Related changes in biodiversity, insolation and climate in the Atlantic rainforest since the last interglacial

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ABSTRACT

The long-term Colônia record is located in the Atlantic rainforest domain in Brazil (23°52′S 46°42′20″W 900 m a.s.l.). The 780 cm long core CO3 provides a coverage of a complete interglacial/glacial cycle for the first time in a neotropical rainforest. Information on the behavior of tropical climates compared to global changes in temperatures indicates specific climate responses in terms of precipitation at these latitudes. Winter extratropical circulation was very active during the last interglacial and most of the glacial. Floristic composition of the rainforest changed several times in each phase of expansion, twice during the interglacial, and three times during glacial episodes. *Araucaria* was well developed in the area of São Paulo until the beginning of the first dry phase of the glacial at ca. 50,000 yr B.P. Changes in insolation controlled the expansion of the rainforest and the tropical hydrological cycle as evidenced by a strong precession signal. However precession had no impact on regional climatic features. The two interglacials (MIS 5e and Holocene) showed completely different patterns attesting to the continuous evolution of the forest. The biodiversity index (Shannon–Wiener Index) remained high during both the interglacial and glacial attesting to the permanence of small patches of rainforest refugia during drier phases. The lowest Shannon-Wiener Indexes were recorded between 23,000 and 12,000 yr B.P. and 40,000 and 30,000 yr B.P. and characterize two marked phases of stress for the rainforest.

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1. Introduction

Global climate fluctuations, and more particularly glacial/interglacial cycles, have major consequences for the distribution of living organisms (Bennett, 1997; Hewitt, 2000). Genetic analysis has already highlighted colonization, refugia, and a mixture of broad spatial scale populations based on their DNA structure (Davis and Shaw, 2001; Petit et al., 2002). However, without a time scale, regional evolution, rates of change, and climate controls cannot be satisfactorily characterized. Low latitude rainforests have the greatest biodiversity, but are also being rapidly deforested and are thus in danger of disappearing before we have had time to study both their richness and their behavior during climate changes. How can their regeneration and conservation be ensured if we do not know how rainforests reacted to global climatic changes in the past? Only well dated paleorecords can provide such information (Willis et al., 2007). The term "biodiversity hotspot" refers to a region with a great diversity based on levels of richness, complementary endemism and, according to Myers et al. (2000), a region where at least 70% of the

original cover has been lost. The Atlantic rainforest in Brazil is one of these hotspots and is seriously threatened – while 20% of the Amazon forest has been destroyed and over 93% of the Atlantic rainforest has already disappeared (Joly et al., 1999; Oliveira Filho and Fontes, 2000; Ledru et al., 2007). A wide range of temperature and topography contributes to the immense variety of plants and animals found in the Atlantic rainforest. Today 130 million people or 70% of the total Brazilian population live in an area that was formerly totally covered by this rainforest. After 500 years of intensive deforestation and associated agriculture (mainly coffee and banana), only small isolated patches of forest remain today. Will global warming shift remaining rainforest to another latitude and threaten another fragile ecosystem as predicted in the Andes with the uplift of the vegetation gradient to paramos (Bush, 2002)? How did the Atlantic rainforest react to increases in temperature in the past? Available pollen records from the Atlantic rainforest cover the late Quaternary. In the southern part of Brazil between 25° and 23°S, the Atlantic rainforest expanded from the last glacial period only during the past 7000 years and was not recorded during the preceding 15,000 years (Behling, 1997; Behling et al., 1997), while in central Brazil the Salitre pollen record (19°S 46°46′W) attests to different phases of expansion, one before the Last Glacial Maximum (LGM), and another between ca. 15,000 and 12,000 yr B.P. indicated by the

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presence of *Araucaria* (Ledru et al., 1996). These results suggest that it is important to take latitudinal and regional effects into consideration when interpreting broad scale changes in the distribution and composition of the Atlantic rainforest (Ledru et al., 2007). Here we present a long-term environmental record located within the Atlantic rainforest domain, in the Colônia crater, São Paulo, Brazil. This is the first South American long-term record that traces the evolution of a neotropical rainforest over a complete glacial/interglacial cycle.

2. Modern settings

2.1. Colônia crater

Colônia is a probable impact crater 3.6 km in diameter filled with 450 m of mainly organic Neogene and Quaternary sediments, located within the city of São Paulo (23°52′S, 46°42′20″W, 900 m a.s.l.) (Riccomini et al., 1991). Its location near the Atlantic Ocean and in the Serra do Mar mountain range, only a few kilometers from the shoreline, means the vegetation is highly sensitive to changes in sea level and temperature. The 780 cm long core CO3 was drilled in the peat in the central part of the crater using a Martin vibra corer (Martin et al., 1995; Ledru et al., 2005).

2.2. Climate

Today the climate features of the Colônia region are characterized by a mean annual precipitation of 1700 mm and a mean winter temperature of ~ 15 °C (Fig. 1). The short (two-month) dry season with around 50 mm precipitation, is attenuated by frequent cloud cover and drizzle brought by maritime winds. Seasonal climate is controlled by the position of the Inter Tropical Convergence Zone or meteorological equator that divides the year into a rainy (austral summer) and a dry season (austral winter). The position of the South Atlantic Convergence Zone (SACZ) also controls seasonal moisture at this latitude (Carvalho et al., 2004). During the austral summer, when the ITCZ is dislocated to the south and the SACZ is located at 20°S±3°, moisture transported by the trade winds from the equatorial Atlantic towards the Amazon basin, named the South American Summer Monsoon (SASM) (Gan et al., 2004). These trade winds are channeled to the south-east by the Andean Cordillera where they are incorporated into the SACZ (Lenters and Cook, 1999; Pezza and Ambrizzi, 2003). The absence of the SACZ induces severe droughts in the area. During the winter season, the ITCZ moves to its northernmost position ~ 10°N and the dry season begins. However, the winter dry season is often attenuated by extratropical circulation and the presence of the SACZ; polar air incursions regularly reach theses latitudes in winter

Fig. 1. Map showing the seasonal atmospheric circulation that controls the distribution of rainfall at the latitude of São Paulo: positions of the ITCZ in austral winter (northernmost) and austral summer (southernmost), austral summer circulation of the SASM, year-round northernshifts of polar advections and mean localization of the SACZ, with location of the Colônia crater (23°S). In the bottom corner the climatic diagram of the city of São Paulo.

(Leroux, 1998; Garreaud, 2000) and when they meet the tropical moist air of the SACZ, high rainfall occurs during winter (June–August) in the Colônia region (Fig. 1) (Marengo et al., 1997).

2.3. Vegetation

The Atlantic rainforest vegetation is broadly distributed and encompasses a large number of biomes that depend on the year-round distribution of precipitation and the range of mean annual temperatures (Oliveira Filho and Fontes, 2000; Oliveira Filho et al., 2006). Today the *Araucaria* forest is located mainly farther south, ca. 300 km from Colônia, where permanent rainfall and drizzle and low temperatures enable it to develop fully. Semideciduous forest, in the Colônia region, is associated with a short dry season and a mean annual temperature of ca. 15 °C. Other patches of Atlantic rainforest, e.g. in northeastern Brazil, are maintained as refugia under favorable edaphic or atmospheric moisture (Ledru et al., 2007).

