radiocarbon dating.

3.2. Pollen and charcoal analyses

For pollen analysis 190 subsamples (0.25 cm^3) were taken mostly at 1-cm intervals along the 211-cm-long core and were processed by standard pollen analytical methods, including acetolysis (Faegri and Iversen, 1989). Pollen preparation included addition of exotic *Lycopodium* spores to determine pollen concentration (grains/cm^{-2}) and pollen influx (grains/cm^{-3}/yr). A minimum of 300 pollen grains in each sample were counted. The total pollen sum includes pollen from herbs, shrubs and trees, while aquatic taxa were excluded from the sum. Fern and moss spores, and algae colonies of *Botryococcus* were counted and expressed as percentages of the total pollen sum. Carbonized particles were counted on the pollen slides as well. Pollen and spore preservation was relatively poor in the sediment between core depths of 141 and 80 cm. Pollen identification relied on the first author's own reference collection containing about 2000 Brazilian species and pollen morphological descriptions (Behling, 1993). Identified taxa were classified into the following ecological groups: Campos, *Araucaria* forest, Atlantic rain forest, aquatics, ferns (excluding *Isoetes*), tree ferns, *Isoetes*, mosses, and *Botryococcus*. For plotting, calculations and cluster analysis the TILIA, TILIAGRAPH and CONISS software was used (Grimm, 1987).

3.3. Multivariate analysis

Eigenanalysis was used to map the 190-sample time series of pollen and spore percentages into a full dimensional ordination to create a lower di-

Table 1
Stratigraphic description of the Cambará do Sul core

Depth (cm)	Description
0–30	Brown, decomposed peat, with abundant roots and rootlets and plant remains
30–56	Dark brown, compact, almost completely decomposed peat, with root and rootlets
56–109	Black, very compact, totally decomposed peat
109–140	Light gray clay, very compact, very poor in organic material
140–212	Gray–brown clay, compact, with decomposed organic material on rocky subsurface

mensional view of compositional transitions in the paleocommunity based on 166 pollen taxa (Orlóci, 2000; Orlóci et al., 2002a and references therein). Eigenanalysis, also known under names such as principal components analysis, principal coordinates analysis, and R- and Q-techniques, is a technique which is used e.g. in exploratory plant community analysis. It was reviewed by Orlóci (1978) and Podani (2000) (cf. references therein) and is implemented in computer application programs (Pillar, 2001; Podani, 2000). We excluded from the ordination indeterminate and spore-bearing taxa, except for the tree ferns.

In one analysis the complete trajectory of 190 records of 166 taxa was examined and interpreted in terms of past taxa dynamics. Further analyses examined segments of the vegetation trajectory in more detail. Rates of composition changes between time steps (velocity) were computed by dividing the Euclidean distance by the time interval in ^{14}C years (see references above). The analyses were performed by Pillar's SYNCSA software (Pillar, 2001).

4. Results

4.1. Stratigraphy

The sediment core starts on the bedrock subsurface 212 cm down from the surface. The material is clay from 212 to 109 cm core depth, overlain by black decomposed peat from 109 to 56 cm, and brown decomposed peat from 56 to 0 cm (Table 1).

4.2. Radiocarbon dates and chronological control

AMS radiocarbon dates were obtained for seven levels (Table 2), suggesting continuous sedimentation during the late Quaternary. The base of the core is dated at 42 658 ± 984 ^{14}C yr BP. Between 144 and 79 cm core depth the sedimentation rate was low. First introduced *Pinus* pollen grains were found at 11 cm core depth. The interpolated age for this depth is 118 ^{14}C yr BP (127 cal BP, i.e. AD 1823). This age coincides with the first known German settlements on the lower

Table 2
Radiocarbon dates for the Cambará do Sul core

Laboratory number	Depth (cm)	^{14}C yr BP	$^{13}C/^{12}C$ ratio	Calendar age (cal yr BP)[a]
Erl-4043	29	394 ± 41	−28.58	AD 1442–1516, AD 1598–1616
Erl-4044	55	1 089 ± 47	−25.98	AD 895–922, AD 939–997
Erl-4045	79	3 523 ± 56	−20.32	1917–1854 BC, 1845–1769 BC, 1757–1748 BC
Erl-4046	109	9 967 ± 91	−23.25	9604–9548 BC, 9541–9518 BC, 9491–9281 BC
Erl-4047	144	28 208 ± 281	−29.77	
Erl-4048	180	37 154 ± 602	−28.64	
Erl-4049	210	42 658 ± 984	−29.00	

[a] 1-σ standard deviation.

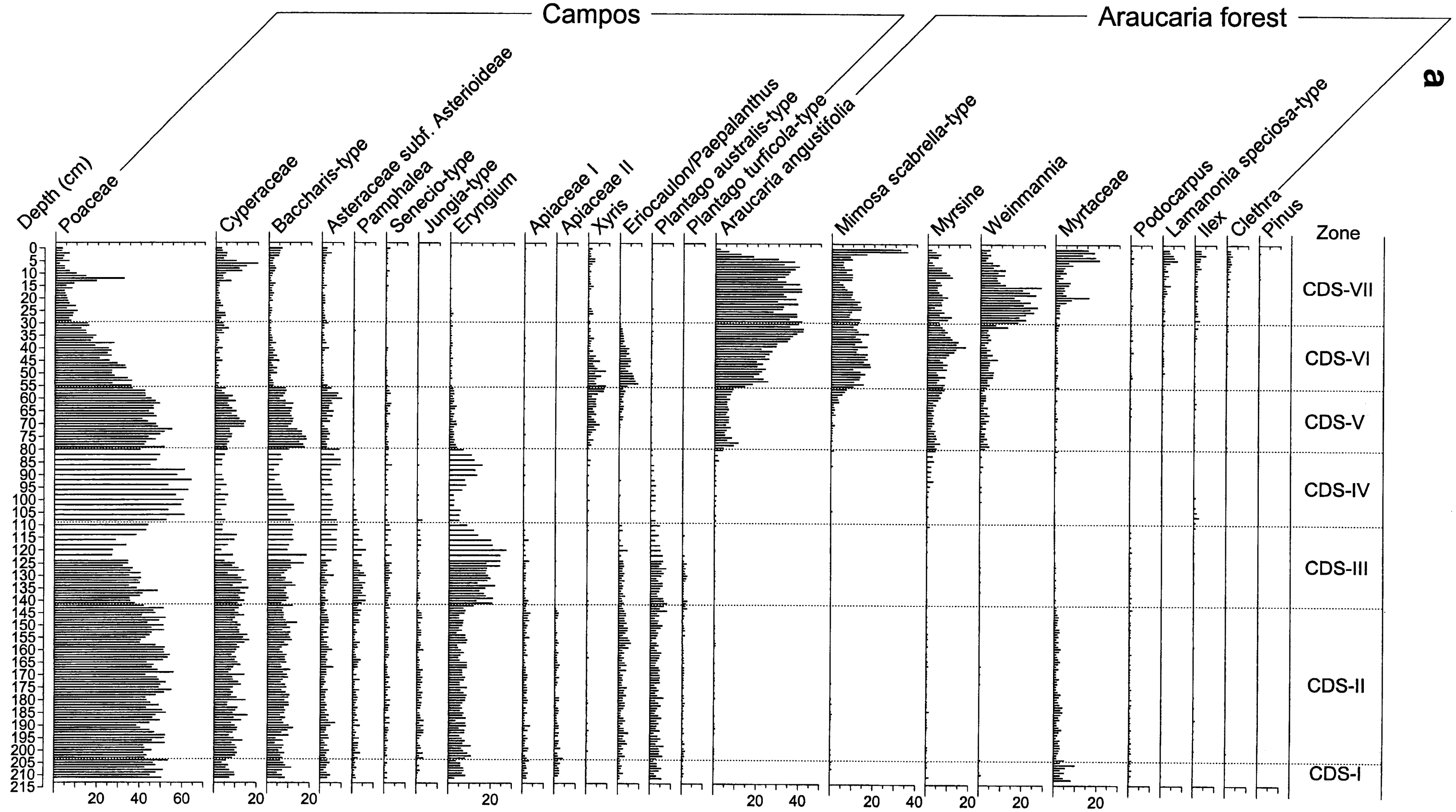

Fig. 2. (a,b) Pollen percentage diagrams for Cambará do Sul. (c) Summary pollen percentage diagram for Cambará do Sul, including the records of pollen concentration, pollen influx, concentration and influx of carbonized particles, and cluster analysis.