A botanical survey was carried out in the region of Colônia (Garcia and Pirani, 2005). Among the local plants identified in the peat bogs inside the crater were *Sphagnum, Baccharis sp.* (Asteraceae), *Tibouchina sp* (Melastomataceae*), Eriocaulon sp* (Eriocaulaceae), *Utricularia sp* (Lentibulariaceae), *Hyptis sp.* (Lamiaceae), *Cuphea sp.* (Lythraceae), *Xyris sp.* (Xyridaceae), *Drosera sp. (Droseraceae)* and the tree fern *Cyathea* (Cyatheaceae). In the Atlantic rainforest, on the margins of the crater, the main tree taxa identified were Myrtaceae with 12 genera, *Myrsine sp.* (Myrsinaceae), *Alchornea sp.* (Euphorbiaceae), *Podocarpus*

sellowii (Podocarpaceae), *Daphnopsis sp.* (Thymeleaceae), *Hedyosmum sp.* (Chloranthaceae), *Drymis winteri* (Winteraceae), Rubiaceae with 16 genera, the palms *Bactris sp., Euterpe sp.* and *Geonoma sp.,* and epiphytes of the Bromeliaceae and Orchidaceae families.

According to our field observations, the region of São Paulo can be classified as « degraded *Araucaria* forest » as only single individuals of *Araucaria angustifolia* (Bert.) Kuntze were found in shadowy ravines. *Podocarpus sellowii* Klotzsch ex Endl., another tropical conifer, is seldom found in this area although we observed this conifer growing in a recently planted *Eucalyptus* forest.

3. Methods

3.1. Lithology of core CO3

We distinguished three different sedimentological units. Between a depth of 760 and 450 cm was black and extremely compacted peat, between 450 and 355 cm the organic layer was very sandy, and from 355 cm to the surface the sediment was characterized by a pure black very moist peat (Fig. 2).

3.2. Pollen analysis

The core was sampled for pollen analysis at 2-cm intervals. Pollen samples were prepared following standard treatment (Faegri and Iversen, 1989) and mounted on microscope slides in silicon oil. Pollen
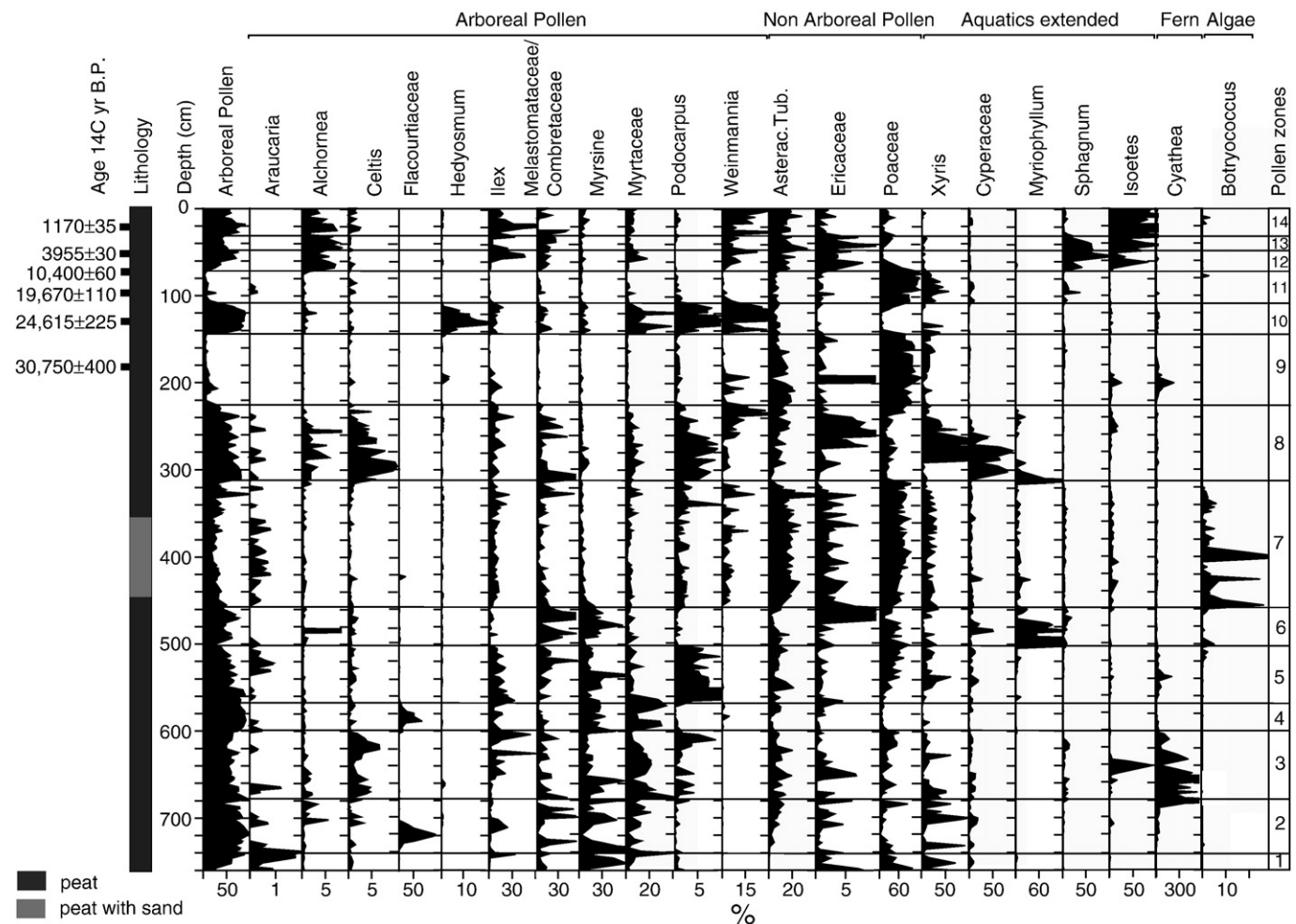

Fig. 2. Synthetic pollen diagram of the Colônia core CO3. The 21 most common selected taxa are expressed as percentages of the total pollen sum that excludes aquatics and ferns, and represented along a depth scale.

counts were performed under 1000X magnification and pollen was identified by comparison with our reference pollen collection. A total of 300 trees and herb pollen grains were counted for each sample. Fern spores and aquatic taxa were excluded from the total sum for percentage calculation. Arboreal Pollen frequencies (AP) are plotted along a depth scale in Fig. 2 and along a time scale in Fig. 4. Tree pollens included all taxa characteristic of the Atlantic rainforest with conifers such as *Araucaria* and *Podocarpus* and a wide range of angiosperms including heliophilous taxa such as *Alchornea, Myrsine* and *Celtis* (see Appendix).