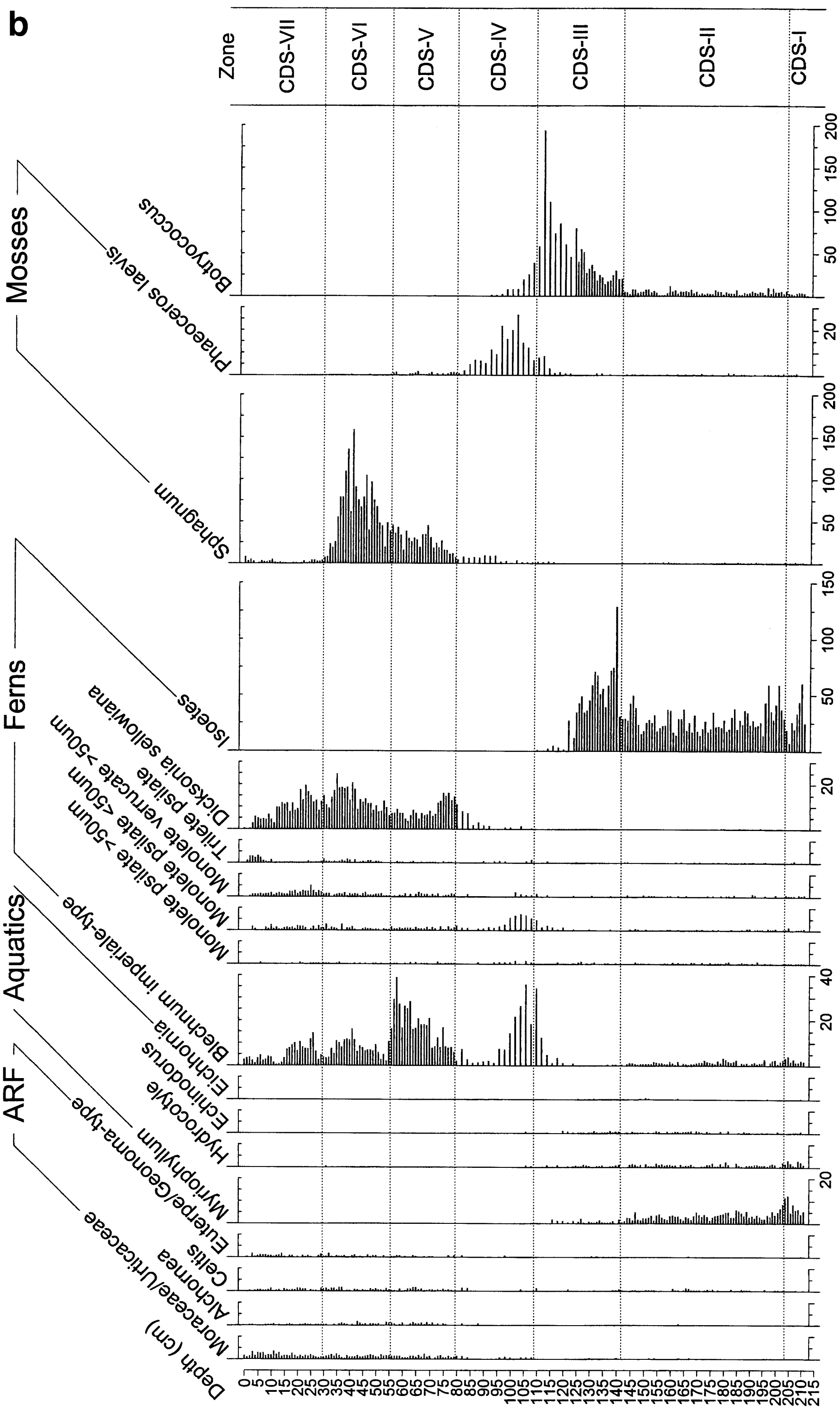

Fig. 2 (Continued).

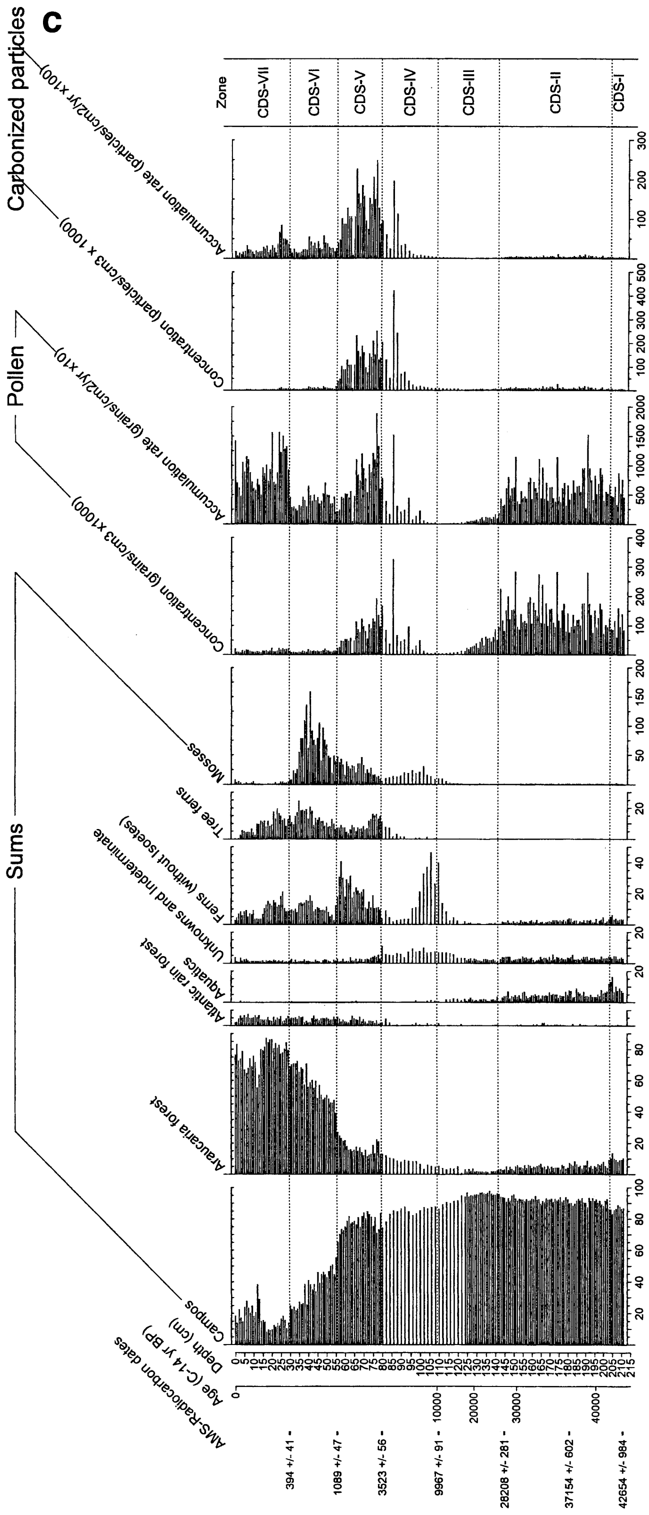

Fig. 2 (*Continued*).

slopes of the Serra Geral in Rio Grande do Sul, around AD 1825. Logging of *Araucaria* trees is also documented in the pollen record, indicating that the top of the core represents the modern surface.

Ages were interpolated from radiocarbon dates for each pollen zone. For the late Holocene period the temporal resolution of the sampling is high, 1 cm of the core corresponding to 100 years between 3950 and 1140 ^{14}C yr BP, to 27 years between 1140 and 410 ^{14}C yr BP, and to only 15 years between 410 ^{14}C yr BP and −50 ^{14}C yr BP (i.e. AD 2000).

4.3. Description of the pollen diagram

The pollen diagram in Fig. 2a,b contains 190 levels. Fig. 2a,b illustrates percentages for the leading taxa out of 140 identified pollen and 26 spore types. In all 24 pollen types could not be identified, but they were found to be distinct. Fig. 2c illustrates the sum of taxa in terms of their ecological affiliation groups, pollen concentration and pollen accumulation rates, concentration and accumulation of carbonized particles, and the cluster analysis dendrogram. Based on the latter, the pollen diagram is zoned into seven pollen zones (CDS-I–VII).

Pollen concentrations of the core subsamples are between 28 000 and 1 900 000 grains/cm^3 and pollen accumulation rates are between 5000 and 19 000 grains/cm^2/yr. Pollen concentration and accumulation rates are about 1 000 000 grains/cm^3 and 5000 grains/cm^2/yr, respectively, in zones CDS-I and CDS-II, lower in zone CDS-III and higher in zone CDS-IV. Higher pollen concentration and accumulation rates with about 1 000 000 grains/cm^3 and about 8000 grains/cm^2/yr, respectively, are found again in zone CDS-V. Pollen concentration values are about 100 000 grains/cm^3 in zones CDS-VI and CDS-VII, and accumulation rates are high, about 4000 grains/cm^2/yr in zone CDS-VI and 8000 grains/cm^2/yr in the uppermost zone.

4.3.1. Zone CDS-I (211–203.5 cm; 42 840–41 470 ^{14}C yr BP; 8 subsamples)

The lowermost zone is characterized by abundant Campos pollen (83–88%), primarily Poaceae, followed by Cyperaceae, *Baccharis*-type, Asteraceae subf. Asterioideae, *Pamphalea*, *Senecio*-type, *Jungia*-type, *Eryngium*-type, Apiaceae types I and II, *Eriocaulon/Paepalanthus*, Iridaceae, *Plantago australis*-type, and *Plantago turficola*-type. Several other Campos taxa (not shown in the diagram) with low amounts include *Alium*-type, *Alstroemeria*, *Alternanthera*, Amaranthaceae/Chenopodiaceae, *Borreria*, Brassicaceae, Caryophyllaceae, *Croton*, *Euphorbia*, Ericaceae, Fabaceae, *Gomphrena/Pfaffia*-type, *Linum*, Malvaceae, *Moritzia dasiantha*, *Oxalis*, *Pavonia–Malvastrum*-type, *Polygala*, *Ranunculus bonariensis*-type, *Salvia*-type, *Scutellaria*-type, *Spermacoce*, *Valeriana*, *Verbena*-type, *Vicia/Lathyrus*, *Trichocline*, and *Trixis*. *Araucaria* forest percentages are low (8–14%), primarily represented by Myrtaceae, a few *Podocarpus* grains (< 1%), and a few single grains of *Araucaria angustifolia* (2 grains), *Mimosa scabrella*-type, *Myrsine*, *Weinmannia*, and *Lamanonia speciosa*-type. *Ilex* and *Clethra* pollen were not found. Atlantic rain forest pollen (0–0.6%) such as Moraceae/Urticaceae, *Alchornea* and *Celtis* are absent, except for one pollen grain of the *Euterpe/Geonoma*-type (Arecaceae). Percentages of aquatics (6–16%) are relatively high, mainly represented by *Myriophyllum*, *Hydrocotyle*, and a few grains of *Echinodorus* and *Eichhornia*. Spores from ferns are low (3–6%), primarily represented by the *Blechnum imperiale*-type and a few spores of the monolete psilate and monolete verrucate types. Spores of the tree fern *Dicksonia sellowiana* are absent, *Isoetes* spores are frequent, and spores of mosses (*Sphagnum*, *Phaeoceros leavis*) are low. Colonies of the alga *Botryococcus* are rare. The concentration and accumulation rates of carbonized particles are very low in this zone.

4.3.2. Zone CDS-II (203.5–141.5 cm; 41 470–26 900 ^{14}C yr BP; 62 subsamples)

Pollen grains representing the Campos vegetation continue to dominate in this zone (87–94%). The pollen sums of *Araucaria* forest taxa (3–9%) decrease slightly due to the lower percentages of Myrtaceae pollen. *Araucaria angustifolia* pollen (0–0.7%) were found in trace amounts. A few single pollen grains of Moraceae/Urticaceae, *Alchor*-

nea, *Celtis*, and *Euterpe/Geonoma* represent the Atlantic rain forest pollen (0–1.6%). Aquatic taxa are lower than before (3–7%), mainly because of the decrease of *Myriophyllum*. Fern spores are also lower (0–3%) and spores of the tree fern *Dicksonia sellowiana* are found in trace amounts. *Isoetes* spores, moss spores and *Botryococcus* remain unchanged compared to the previous zone. Carbonized particles are also low in this zone.

4.3.3. Zone CDS-III (141.5–109 cm; 26 900–10 120 ^{14}C yr BP; 25 subsamples)

Pollen percentages of the Campos group continue to be high (87–97%), while Poaceae decrease and the *Eryngium*-type pollen increase markedly. Apiaceae types I and II are less frequent. The pollen sums of *Araucaria* forest and the Atlantic rain forest taxa are at their lowest in this zone (1–5% and 0–0.3%, respectively). Myrtaceae percentages are low and a few single grains of *Araucaria angustifolia* pollen were found. Percentages of aquatic taxa are low (1–3%), primarily because of very low amounts of *Myriophyllum*. Fern spores show the lowest values in this zone, but the *Blechnum imperiale*-type (max 40%) increases markedly at the end of this zone. *Dicksonia sellowiana* spores are absent. *Isoetes* spores have their highest values at the beginning of this zone, but decrease markedly in the upper section of the zone. Moss spores are rare. Colonies of *Botryococcus* are common and increase continuously to the end of this zone. Carbonized particles are rare in the deposits.

4.3.4. Zone CDS-IV (109–81 cm; 11 540–4320 cal yr BP, 10 120–3950 ^{14}C yr BP; 15 subsamples)

Campos pollen types form the most abundant group in this zone (74–88%), although they decrease slightly towards the top of this zone. Poaceae pollen are markedly higher than in the previous zone, while pollen of several other taxa such as Cyperaceae, *Baccharis*-type, *Pamphalea*, *Jungia*-type, *Eriocaulon/Paepalanthus*, and *Plantago* are less frequent. Pollen grains of the *Eryngium*-type are less frequent in the lower core section than in the upper core section. Pollen from the *Araucaria* forest taxa increase slightly (3–13%) due to increases of *Araucaria angustifolia* (0–2%) and *Myrsine*. The Atlantic rain forest pollen types increase slightly (0–4%). Aquatic pollen taxa are found only in trace amounts ($<1\%$). There is a pronounced increase of fern spores (maximally 46%), mainly of the *Blechnum imperiale*-type, which started already in the previous zone, followed by a decrease in the upper part of the zone (minimally 9%). Spores of *Dicksonia sellowiana* increase at the top of the zone (0–14%). Moss spores of *Phaeoceros leavis* are frequent and have their highest values in this zone. *Botryococcus* is absent in the lower section of this zone. In the upper section carbonized particles are abundant.