3.3. Biodiversity measure

To measure the changes in plant life forms within the Atlantic rainforest we used the Shannon–Wiener diversity index (S–W). This index accounts for both abundance and representation of the species and characterizes species diversity within a community. The proportion of species *i* relative to the total number of species (*pi*) was calculated, and then multiplied by the natural logarithm of this proportion (ln*pi*). The resulting product was summed across species, and multiplied by −1 (Fig. 5).

At Colônia, values of the S–W Index ranged between 1.1 at a depth of 75 cm (the lowest) and 4.4 at a depth of 137 cm (the highest). The mean values of the S–W Index were calculated for each pollen zone and are presented in Fig. 4.

3.4. Chronology

The original chronology is based on six radiocarbon ages derived from the top two metres of sediments (Table 1). As the limit of radiocarbon dating was obtained with an age of 30,750± 400 ^{14}C yr B.P. at a depth of 182 cm, we then compared our record with a speleothem record located ca. 200 km south of Colônia and dated by Ur/Th ratio (Cruz et al., 2006). Strong similarities appeared between the records and we correlated peaks in AP with peaks in $\partial^{18}O$ to give an estimated age of 100,000 years at the base of the core. Extrapolated age/depth and extrapolated age/AP% curves were built based on these matches (Ledru et al., 2005). This extrapolated curve was then compared to summer insolation at 20°S. We observed that peaks in arboreal pollen closely coincided with insolation maxima in the dated top part of the record (Fig. 5). However, the extrapolated dates from Ledru et al. (2005) obtained at the base of the record did not match the insolation maxima. The age curve was extrapolated and was consequently subject to "incertitude"; we re-adjusted our first age model so that each peak in insolation would fit a peak in arboreal pollen. We conducted a spectral analysis with the free software AnalySeries (Paillard et al., 1996). Only one signal was obtained: the precession cycle, 20,000 yr (Fig. 3). The resulting extrapolated age model showed that the base of the core is approximately at 130,000 years old and that the record of Colônia covers the last interglacial, the last glacial stage and the Holocene. However in the text we use the words "approximately" or "ca." and show these ages in grey in

Table 1
Radiocarbon ages of Total Organic Matter from core CO3. Calibrated ages are calculated from Stuiver et al. (1998) and Jöris and Weninger (1998)

Depth in cm	Age (^{14}C yr B.P.)	Laboratory number	$\partial^{13}C$	Age range (cal yr BP)*
21–23	1170±35	LY 11500	−28,47	2980–2775
51–53	3955±30	LY 11501	−27,6	4565–4350
71–73	10,400±60	LY 11502	−23,11	12,885–11,980
101–103	19,670±110	LY 11503	−23,48	25,200–23,615
129–131	24,615±225	LY 11504	−28,72	30,400–28,225
181–183	30,750±400	LY 11505	−24,27	36,700–33,150

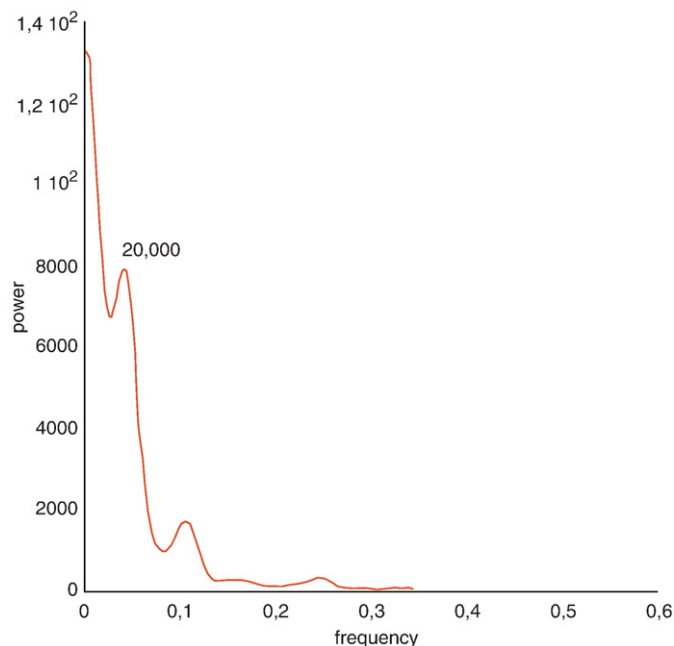*Range at two standard deviations with error multiplier of 1.0; cal.=calibrated.

Fig. 3. Spectral analysis performed on the pollen spectra of core CO3 showing the 20,000 yr cycle signal (Analyseries 2.0 Paillard et al., 1996).

Figs. 4–6 to indicate that these values are extrapolated and should be interpreted with caution.

4. Results

Based on changes in the proportions of AP we recognized 14 pollen zones in the simplified diagram numbered from 1 (the oldest) to 14 (the youngest) (Figs. 2 and 4). Over 239 taxa were identified, all of which are found in the Atlantic rainforest domain today (Appendix). Twenty-one of the most representative taxa were selected for presentation in a simplified synthetic diagram (Fig. 2). Interpretation of the results is based on analysis of surface pollen samples (Ledru, 1993; Ledru, 2002).

Pollen zone COL 1 extends from 760 to 740 cm, and includes 6 samples whose age was estimated at between 134.5 and 130.9 cal kyr B.P.

Zone 1 is characterized by high percentages of Arboreal Pollen (ranging from 25% to 88%). Among the main taxa, we distinguished *Araucaria* (ranging from 0.5 to 2%) i.e. the highest frequencies of *Araucaria* recorded in the whole core CO3, *Myrsine* (5–40%), *Celtis* (~0.5%), *Podocarpus* (0–2%), Melastomataceae/Combretaceae (4–12.5%), *Ilex* (0.5%), Myrtaceae (1.5–40%). Pollen grains of *Araucaria* are not transported very far and surface samples show frequencies of 5 to 10% within the forest. In the middle of a 3.6 km diameter crater, these frequencies drop down to less than 1%. Therefore we consider that a frequency of 1% *Araucaria* pollen together with the *Araucaria* forest association of taxa as a whole indicates the presence of a well developed *Araucaria* forest at the beginning of the record. Among the herbs, Poaceae (6–68%) and Ericaceae (0.25–8%) are dominant. The aquatics, ferns, algae and bryophytes represented by *Myriophyllum* (3–0%), Cyperaceae (0.2–10%), *Xyris* (0–7%), *Cyathea* (0–4%), *Isoetes* (0–2%) and *Sphagnum* (1% –0) attesting to moisture within the crater. The mean biodiversity index of this zone is rather low at 2.7 (Fig. 4). The climate of zone COL 1 is characterized by permanent moisture (precipitation or drizzle) and a mean winter temperature of ~12 °C according to Ledru (1993).