4.3.5. Zone CDS-V (81–55.5 cm; 4320–1100 cal yr BP, 3950–1140 ^{14}C yr BP; 24 subsamples)

The pollen sums of the Campos taxa are slightly lower (65–84%) compared to the previous zone, but the percentage values are still high. Pollen grains of Poaceae and of the *Eryngium*-type are less common, while pollen of Cyperaceae, the *Baccharis*-type and *Xyris* increase. The pollen sum of the *Araucaria* forest taxa is higher (13–27%), related to the increase of *Araucaria angustifolia* (4–7%), *Myrsine* and *Weinmannia*. Other taxa of the Araucaria forest, which are now slightly more frequent (not shown in the diagram), include such types as *Buddleja*, *Daphnopsis*, *Drimys*, *Luehea*, *Mimosa*, *Mimosa taimbensis*-type, *Ocotea*, *Phrygilanthus acutifolius*, *Sebastiania commersionia*, *Struthanthus*, and *Stryax*. Pollen of the Atlantic rain forest taxa are more frequent (2–5%) in this zone, primarily owing to increase in Moraceae/Urticaceae, *Alchornea*, *Celtis*, and the *Euterpe/Geonoma*-type. Other taxa in this group, which are found sporadically (not shown in the diagram), include *Acalypha*, *Cecropia*, *Didymopanax*, *Dodanea*, *Hyeronima*, *Matayba*, *Meliosma*, *Pera*, *Piper*, *Tetrochidium rubrivenium*, and *Trema*-type. The group of fern spores increases again (9–40%), mainly owing to *Blechnum imperiale*-type and a few spores of the monolete psilate and verrucate type. Spores of *Dicksonia sellowiana* are common (9–16%). There is a marked increase of *Sphagnum* spores. Carbonized particles are very frequent.

4.3.6. Zone CDS-VI (55.5–29.5 cm; 1100–430 cal yr BP, 1140–410 ^{14}C yr BP; 26 subsamples)

The representation of Campos pollen taxa, primarily Poaceae, is markedly lower and decreases continuously towards the top of the zone (from 55 to 24%). All other pollen of the Campos group are markedly less frequent, except for *Xyris* and *Eriocaulon/Paepalanthus*. Pollen of the *Araucaria* forest increase continuously (from 39 to 80%) and become predominant. The most striking feature of the zone is the strong increase of *Araucaria angustifolia* (from 14 to 42%). Also, the *Mimosa scabrella*-type increases markedly, but the *Myrsine*-type increases only moderately and *Weinmannia* only slightly. The Atlantic rain forest group remains unchanged (2–6%). Fern spores are less frequent (5–19%) due to the decrease of the *Blechnum imperiale*-type. *Dicksonia sellowiana* spores have the highest percentages in this zone (9–26%). Mosses, almost exclusively *Sphagnum* spores, have their highest values, but decrease towards the top of the zone. The concentrations of carbonized particles are low, but accumulation rates are higher than in zones CDS-I and CDS-III.

4.3.7. Zone CDS-VII (29.5–0 cm; 430 to −50 cal yr BP, 410 to −50 ^{14}C yr BP; 30 subsamples)

Pollen of the Campos group are the lowest (down to minimally 11%) in the bottom portion of the zone, but increase further up (maximally 38%), first by an increase of Cyperaceae and subsequently by Poaceae. At the top of this zone the Campos pollen sums decrease. The sum of the *Araucaria* forest group is the highest in the lower section of the zone (maximally 87%), but decreases in the upper part (minimally 65%). The *Araucaria angustifolia* pollen remain high, but they decrease sharply at the top of the zone (from 41 to 2%). The *Mimosa scabrella*-type increases markedly. *Weinmannia* pollen are abundant in the lower part of the zone and decrease continuously in the upper section. The Myrtaceae pollen decrease, especially in the top part of the zone. Also, *Ilex* and pollen of the *Lamanonia speciosa*-type increase at the top of the zone. The pollen sums of the Atlantic rain forest taxa are similar to those in the previous zone (2–7%). Fern spores decrease (from 21 to 2%), spores of *Dicksonia sellowiana* decrease and become rare in the upper section of the zone (from 19 to 0.3%). Moss spores are low. The frequency of carbonized particles is similar to that in the previous zone.

4.4. Description of the results of the multivariate data analysis

The ordination diagram in Fig. 3a,b provides a map of the pollen compositional changes along a time trajectory, spanning the period from 42 841 ^{14}C yr BP to −50 ^{14}C yr BP (AD 2000). The 2-D ordination diagram accounts for 84.7% of the total variation in the 183 taxa by a 190-subsample record set. Dramatic changes in pollen composition occurred during the mid-Holocene (starting around 4575–4059 cal yr BP), from predominantly Campos vegetation (cf. Fig. 3b, on the right) to *Araucaria* forest (Fig. 3b, on the left).

Vegetation dynamics progresses through trajectory phases isolated by sharp directional changes. The process in some phases is highly directional (e.g. between 1277 and 1023 cal yr BP or in the last 80 years), while it appears essentially random in other intervals (e.g. between 4059 and 1277 cal yr BP, after the first expansion of *Araucaria* forest, roughly corresponding to zone CDS-V).

After 1023 cal yr BP, corresponding to zones CDS-VI and CDS-VII, the pollen composition is dominated by *Araucaria* forest taxa, including *Araucaria angustifolia*, Myrtaceae, *Ilex*, *Dicksonia sellowiana*, by Atlantic rain forest taxa including *Celtis*, *Alchornea*, *Euterpe*, *Cecropia*, Moraceae, and by cloud forest taxa such as *Weinmannia*. The rates of pollen composition change between adjacent time points (Fig. 4) slightly decrease between 26 000 and 12 000 ^{14}C yr BP, increase in the Holocene and sharply increase in the last 1000 cal yr BP.

Fig. 3c,d displays the vegetation dynamics from 42 841 ^{14}C yr BP to 5091 cal yr BP in a separate ordination. Here, too, phases of randomness are followed by phases of strong directionality of change. Interestingly, the trajectory shows definite directional trends in the vegetation process over long periods of time (e.g. from 27 166 to 15 700 ^{14}C yr BP). At shorter time scales random com-