Pollen zone COL 2 extends from 740 to 680 cm in depth and includes 17 samples whose age is estimated at between 130.9 and
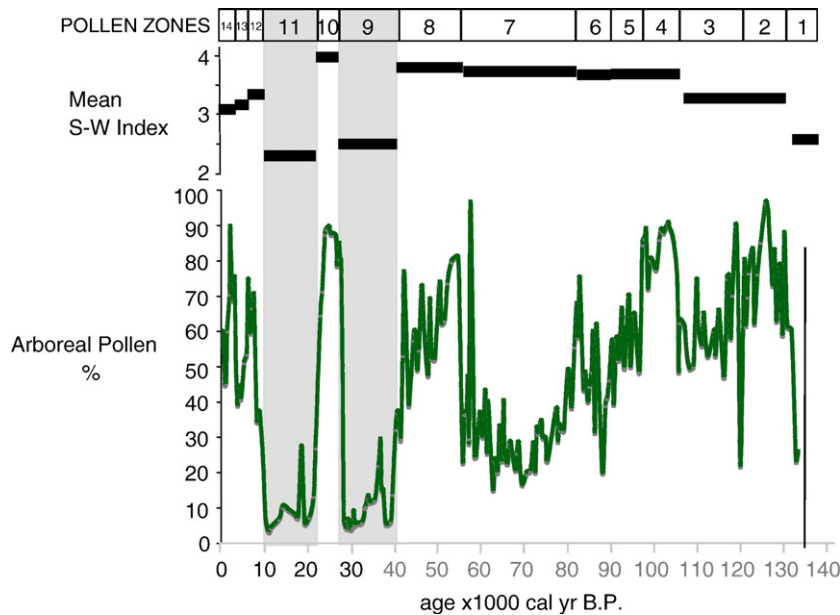
Fig. 4. Changes in tree pollen frequencies of core CO3 represented along a time scale. For a description of the pollen zones see the text. The mean value of the Shannon–Wiener index is shown for each pollen zone. Ages shown in grey are extrapolated and should therefore be interpreted with caution.

120.5 cal kyr B.P. This zone is characterized by high percentages of AP ranging from 96% to 21% with a peak of 81–82%, Flacourtiaceae sp. at a depth of 718–720 cm and, in general, the dominance of Flacourtiaceae sp. between 726 and 707 cm. Among the other tree taxa, Melastomataceae/Combretaceae (0.5–48%), *Myrsine* (2–64%), Myrtaceae (2–20%), *Podocarpus* (0–3%), *Weinmannia* (0–0.3%) *Alchornea* (0–5%), *Celtis* (0–3%), *Hedyosmum* (0–0.3%), Ilex (1–16%) are observed. We noted a progressive increase in the herb Asteraceae tubuliflorae (0.2–12%) along with a progressive decrease in Poaceae (0–59%). Ericaceae (0–6%), the aquatics *Myriophyllum* (0–0.3%), Cyperaceae (0–18%) and *Xyris* (0–10%), ferns and bryophytes *Cyathea* (0–>100%), *Isoetes* (0–9%), *Sphagnum* (0–2%) and algae *Botryococcus* (0–1%) were recorded. The mean S–W Index increases to 3.2 characterizing high species and biodiversity richness. The forest was still present although its composition had changed. *Araucaria* trees disappeared in favour of a moist tropical forest with a floristic composition similar to the one we observed today around the crater. The only anomaly is the high frequencies of Flacourtiaceae spp. for which we do not have any modern analogs. The abundantly represented tree fern *Cyathea* probably extended to the middle of the crater as it does today.

Pollen zone COL 3 extends from 678 to 600 cm in depth, and includes 22 samples with an estimated age of between 120 and 106.4 cal kyr B.P. This zone is characterized by a decrease in AP (from 90% to 47%) and the absence of Flacourtiaceae compared with the previous pollen zone. The peak of 90% at a depth of 680 cm is due to high frequencies of the *Myrsine,* Myrtaceae and Melastomataceae/Combretaceae association. Among the tree taxa were observed *Araucaria* (1–0%), *Alchornea* (0–1.7%), *Celtis* (0.5–7%), *Hedyosmum* (0–1.4%), Ilex (0–35%), Melastomataceae/Combretaceae (3–26%), *Myrsine* (4–31%), Myrtaceae (4–43%) and *Podocarpus* (0–8.6%). The herbs Asteraceae tubuliflorae (3–19%), Ericaceae (0–6%) and Poaceae (0–40%) were observed. Aquatics *Myriophyllum* (0–0.2%), Cyperaceae (0–13%), Xyris (0–6%), ferns and bryophytes *Cyathea* (155–11%), *Isoetes* (0–93%), *Sphagnum* (0–13%), and algae *Botryococcus* (0–0.4%) are also well represented. The mean biodiversity index (S–W) is the same as in the previous zone at 3.2. This pollen association characterizes a tropical forest with *Araucaria* trees on the margins and tree ferns in the crater. This type of forest is adapted to a cold and moist climate with permanent moisture.

Pollen zone COL 4 extends from 595 to 572 cm in depth and includes 8 samples with an estimated age of between 105.5 and 98.5 cal kyr B.P. This zone is characterized by an increase in AP (77–90%) mainly composed of the second and final increase in the frequency of Flacourtiaceae (7–35%). Other dominant tree taxa were *Ilex* (3.5–11.5%), *Myrsine* (7.5–22%), Myrtaceae (6.5–34%) and Melastomataceae/Combretaceae (1–19.5%). *Araucaria* (0.3–0%), *Alchornea* (0–0.7%), *Celtis* (0–1.5%), *Hedyosmum* (0–0.3%), *Podocarpus* (0–0.6%), *Weinmannia* (0–1%) are the other tree taxa represented. Asteraceae tubuliflorae (5–10%), Ericaceae (0–1.5%), Poaceae (1.5–7%), Cyperaceae (0–8%), *Xyris* (0–1.5%), *Cyathea* (0–9%), *Isoetes* (0–1%), *Sphagnum* (0–0.3%), *Botryococcus* (0–0.7%) are also observed. The mean S–W Index is higher than in the previous zone at 3.5. *Araucaria* forest was well represented although there is a change in the frequencies of herbs and local taxa. This change could be attributed to a change in soil moisture levels.

Pollen zone COL 5 extends from 565 to 505 cm in depth and includes 19 samples with an estimated age of between 98 and 89 cal kyr B.P. This zone is characterized by a decrease in AP (80–39%) but an increase in *Podocarpus* (2–58%), and the presence of *Ilex* (2–22%), Melastomataceae/Combretaceae (2–35%), *Myrsine* (5–52%), and *Araucaria* (0.9–0%); concomitantly a progressive increase in Poaceae (3–50%) is observed.

Other associated taxa are *Alchornea* (0–0.2%), *Celtis* (0–2%), *Hedyosmum* (0–0.4%), Myrtaceae (2–27%), *Weinmannia* (0–0.5%), Asteraceae tubuliflorae (2–21%) Ericaceae (0–4%), *Myriophyllum* (0–1%), Cyperaceae (0.3–20%), *Xyris* (0.2–6%), *Cyathea* (1–66%), *Isoetes* (0–9%), *Sphagnum* (0–5%), *Botryococcus* (0–2.5%). The mean S–W Index was still high at 3.5, i.e the same value as in the previous zone. The decrease in moisture rates observed at the end of the previous pollen zone is indicated by a peak in *Podocarpus* and the marked decrease in the herbs Poaceae and Asteraceae at the beginning of this zone. However the tendancy reversed in the middle of this zone with marked increases in *Cyathea* and *Myrsine*. The marked decrease in the frequency of heliophilous taxa (*Alchornea, Hedyosmum, Celtis*) that started in the previous zone continued.