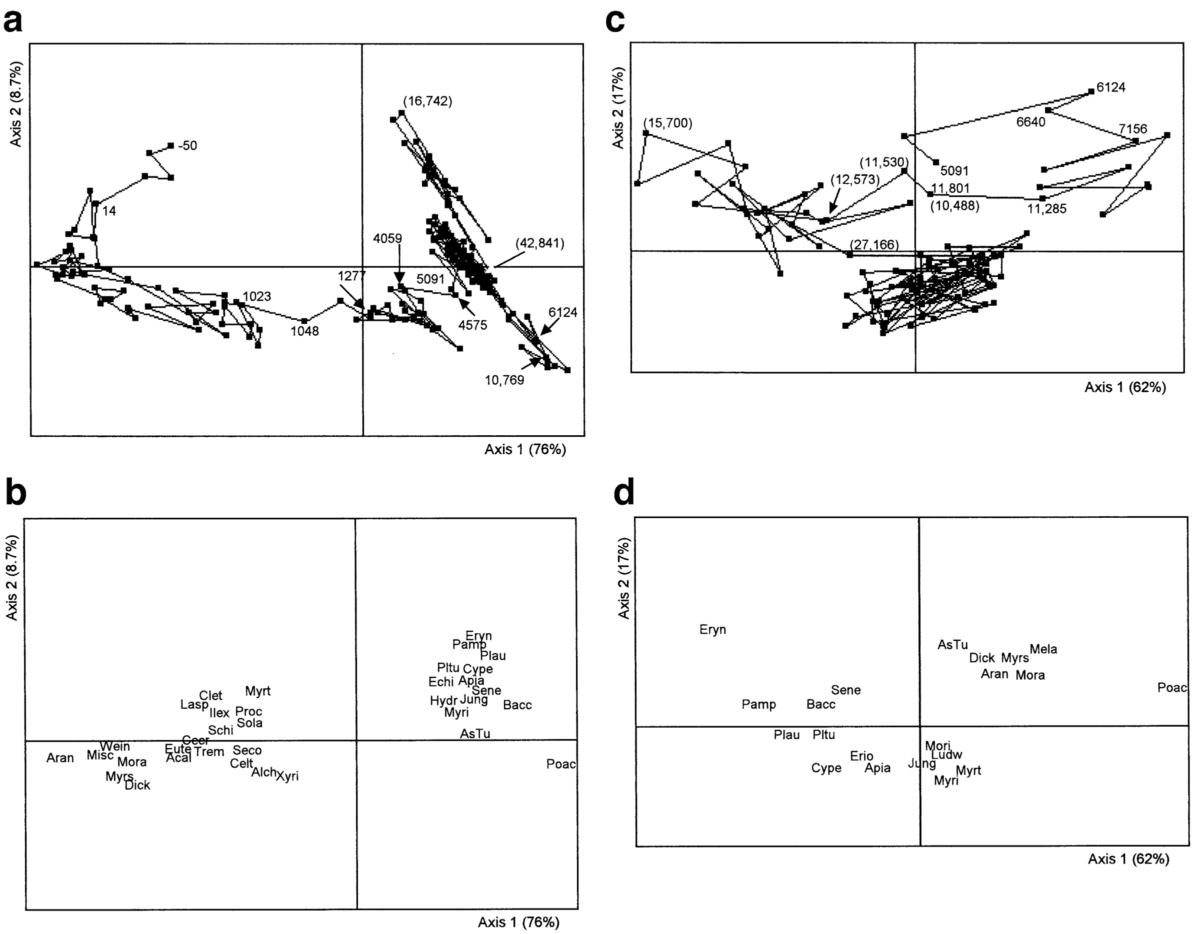

Fig. 3. Ordination diagrams of pollen taxa described from sediment core Cambará do Sul, Brazil. The diagrams map the complete vegetation trajectory over 42 840 ^{14}C yr BP in (a,b), and parts of the trajectory in (c,d), (e,f) and (g,h). Dates after 11 540 are calibrated years BP (i.e. before AD 1950); uncalibrated dates are in parentheses. The ordination method is the principal coordinates analysis based on Euclidean distances between sampling units, using percentages of pollen taxa of 138, 106, 92 and 92 taxa in diagrams (a,b), (c,d), (e,f), and (g,h), respectively. In (b), (d), (f) and (h) taxa with the highest correlations with the ordination axes are shown in positions proportional to the correlation level; the corresponding diagrams overlapped would form biplots. Taxa abbreviations are in Table 4.

positional transitions are more common, suggesting short-term random variation is superimposed on the long-term deterministic trend.

As seen in Fig. 2a,b, the vegetation during the glacial period was predominantly Campos. From 42 841 to around 27 687 ^{14}C yr BP, roughly corresponding to zones CDS-I and CDS-II, the vegetation was characterized by increased quantities of Myrtaceae, *Mortizia*, *Ludwigia*, the *Jungia*-type, and *Myriophyllum* (see Fig. 3d). A detailed ordination for this period (not shown here) revealed a trajectory which was random in the short term, but directional in the long term. Myrtaceae and *Myriophyllum* were initially the characteristic taxa, and Cyperaceae, *Eriocaulon*/*Paepalanthus* and Poaceae dominated towards the end. From around 27 000 to 12 573 ^{14}C yr BP, roughly corresponding to zone CDS-III, Campos taxa increased, including *Eryngium*, *Pamphalea*, *Plantago*, *Baccharis*, and *Senecio*. From 12 573 to 9752

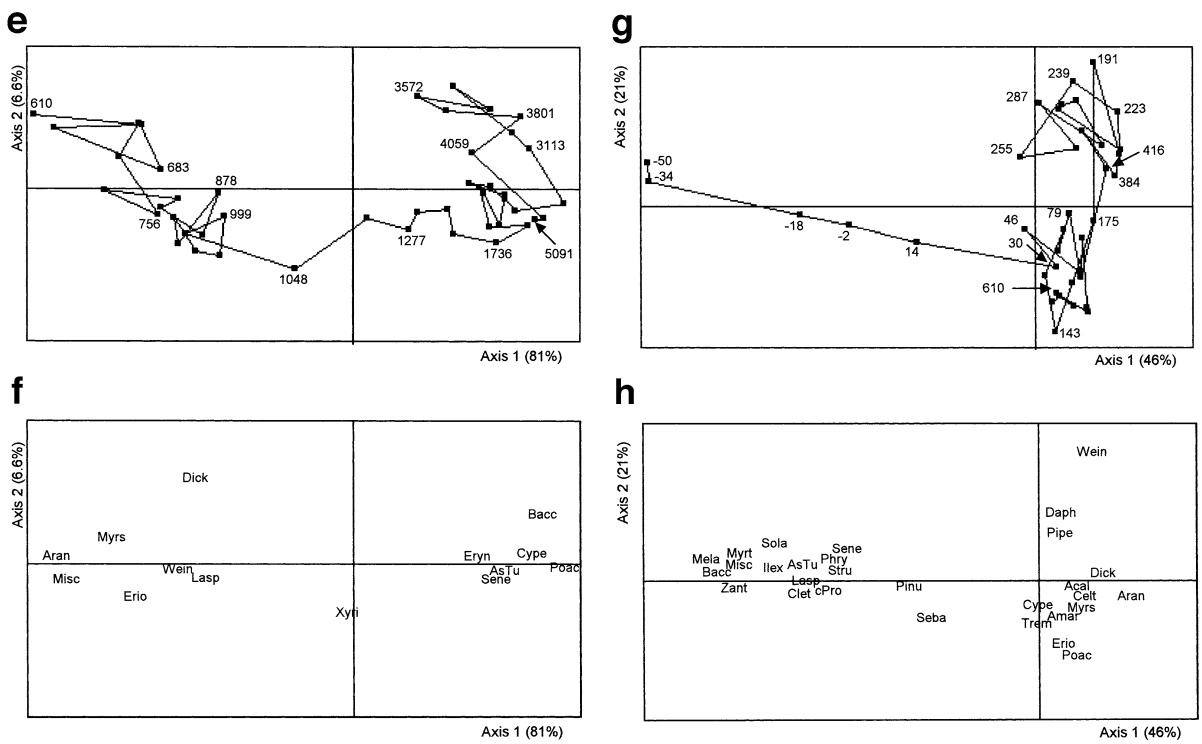

Fig. 3 (*Continued*).

^{14}C yr BP (11 285 cal yr BP) Poaceae sharply increased, followed by a period of mainly random changes until 7156 cal yr BP, when once again directional change dominated with increased numbers of the *Araucaria* forest taxa (e.g. *Araucaria angustifolia*, *Dicksonia sellowiana*) and Atlantic rain forest (e.g. Moraceae/Urticaceae).

The ordination in Fig. 3e,f shows details of the vegetation dynamics from 5091 to 610 cal yr BP, mostly corresponding to zones CDS-V and CDS-VI. The main ordination axis indicates a clear trend from predominantly Campos taxa on the right to *Araucaria* forest taxa on the left of the diagram (see Fig. 3f). This ordination axis accounts for 81% of the total variation, compared to 6.6% of the second (vertical axis). After the first spatial expansion of the *Araucaria* forest, a random phase occurs in the trajectory lasting until around 1736 cal yr BP. Subsequently, a linear phase occurs which lasted until around 1000 cal yr BP, the time when random variation superimposed on a general directional trend towards *Araucaria* forest is evident, coinciding with the first part of zone CDS-VI.

The interesting nature of the vegetation dynamics in the last 600 cal yr BP, including zone CDS-VII, is revealed in the ordination diagram of Fig. 3g,h. During this period the pollen composition represented the *Araucaria* forest with only negligible presence of the Campos taxa, except in the last 80–65 years when changes reflect the effect of logging. Notwithstanding the relative brevity of the period, a two-phase structure is evident, strongly directional as well as chaotic. From 610 to 440 cal yr BP the vegetation dynamics was largely chaotic, characterized by compositional oscillations in the *Araucaria* forest taxa (*Araucaria angustifolia* and *Dicksonia sellowiana*) and including some Atlantic rain forest taxa (*Acalypha* and *Celtis*, see Fig. 3h). Around 416 cal yr BP pollen composition entered a new chaotic phase, mainly characterized by fluctuations in *Weinmannia* proportions, until around 180 cal yr BP, when

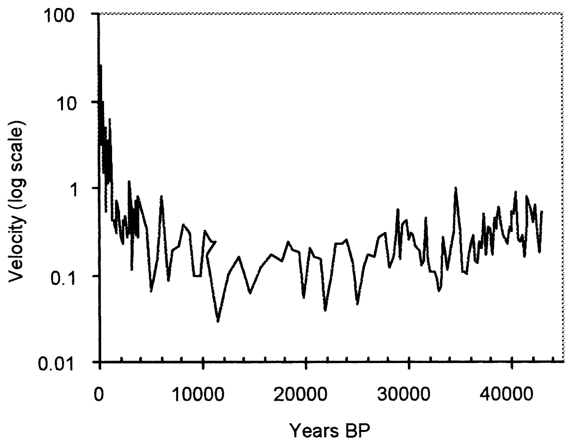

Fig. 4. Rates of pollen composition change (velocity), computed for 189 time steps based on the sediment profile at Cambará do Sul, Brazil. Computation was based on Euclidean distances between adjacent sampling units, using percentages for counts of 138 pollen taxa, divided by time intervals in ^{14}C years. Years on the horizontal scale are in calibrated years BP (i.e. before AD 1950) after 10 000 years, and not calibrated before that.

pollen composition returned to the previous compositional phase.

5. Palaeoecological and palaeoclimatic interpretations and discussion

5.1. Last glacial period (zones CDS-I to CDS-III: 42 840–10 120 ^{14}C yr BP)

The peat bog evolved from a shallow lake during the last glacial period, shown by the occurrence of *Myriophyllum* and *Isoetes*, both shallow-water indicators. The lake started to fill up with sediment from about 41 470 ^{14}C yr BP and became even shallower suggested by the reduction in *Myriophyllum*. At about 26 900 ^{14}C yr BP the lake ceased to be permanent as indicated by the further reduction of *Myriophyllum* and abundance of *Botryococcus* colonies. The seasonal drying of the lake during the Last Glacial Maximum (LGM) and the late-Glacial era may be responsible for the poor pollen and spore preservation, and for the low sedimentation rate and low pollen concentration and accumulation rates.

The pollen data indicate dominance of a diverse Campos vegetation between 42 840 and 10 120 ^{14}C yr BP, including the pre-LGM episode (zones CDS-I and CDS-II), the LGM and late-Glacial period (zone CDS-III). The grassland was rich in Poaceae, Asteraceae (primarily *Baccharis*-type), and Apiaceae (primarily *Eryngium*-type), reflecting a type of Campo with shrubs. The highland region of northwestern Rio Grande de Sul was probably almost treeless. Myrtaceae pollen, specially during zone CDS-I, probably originated from small shrub species found in the Campos vegetation and/or from shrubs and trees which may have grown at some distance on coastal slopes. Studies from the Atlantic lowland near the border of Paraná and Santa Catarina indicate that this region was covered by grassland and patches of Myrtaceae forest (Behling and Negrelle, 2001). The occurrence of a few single pollen grains representing *Araucaria* forest and Atlantic rain forest vegetation in the late Pleistocene sediments were probably wind transported over some distance from forest refugia in deep and protected valleys in the highlands or from the 6–7-km-distant slopes of the Serra Geral mountains or from the lowland vegetation of the coastal region, respectively.

During the pre-LGM between 42 840 and 26 900 ^{14}C yr BP (zones CDS-I and CDS-II) vegetation dynamics was characterized by small random changes in pollen composition, which is indicative of rather stable climatic conditions and plant communities. This was followed by a sharp change, beginning around 27 000 ^{14}C yr BP, to a new phase during the LGM (zone CDS-III), when changes were undirectional in short time scales but strikingly directional in the long term towards Campos, characterized by more *Eryngium* and less Poaceae and Myrtaceae species. This pattern supports the idea that vegetation dynamics is a convolution of alternating determinism during directional phases, and chaos during random phases (Orlóci et al., 2002a; Anand, 2000; Anand and Orlóci, 1997). During the pre-LGM, pollen compositional changes between adjacent time points occurred with more frequent high velocity than during the LGM. This corroborates evidence from other pollen profiles indicating that compositional changes of vegetation tend to slow down during cooler climatic periods (Orlóci, 2000; Orlóci et al., 2002a,b).

The reconstructed palaeovegetation of widespread treeless Campos vegetation suggests a cold climate with repeated frost events and minimum austral winter temperatures below −10°C, which do not permit the growth of *Araucaria* on the highlands. Mean annual temperature depression on the southeastern Brazilian highlands was probably in the range of 5–7°C for the LGM period (Behling and Lichte, 1997). A similar magnitude of depression is suggested for the LGM period in southern Brazil. The evidence of a shallow lake surrounded by a treeless landscape indicates a relatively dry late Pleistocene climate. The periods between 42 840 and 41 470 ^{14}C yr BP and between 41 470 and 26 900 ^{14}C yr BP were wetter than the LGM and the late-Glacial period. During the LGM, the driest period recorded, pollen of *Eryngium*-type were abundant, indicating drier conditions, and the shallow lake was not permanent, indicating a seasonally dry climate. Based on the Cambará do Sul record, it is suggested that seasonal climatic conditions developed after 26 900 ^{14}C yr BP. Seasonal climate with a long annual dry periods since the LGM prevailed until the late Holocene.

The relatively low amount of carbonized particles documents that natural grassland fires were rare during the glacial periods between 42 840 and 10 120 ^{14}C yr BP (CDS-I to CDS-III), even during the drier LGM and the late-Glacial period. A similar fire history was reported from the Serra Campos Gerais record in Paraná State for the late-Glacial period (Behling, 1997).

5.2. Early and mid-Holocene (zone CDS-IV: 11 540–4320 cal yr BP, 10 120–3950 ^{14}C yr BP)

With the beginning of the Holocene, the non-permanent lake changed to a peat bog, indicated by the accumulation of black organic-rich material and sporadic *Botryococcus* colonies. The fern *Blechnum imperiale*, with pseudo-trunks reaching ca. 50 cm in height, initially was common on the bog before it became rare during the mid-Holocene period.

During early and mid-Holocene times Campos vegetation still dominated the landscape. The lower frequency of Asteraceae (*Pamphalea*, *Senecio*, *Jungia*), Apiaceae (*Eryngium*, Apiaceae types I and II), *Eriocaulon*/*Paepalanthus* and *Plantago australis* indicates a change in plant composition within the grassland at the beginning of the Holocene. The frequent abundance of the moss *Phaeoceros leavis* indicates soil dryness and reduced vegetation cover in the areas surrounding the peat bog. The *Araucaria* forest taxa increased slightly but were still rare, indicating that populations migrated into the study region, probably along small streams. The Atlantic rain forest taxa became more common, suggesting an expansion on the Serra Geral coastal slopes closer to the study site.

During the early Holocene until about 7156 cal yr BP vegetation dynamics is characterized by low amplitude, undirectional fluctuations in taxa composition, indicative of a rather stable plant community and climate. This was followed by an interval of rapid changes, coinciding with the onset of probably human-set fires (see below) and subsequently by expansion of the *Araucaria* forest and Atlantic rain forest. The vegetation changes were more rapid during the early Holocene than during the LGM.

Widespread Campos vegetation coupled with the rare occurrence of *Araucaria* forest taxa suggest a dry climate. Changes in the composition of the Campos vegetation, including the presence of *Phaeoceros leavis*, document a change to a warm and dry climate. Annual precipitation must have been lower than 1400 mm and the climate was seasonal, with a dry season lasting about 3 months. The climatic conditions did not favor the expansion of *Araucaria* forest taxa in the study area during the early and mid-Holocene, which has been documented from several other sites on the south Brazilian highlands (e.g. Behling, 1995, 1997).