Pollen zone COL 6 extends from 501 to 460 cm in depth and includes 14 samples with an estimated age of between 89 and 81.8 cal kyr B.P. This zone is characterized by an increase in AP (20–74%) with high frequencies of *Myriophyllum* (0–17%), and the presence of Melastomataceae/Combretaceae (0–53%), *Myrsine* (3–37%) and Poaceae (8–61%).
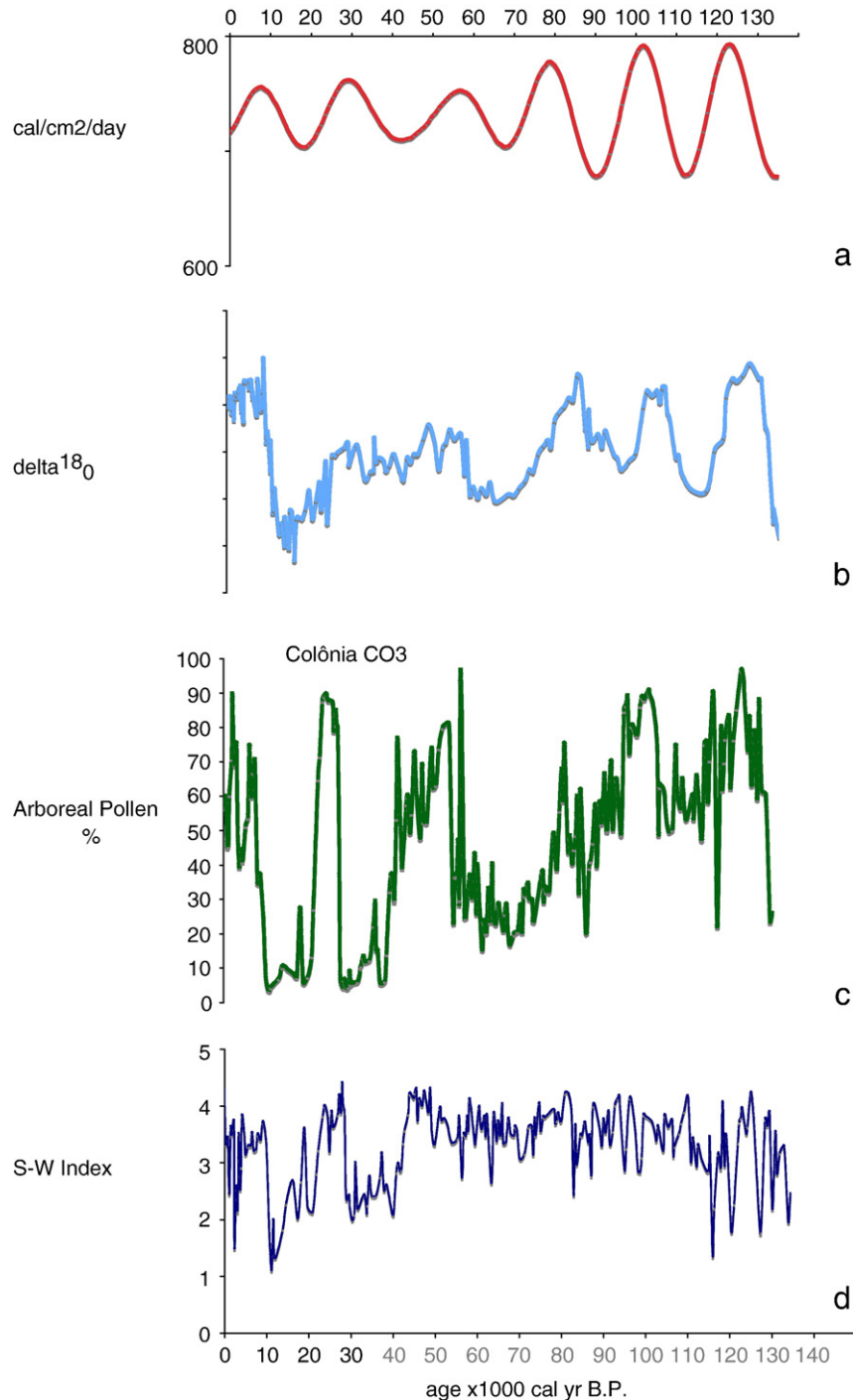
Fig. 5. Changes in a) insolation at 20°S during the austral summer (February) (Berger and Loutre, 1991), b) temperatures of Antarctica (EPICA, 2004), c) tree cover and d) biodiversity (Shannon–Wiener index) of the rainforest at Colônia São Paulo, Brazil. Ages shown in grey are extrapolated and should therefore be interpreted with caution.

Other associated taxa are *Araucaria* (0.3–0%), *Alchornea* (0–0.7%), *Celtis* (0.3–2%), *Hedyosmum* (0–0.3%), *Ilex* (0–3.6%), Myrtaceae (0–9%), *Podocarpus* (0–2%), *Weinmannia* (0–0.4%), Asteraceae tubuliflorae (1–16%), Ericaceae (0–20%), Cyperaceae (1–52%), *Xyris* (0–3.5%), *Cyathea* (0–5%), *Isoetes* (0–9%), *Sphagnum* (0–18%), *Botryococcus* (0–3%). Although changes in the frequencies of AP are observed in COL 4, 5 and 6, the biodiversity index is stable and high at 3.5.

The sediment in the crater changed toward that deposited in a shallow lake under cooler temperatures and/or less evapotranspiration as attested by the presence of *Myriophyllum*. The *Araucaria* forest was no longer represented and the forest is characterized by the dominance of pioneer taxa such as Melastomataceae/Combretaceae

and *Myrsine*. Today these taxa grow on the margins of the Andean forest at 3700 m asl. in Bolivia where they form sparse shrubs on the transition to the puna or in Brazil where different species grow either as trees or shrubs in Atlantic rainforest or Cerrado domains. These pollen spectra attest to a degradation of the rainforest that grew around the flooded crater.

Pollen zone COL 7 extends from 456 to 316 cm in depth and includes 42 samples with an estimated age of between 81 and 56.5 cal kyr B.P. This zone is characterized by a decrease in AP (47 to 17%), although a single peak of tree pollen taxa of 96% is observed at a depth of 328 cm composed of 17% *Ilex* (32%) Melastomataceae/Combretaceae (3%), *Myrsine* (14%), Myrtaceae (3%), *Symplocos* (3%), *Podocarpus*
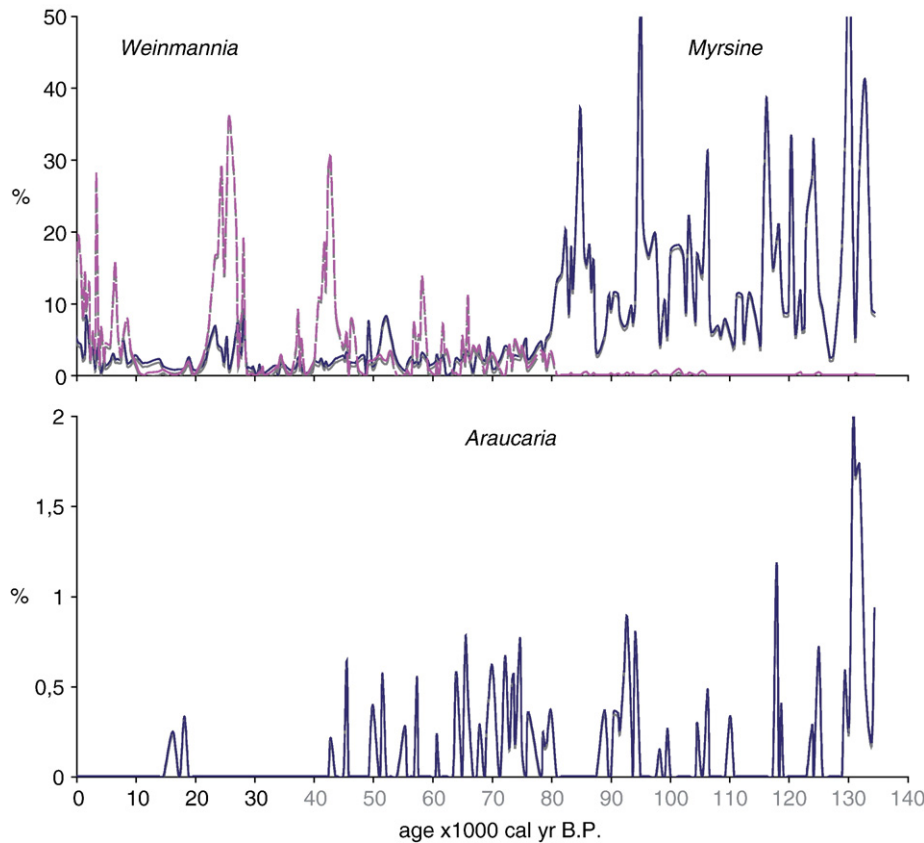
Fig. 6. Changes in floristic composition of the Atlantic rainforest: examples of *Myrsine/Weinmannia* (a) and *Araucaria* (b), where pollen frequencies are expressed along a time scale. Ages shown in grey are extrapolated and should therefore be interpreted with caution.

(13%), *Weinmannia* (14%). Other associated taxa are *Araucaria* (0,.8–0%), *Alchornea* (0–1.5%), *Celtis* (0–1.7%), *Hedyosmum* (0–1%), *Ilex* (0–17%), Melastomataceae/Combretaceae (1–32%), *Myrsine* (0–13%), Myrtaceae (0–14%), *Podocarpus* (0–10%), *Weinmannia* (0–14%), Asteraceae tubuliflorae (6–61%), Ericaceae (0.3–7%), Poaceae (26–66%), *Myriophyllum* (0–1.4%), Cyperaceae (0–18%), *Xyris* (0.2–3%), *Cyathea* (0–7%), *Isoetes* (2–19%), *Sphagnum* (0.3–13%) and *Botryococcus* (0–46%). The biodiversity index is high at 3.6 attesting to the permanence of rainforest flora in the area during a forest regression phase. The degradation of the rainforest that started in the previous zone continues. The pollen association suggests an open landscape with some trees or shrubs including *Araucaria* near springs. *Myriophyllum* was replaced by *Botryococcus* and sand was deposited in the sediment, as the shallow lake was still present in the crater at the time, probably seasonally. At the beginning of this pollen zone *Weinmannia* started to increase while *Myrsine* almost disappeared. It is difficult to infer to a climatic change to explain the interplay between these two taxa as they both characterize moist forested environments and grow in the *Araucaria* forest, the Atlantic rainforest, and the Andean forest. One taxon (*Weinmannia)* appears to have taken over the niche of another taxon, *Myrsine*, due to some marked change in environmental conditions (Fig. 6). The peak in tree pollen taxa at 328 cm, ca. 58 kyr B.P., corresponds to the abrupt development of the moist tropical forest due to warmer temperatures that lasted a short period. Moisture rates remained high as indicated by the algae and the *Araucaria*.

Pollen zone COL 8 extends from 312 to 227 cm in depth and includes 26 samples with an estimated age of between 55.8 and 40.9 cal kyr B.P. This zone is characterized by an increase in AP (30 to 81%) with conspicuous *Celtis* (0–10%), *Podocarpus* (1–9%), and *Alchornea* (0–13%). *Ilex* (2–14%), *Araucaria* (0.5–0%), Ericaceae (0–34%), *Xyris* (0–22%) and Cyperaceae (0–93%) are also well represented. *He-*

dyosmum (0–0.8%), Melastomataceae/Combretaceae (3–51%), *Myrsine* (0–8%), Myrtaceae (1–14%), *Weinmannia* (0–30%), Asteraceae tubuliflorae (1–17%), Poaceae (7–53%), *Myriophyllum* (0–18%), *Cyathea* (0–10%), *Isoetes* (0–18%), *Sphagnum* (0–1.5%), *Botryococcus* (0–0.4%) are also recorded. This pollen zone characterizes the re-expansion of the tropical forest, although the mean S–W Index of this zone is not very different from that of the previous zone at 3.7. Re-expansion of the forest was facilitated by the permanence of all the rainforest species in the area. Soil moisture decreased and there was the development of a *Xyris*-Cyperaceae herb field. Moisture was probably atmospheric and was able to maintain a dense cloud forest around the crater. Temperatures were cool as indicated by the presence of *Araucaria*.

Within this pollen zone, many abrupt brief changes in forest composition were observed. The progression of *Celtis* to *Podocarpus* and *Weinmannia,* and, among the non-arboreal pollen, from *Myriophyllum*–Cyperaceae–*Xyris*–Ericaceae–Poaceae for the local taxa, attest to gradual changes.

Pollen zone COL 9 extends from 223 to 144 cm in depth and includes 22 samples with an estimated age of between 40.2 to 28.8 cal kyr B.P. This zone is characterized by a decrease in AP (5–29%) and the dominance of Poaceae (38–74%) and Asteraceae tubuliflorae (4–22%). The other taxa observed are *Alchornea* (0–0.2%), *Celtis* (0–1%), *Hedyosmum* (0–1%), *Ilex* (0–11%), Melastomataceae/Combretaceae (1–3%), *Myrsine* (0–2%), Myrtaceae (0–3%), *Podocarpus* (0–1%), *Weinmannia* (0–9%), Ericaceae (0–3%), Cyperaceae (0–3%), *Xyris* (0–3%), *Cyathea* (0–75%), *Isoetes* (0–26%), *Sphagnum* (0–8%), *Botryococcus* (0–0.2%). This pollen zone displays the lowest frequencies of arboreal pollen of the record with the disappearance of *Araucaria*, which never recovered from this drastic climatic change. The mean S–W Index of this zone is very low at 2.4 indicating the stress to which the rainforest is subjected during this episode. An abrupt brief increase in moisture is

recorded at ca. 39 kyr B.P. Arboreal taxa were probably maintained as sparse shrubs growing near springs. The vegetation was dominated by Poaceae and Asteraceae tubuliflorae. The climate was dry with cool temperatures.