Fire became frequent for the first time at about 7400 cal BP (6500 ^{14}C yr BP), perhaps in response to the onset of occupation by Amerindians (Dillehay et al., 1992), who may have used fire for hunting, coupled with seasonal climatic conditions leading to accumulation of flammable biomass. In the Serra Campos Gerais region in Paraná fire became common already at the beginning of the Holocene, suggesting an earlier occupation than in the southernmost highland region. Fire was facilitated by the presence of Poaceae species, likely tall grasses that can lead to accumulation of large amounts of highly flammable biomass during the growing season (Pillar and de Quadros, 1997). The abundance of Poaceae and the decrease of some other Campos taxa suggest that frequent fires may have been a driving factor changing the floristic composition of the Campos (Bond and van Wilgen, 1996).

5.3. Late Holocene (zones CDS-V to CDS-VII: 4320 cal yr BP to modern, 3950 ^{14}C yr BP to modern)

During the older interval (zone CDS-V), the fern *Blechnum imperiale* was a common element on the bog, before becoming rare during the two following periods. *Sphagnum* became abundant in the peat bog during the second period (zone CDS-VI), but rare thereafter.

During the initial late Holocene period (zone CDS-V; 4320–1100 cal yr BP), *Araucaria* forests expanded in the region, forming a net of gallery forests along streams, while regionally grassland vegetation dominated. During this period, forest expansion was not continuous and the occupied area remained relatively constant. *Araucaria* forests included populations of *Myrsine* and less frequently individuals of arboreal plants such as *Mimosa scabrella*, Myrtaceae, *Podocarpus* and *Ilex*. The tree fern *Dicksonia sellowiana* was common in the gallery forests. *Weinmannia* was perhaps also present with few individual trees in the *Araucaria* forests and was possibly common on the slopes of the coastal mountains. Pollen grains of *Weinmannia* could have been transported by wind over some distance. The Atlantic rain forest taxa and probably also cloud forest species were well established on the upper coastal slopes, located about 6–10 km distance to the study site since the late Holocene.

The rate of vegetation change increased sharply during the late Holocene. The undirectional phase that characterized the vegetation trajectory after the initial expansion of the *Araucaria* forest taxa, until around 1736 cal yr BP, coincides with an interval of highly stable pollen composition, including presence of Campos taxa. This situation could be similar to present-day *Araucaria* forest patches occurring in a matrix dominated by Campos grassland.

The first expansion of the *Araucaria* forest has been dated between 2400 and 3400 ^{14}C yr BP at other sites on the southern highlands: at 2850 ^{14}C yr BP, interpolated age (Serra Campos Gerais), 3460 ± 195 ^{14}C yr BP (Serra da Boa Vista) and 2385 ± 225 ^{14}C yr BP (Serra do Rio Rastro) (Behling, 1995, 1997). In São Francisco de Paula (Rio Grande do Sul) pollen preservation in the deposits started after 4000 ^{14}C yr BP, indicating wetter climatic conditions (Behling et al., 2001). The new radiocarbon date from the Cambará do Sul site at 4320 cal yr BP (3950 ^{14}C yr BP) may date the changes much precise than the earlier dates.

During the second period in the late Holocene (zone CDS-VI; 1100–430 cal yr BP), a remarkably strong expansion of *Araucaria* forest taxa took place, primarily *Araucaria angustifolia* and *Mimosa scabrella*, within 100 years replacing the Campos vegetation. *Dicksonia sellowiana* followed the expansion of the *Araucaria* forests.

At about 1100 cal yr BP (1140 ^{14}C yr BP), carbonized particles became less frequent in the sediments. The expansion of the *Araucaria* forests reduced the area of Campos near the peat bog and fires became rare near the peat bog during the entire late Holocene period. The somewhat higher accumulation rates of carbonized particles indicate that fires were still frequent in the wider region.

The increase in Araucaria forest taxa occurred rapidly between 1736 and 1000 cal yr BP, as is depicted by the clearly directional phase in vegetation dynamics of this period. The cause of this change is primarily related to the climate but could as well be the consequence of the reduction of Campos vegetation which then tended not to burn as frequently.

The increase of *Araucaria angustifolia* from 14 to 42% of the total pollen grains is due to the fact that the studied peat bog became surrounded by forest. In other records from peat bogs in the southern Brazilian highlands surrounded by Campos vegetation, *Araucaria* pollen increase only by 3–10% (Behling, 1995, 1997). The marked expansion of the *Araucaria* forest has been dated at other sites on the highlands at 1530 ^{14}C yr BP (Serra Campos Gerais) and about 1000 ^{14}C yr BP (Morro da Igreja and Serra do Rio Rastro). In the São Francisco de Paula area the expansion started at 1060 ^{14}C yr BP, but the expansion of the *Araucaria* trees themselves at 850 ^{14}C yr BP (interpolated age). At present the radiocarbon date of 1100 cal yr BP (1140 ^{14}C yr BP) from Cambará do Sul is the best date for this vegetational and climatic event. It is still unclear whether the recorded strong *Araucaria* expansion in Paraná was earlier, as is suggested by the radiocarbon date of 1530 ^{14}C yr BP, than on the southernmost highlands or corresponds to the same time period.

During the uppermost late Holocene period (zone CDS-VII; 430 cal yr BP to modern), the *Araucaria* forests kept expanding, reducing the Campos area in the study region. Most striking in this zone is the expansion of the *Weinmannia* population within the *Araucaria* forests, probably starting from the coastal slopes into the highlands, from 430 cal yr BP (410 ^{14}C yr BP) onwards. After 183 cal yr BP (172 ^{14}C yr BP) the *Weinmannia* population decreased significantly, before human disturbance of the *Araucaria* forest began.

The increase of Poaceae pollen (13.5 cm core depth) and then Cyperaceae pollen (9.5 cm) at about 167 cal yr BP, AD 1783 (157 ^{14}C yr BP) and about 103 cal yr BP, AD 1847 (96 ^{14}C yr BP), respectively, indicate a disturbance of the *Araucaria* forest, probably by cattle in the forest. The village of Cambará do Sul (7 km distance to the study site) was founded in 1864. The first farmers had free-range cattle likely entering the forest somewhat earlier. The first *Pinus* pollen grains (11 cm core depth) have been found at about 127 cal yr BP, AD 1823 (118 ^{14}C yr BP). This coincides with the first German settlements on the lower slopes of the Serra Geral in Rio Grande do Sul, around AD 1825, which may have introduced the exotic taxa. A decrease in *Araucaria angustifolia* pollen was detected between 30 and 14 cal yr BP (AD 1920 and 1936), signalling the start of intense selective logging. The sharp directional change in the pollen composition trajectory by this time forms another indication of this. An enormous reduction of *Araucaria angustifolia* (decrease of pollen from 41 to 2%, starting at 3.5 cm core depth) begins at about 8 cal yr BP, AD 1942 (6 ^{14}C yr BP), with intensified selective logging of *Araucaria* trees during the last 50–60 years, but still not in the surroundings of the peat bog. Due to cattle grazing in the forest and the logging of the *Araucaria* trees, other tree species, especially *Mimosa scabrella*, and Myrtaceae, *Lamanonia speciosa*, and *Ilex*, became more frequent in the now secondary vegetation. Also, *Dicksonia sellowiana* were removed from the *Araucaria* forest during the last 50–60 years. Tree fern trunks are used for orchid and other ornamental plant cultivation.