Pollen zone COL 10 extends from 142 to 113 cm in depth and includes 12 samples with an estimated age of between 28.5 and 23.5 cal kyr B.P. This zone is characterized by a sharp increase in AP (50–89%). High frequencies of *Hedyosmum* (1–20%), *Podocarpus* (0.3–17%) and *Weinmannia* (2–36%) characterized this pollen zone as do the presence of *Ilex* (2–11%), Melastomataceae/Combretaceae (3–12%), *Myrsine* (2–9%), Myrtaceae (6–55%). Also observed were *Alchornea* (0.3–3%), *Celtis* (0–1%), Asteraceae tubuliflorae (4–9%), Ericaceae (0–0.9%), Poaceae (1–29%), Cyperaceae (0–2%), *Xyris* (0–4%), *Cyathea* (1–14%), *Isoetes* (0–4%), *Sphagnum* (0–7%), *Botryococcus* (0–0.2%). The mean S–W Index of this zone increases sharply to reach 3.8, the highest value of the whole record.

This pollen zone marks the development of a tropical cloud forest under cool temperatures as attested by the presence of *Hedyosmum,* a taxon that today grows at the top of the serras in central Brazil, and at 2500 m asl. in the cloud forest of the eastern Andean Cordillera. The crater was entirely covered with forest as shown by the fact that non-arboreal pollen taxa were completely absent from this zone. Climate was moist with no dry season but with a permanent supply of moisture.

Pollen zone COL 11 extends from 108 to 68 cm in depth and includes 15 samples with an estimated age of between 23 and 9.9 cal kyr B.P. This zone is characterized by a decrease in AP (3–27%) and between a depth of between 90 and 95 cm a limited increase in *Araucaria* (up to 0.3%), *Celtis* (0–2%) and Melastomataceae/Combretaceae (0.4–7%) between ca. 18 and 16 kyr B.P. at the end of the glaciation. *Alchornea* (0–6%), *Hedyosmum* (0–0.1%), *Ilex* (0–4%), *Myrsine* (0.7–4%), Myrtaceae (0–6%), *Podocarpus* (0–3%), *Weinmannia* (0–6%) were also represented as trees, Asteraceae tubuliflorae (0–17%), Ericaceae (0–3%), Poaceae (46–85%) among the herbs, the aquatics Cyperaceae (0–11%), *Xyris* (0.3–5%), ferns and bryophytes *Cyathea* (0–12%), *Isoetes* (0–9%), *Sphagnum* (0–40%) and algae *Botryococcus* (0–3%). The mean S–W Index of this zone, 2.3, is the lowest of the whole pollen record attesting to extremely low biodiversity. This pollen zone includes the LGM, the Late Glacial and the beginning of the Holocene. The differences in sedimentation rates can be attributed to erosive conditions during the LGM and the beginning of the Holocene. The first change was a global climatic change; the second was due to the precession signal which was strong at these latitudes and was characterized by strong erosive climatic conditions and reduction in the tropical forest at different latitudes (Ledru et al., 1998a,b). The higher moisture rates that led to an increase in the frequency of *Araucaria* can be attributed to an abrupt shift in moisture rates during the deglaciation.

Pollen zone COL 12 extends from 64 to 50 cm in depth and includes 6 samples and with an estimated age of between 9 and 6.6 cal kyr B.P. This zone is characterized by an increase in AP (34–74%) related to the dominance of *Alchornea* (3–7%), Melastomataceae/Combretaceae (6–13%), Myrtaceae (1–18%), *Ilex* (1–31%) and *Weinmannia* (2.5–15.5%) with the presence of Asteraceae tubuliflorae (8–22%), Ericaceae (2–8%), *Isoetes* (13–83%), *Sphagnum* (16–114%) and *Botryococcus* (0–0.5%). *Celtis* (0–1%), *Hedyosmum* (0–0.5%), *Myrsine* (1.6–5%), Poaceae (3–30%), *Myriophyllum* (0–0.3%,) Cyperaceae (0–3%), *Xyris* (0–0.5%), *Cyathea* (0–9%) are recorded at low frequencies. The mean S–W Index increases abruptly to 3.4 attesting to the fact that the forest was fully developed. Dominance of heliophilous taxa and the beginning of the formation of a *Sphagnum* peat bog are other features that define this ecological zone. This pollen association suggests a seasonal climate with a summer precipitation regime and dry winters.

Pollen zone COL 13 extends from 48 to 30 cm in depth and is represented by 7 samples with an estimated age of between 6.2 and 3.7 cal kyr B.P. This zone is characterized by a decrease in AP (39–54%), *Alchornea* (1–8.5%), Melastomataceae/Combretaceae (4–16%), Asteraceae tubuliflorae (11–32%), Ericaceae (2–12%), *Isoetes* (28–144%) and *Sphagnum* (9.5–64%). Also recorded but at low frequencies are *Celtis* (0–1%), *Hedyosmum* (0–0.3%), *Ilex* (2–22%), *Myrsine* (0.3–4.5%), Myrtaceae (1–7%), *Podocarpus* (0–1%), *Weinmannia* (1–11%), Poaceae (5–28%), Cyperaceae (0–3%), *Xyris* (0–1%), *Cyathea* (0–1.5%). The biodiversity index remains high at 3.2. This mid-Holocene decrease in arboreal pollen in favor of Asteraceae tubuliflorae attests to the fact that the climate was much drier at this time.

Pollen zone COL 14 extends from 27 to 1 cm in depth and includes 11 samples with an estimated age of 3.5 cal kyr B.P. to the present. This zone is characterized by an increase in AP (44–89%) associated with the following taxa: *Alchornea* (1–7%), *Celtis* (0–2.5%), *Ilex* (3–68%), and *Weinmannia* (2–28%) and local plants: *Isoetes* (0–251%) and *Sphagnum* (0–5%). *Hedyosmum* (0–0.7%), Melastomataceae/Combretaceae (1–26%), *Myrsine* (1–8%), Myrtaceae (1–8.5%), *Podocarpus* (0–1%), Asteraceae tubuliflorae (9–28%), Ericaceae (0–3%), Poaceae (0.5–29%), Cyperaceae (0–7%), *Xyris* (0–0.7%), *Cyathea* (0–6%), *Botryococcus* (0–3.5%) are also recorded within this zone. The modern forest was fully developed at this time with all indicator taxa of the cloud forest. The mean S–W Index is high at 3.1 although within the pollen zone it fluctuates between 1.4 and 4.2.