The expansion of the *Araucaria* forests, including tree ferns, is probably related to a change to a wetter climate, with higher rainfall rates and a shorter annual dry season, during the period between 4320 and 1100 cal yr BP (3950 and 1140 ^{14}C yr BP). Remarkable is the pronounced presence of *Weinmannia* populations within the *Araucaria* forest between 430 and 183 cal yr BP (410 and 172 ^{14}C yr BP), i.e. between AD 1520 and 1767. This signal is also clearly detected in the vegetation trajectory, where a switch in pollen composition towards *Weinmannia* and other species is reversed back to the typical composition of the *Araucaria* forest at the end of the period. This signal captured in the vegetation dynamics is not related to the introduction of cattle. Cattle was introduced to the highland Campos only in the first decade of the 18th century by the Jesuits from the missions on the east side of the Uruguay River (Porto, 1954). Today, *Weinmannia* does not frequently occur in the *Araucaria* forest (Cuatrecasas and Smith, 1971). These vegetational changes document a warm period of about 250 years during the period of the so-called Little Ice Age. In the Northern Hemisphere the Little Ice Age cooling occurred between AD 1450 and 1850 (e.g. Eddy, 1976). *Weinmannia* needs warmer climatic conditions and a certain amount of precipitation to grow on the southernmost Brazilian highlands (Behling, 1995). The slight increase of *Piper* during this period supports this interpretation, for most species of this genus grow in the Atlantic rain forest (Klein, 1979). After this period *Weinmannia* became rare in the *Araucaria* forests, indicating somewhat cooler, modern climatic conditions.

6. Conclusions

The pollen and charcoal records from Cambará do Sul (Table 3) reveal for the first time insight into the palaeoenvironment of the southern Brazilian highlands during the pre-LGM and LGM periods. Seven AMS radiocarbon dates and high-resolution sampling of the lake and peat bog deposits allow a detailed analysis and decadal resolution of the last 1100 years. Furthermore, the Cambará do Sul record documents for the first time how a peat bog site became surrounded by *Araucaria* forest, allowing realistic interpretation of the vegetation dynamics within the *Araucaria* forest of northeastern Rio Grande do Sul.

Multivariate analysis of the pollen data, with examination of the palaeovegetation trajectory in ordination space and the measuring of velocity of compositional change, brings new insight into the dynamics of the vegetation in the south Brazilian highlands. The pollen composition revealed both undirectional, chaotic, phases and phases with directional, sometimes fast moving, vegetation changes, supporting the theory that vegetation is a complex system with a dynamics characterized by a convolution of alternating determinism and chaos. Our results give additional evidence that vegetation dynamics is slower in cooler periods (LGM compared to pre-LGM) and faster in warmer periods (Holocene).

Initially, the studied peat bog was a permanent shallow lake (42 840–41 470 ^{14}C yr BP). Later, the water level decreased (41 470–26 900 ^{14}C yr BP) and then the lake changed to a non-permanent lake (26 900–10 120 ^{14}C yr BP). The peat bog started to develop at the beginning of the Holocene.

Since the beginning of the record at 42 840 ^{14}C yr BP, species rich Campos (grassland) vegetation characterized the south Brazilian highlands. *Araucaria* forests were not found on the highlands themselves during glacial times. The pollen data suggest that small populations of the *Araucaria* and the Atlantic rain forest trees may have been present on the wetter coastal slopes, which may have served as a refugium. It is also suggested that deep and protected river valleys on the southern highlands (probably at some distance from the study site) may have served as forest refugia for species of the *Araucaria* forest.

Campos vegetation prevailed on the southernmost highlands during early and mid-Holocene times, but the first small *Araucaria* forest populations migrated along the river valleys to the study region. At the beginning of the Holocene the species composition of the grassland changed, which is probably related to the Holocene warming. During the late Holocene period, i.e. at 4320 cal yr BP, the *Araucaria* forests expanded and created a net of gallery forests along the streams. Campos still formed the predominant vegetation until 1100 cal yr BP. Then the *Araucaria* forest trees, especially *Araucaria angustifolia* itself, overtook the

Table 3
Pollen zones of Cambará do Sul, showing core depth, the calculated radiocarbon age and the number of pollen subsamples of each pollen zone

Zone	Depth (cm)	Age range (^{14}C yr BP)	Age range (cal yr BP)	Number of subsamples
Zone CDS-I	211–203.5	42 840–41 470		8
Zone CDS-II	203.5–141.5	41 470–26 900		62
Zone CDS-III	141.5–109	26 900–10 120		25
Zone CDS-IV	109–81	10 120–3950	11 540–4320	15
Zone CDS-V	81–55.5	3950–1140	4320–1100	24
Zone CDS-VI	55.5–29.5	1140–410	1100–430	26
Zone CDS-VII	29.5–0	410 to −50	430 to −50	30

Table 4
Pollen taxa abbreviations used in the ordination diagrams

Abbreviations	Pollen taxa
Acal	*Acalypha*
Alch	*Alchornea*
Amar	Amaranthaceae/Chenopodiaceae
Apia	Apiaceae
Aran	*Araucaria angustifolia*
AsTu	Asteraceae subf. Asterioideae
Bacc	*Baccharis*-type
Cecr	*Cecropia*
Celt	*Celtis*
Clet	*Clethra*
Cype	Cyperaceae
Daph	*Daphnopsis*
Dick	*Dicksonia sellowiana*
Echi	*Echinodorus*
Erio	*Eriocaulon/Paepalanthus*
Eryn	*Eryngium*-type
Eute	*Euterpe/Geonoma*-type
Hydr	*Hydrocotyle*
Ilex	*Ilex*
Jung	*Jungia*-type
Lasp	*Lamanonia speciosa*-type
Ludw	*Ludwigia*
Mela	Melastomataceae
Misc	*Mimosa scabrella*-type
Mora	Moraceae/Urticaceae
Mori	*Moritzia dasiantha*
Myri	*Myriophyllum*
Myrs	*Myrsine*
Myrt	Myrtaceae
Pamp	*Pamphalea*
Phry	*Phrygilanthus acutifolius*
Pinu	*Pinus*
Pipe	*Piper*
Plau	*Plantago australis*-type
Pltu	*Plantago turficola*-type
Poac	Poaceae
Proc	*Prockia curis*-type
Schi	*Schinus*-type
Seba	*Sebastiana brasiliensis*
Seco	*Sebastiania commersionia*
Sene	*Senecio*-type
Sola	*Solanum*
Stru	*Struthanthus*
Trem	*Trema*-type
Wein	*Weinmannia*
Xyri	*Xyris*
Zant	*Zanthoxylum*
cPro	cf. *Prockia*

Campos vegetation of the study region. For a certain time interval, between AD 1520 and 1780, *Weinmannia* became frequent in the *Araucaria* forest. Some years later, Poaceae and subsequently Cyperaceae pollen increased, indicating that cattle invaded the forest. The introduction of the exotic pine into southern Brazil about 180 years ago, the collection of tree fern trunks, the very strong logging of *Araucaria* trees during the last 50–60 years, and the alteration of the original forest to a secondary forest, are registered in the pollen record as well.

The charcoal record documents that natural fires were rare during glacial times. Fire became very frequent only after about 7400 cal BP, suggesting anthropogenic fires due to the first human occupation of the southernmost highlands. Frequent fires may have been an important factor changing the floristic composition of the grassland at that time. Due to the marked expansion of the *Araucaria* forest since 1100 cal yr BP, fire was rare in the surroundings of the peat bog, but human-related fires were probably still frequent in the Campos of the studied region.

The reconstructed palaeovegetation indicates cold and relatively dry climatic conditions for the glacial period. Late Pleistocene cooling, especially during the LGM period, of 5–7°C is also suggested for the south Brazilian highlands. The absolute minimum temperatures were probably below −10°C. Shallower lake conditions suggest that the period between 41 470 and 26 900 ^{14}C yr BP was somewhat drier than the episode between 42 840 and 41 470 ^{14}C yr BP. The pollen data indicate that the LGM formed the driest period recorded. During the LGM and the late-glacial era, the shallow lake was not permanent, pointing to a seasonal climate with a long annual dry period. The Cambará do Sul record suggests that on the south Brazilian highlands a seasonal climate developed after 26 900 ^{14}C yr BP. The warm early and mid-Holocene periods were still dry with a dry season of probably about 3 months. Annual precipitation must have been below 1400 mm. After 4320 cal yr BP climate became wetter, but a permanently wet climate without seasonality is found only since 1100 cal yr BP. The frequent distribution of *Weinmannia* trees within the *Arau-*

caria forest between AD 1520 and 1770 documents a warm period on the south Brazilian highlands during the Little Ice Age.

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