5. Changes in forest extent and floristic composition

Studies of low latitude lake (Baker et al., 2001) and speleothem (Cruz et al., 2005) records previously showed that precession cycles control changes in solar radiation and variability in the tropical hydrological cycle. The Colônia pollen record shows that the development of the tropical forest was moisture dependant and controlled by changes in insolation over a 20,000-year cycle with maximum forest expansion and long wet periods occurring when summer insolation was highest. However, within these moist episodes, changing floristic composition was apparently neither related to insolation nor to atmospheric CO_2 concentrations (Barnola et al., 1987) or temperature (Dansgaard et al., 1993; EPICA, 2004), but rather had different regional causes that differenciated the tropical climate and circulation from those at higher latitudes (Fig. 5).

5.1. The last interglacial

The last interglacial interval is represented by Marine Isotope Stage (MIS) 5e, a period of low global ice volume and high sea level. In the northern hemisphere, where it was first described, it is characterized by a warm interval arbitrarily dated between ~130,000 and 116,000 yr B.P. (Kukla et al., 2002). This interval has not been yet documented in other paleoenvironmental studies of the region and only rarely within terrestrial pollen records in the tropics of the southern hemisphere (Kershaw, 1978; Kershaw and Whitlock, 2000). Fluctuations in arboreal pollen frequencies were observed, and two pollen zones (COL 1 and 2) described the floristic composition of the interglacial rainforest. The first part of the interglacial was characterized by the presence of the southern conifer *Araucaria* between approximately 134.5 and 130.9 cal kyr B.P. and a low biodiversity index that increased in the next ecological zone. In the second part, *Araucaria* is not recorded and another taxon is observed, Flacourtiaceae sp., between approximately 130.9 and 120.5 cal kyr B.P. No modern analogs for the assemblage with Flacourtiaceae sp. have been found so far. *Araucaria* attests to a winter precipitation regime in the area at this time, induced by extratropical circulation (Ledru, 1993). Rainfall and drizzle are caused by the meeting of the polar air masses with moist air from the Atlantic. This climatic feature changed in the second half of the interglacial as *Araucaria* was no longer observed (Fig. 6). These results are in good agreement with paleoclimatic interpretations based on isotopic analysis of speleothems. High values of $\partial^{18}O$ in Santana cave,

24°31′51″S 48°43′36″W 1000 m asl., ca. 200 km south of the Colônia crater, indicate an extratropical regime with rainfall occuring mainly in winter at this time (Cruz et al., 2006). However, the presence of the tree *Araucaria* and of a dense rainforest at Colônia during the interglacial provides evidence for the occurrence of both winter and summer precipitation regimes in the area. The change from interglacial to glacial times does not appear to have had any impact on the vegetation diversity (Figs. 4 and 5).

5.2. The last glacial stage

The last glacial stage started at approximately 116,000 yr B.P. with an episode named MIS 5d, and ended 12,000 years ago with the onset of the present interglacial, the Holocene. Major fluctuations in forest expansion and composition were observed throughout this interval and nine pollen zones (COL 3 to COL 12) have been defined. The rainforest expanded three times, each time showing a different floristic composition. The beginning of the glacial was characterized by a slight decrease in tree pollen frequencies, a considerable increase in the frequency of *Podocarpus*, a conifer indicator of a cool and moist climate, and a high biodiversity index attesting to the permanence of a dense tropical forest in this region. In pollen zone COL 3, between ca. 120 and 106.4 cal kyr B.P., we observed a very similar association of taxa to that in the modern *Araucaria* forest with abundant tree ferns (*Cyathea*) in the crater attesting to a winter precipitation regime in the area. The first glacial expansion of the rainforest occurred between approximately 105.5 and 101.5 cal kyr B.P. when *Araucaria* and Flacourtiaceae sp. were recorded together although discontinuously. Low summer insolation values could explain this change in environment. The second glacial expansion of the rainforest was observed between approximately 55.8 and 40.9 cal kyr B.P. Here again, the floristic composition was very similar to that observed during the interglacial. The continuous presence of *Araucaria* shows that the winter precipitation regime was still active in this region at this time (Fig. 6).

The third rainforest expansion occurred between 30 and 23 cal kyr B.P. and was characterized by different floristic assemblages than those previously described, this time with *Hedyosmum-Podocarpus-Weinmannia*. Today *Hedyosmum* grows in the coastal moist Atlantic forest up to latitude 30°S and in the Andes up to 2500 m asl., in gallery forests of the cerrado, and in the *Araucaria* forest. The presence of *Weinmannia* excludes the possibility of a cerrado-type landscape and climate. Conversely, the *Hedyosmum-Podocarpus-Weinmannia* association observed in this glacial rainforest argues in favor of cold temperatures and therefore of a cold rainforest.

During the last glacial stage, two major rainforest regressions were observed. Between ca. 40 and 30 kyr and between 23 and 12 kyr, the biodiversity index abruptly decreased and the rainforest was replaced by open vegetation dominated by Poaceae. The rare trees observed during these phases were pioneer and heliophilous species such as Melastomataceae/Combretaceae and *Celtis*. Lack of moisture may explain this drastic change in environment. Few pollen data were recovered for the time period 23–12 kyr B.P. in southeastern Brazil. Where the LGM has been recorded, strong hiatuses in sedimentation are evident due to dry and erosive climatic conditions (Ledru et al., 1998a). Problems in sediment deposition between 23 and 12 kyr B.P. (Behling and Negrelle, 2001), or age inversions (Behling et al., 2002), are rarely discussed although they attest to dry LGM and Late Glacial climatic conditions at this latitude. The development of a pre-LGM Atlantic rainforest has already been characterized at Salitre (19°S) (Ledru et al., 1996) and in the GeoB 3202-1 (21°37′S) marine record (Behling et al., 2002) although it was, for both records, poorly dated and not commented on the marine record.

The whole Atlantic forest did not survive these dry episodes but probably survived as patches in protected areas around the crater.

These « refugia » of rainforest enabled its regeneration when the climate again became more favorable. Another rainforest regression was observed after the beginning of the glacial, between ca. 100 and 56 kyr (Pollen zones COL 5-6-7), although this time the regression was less drastic than the two other times. At this time the rainforest was progressively reduced to shrubs and a shallow lake formed in the crater. However biodiversity remained high during the same period, indicating that permanent moisture was able to maintain biodiverse refugia without stressing the floristic associations.

At approximately 80 kyr a change was observed in insolation amplitude (Berger and Loutre, 1991). This change in energy induced a change in the floristic composition of the forest. Two taxa appeared to react to the change in insolation: *Myrsine* which was abundant before 80 kyr decreased or disappeared from the Colônia record while *Weinmannia* started to increase. The expansion of *Weinmannia* in this region is still underway even though trees are seldom observed in the area (Fig. 6).

During this interval, precipitation appears to have been the limiting factor in the development of the rainforest. As cold indicator taxa such as *Araucaria, Podocarpus, Weinmannia* were consistently well represented, the major changes in the environment that resulted in a drier landscape when the forest disappeared are attributed to drier climatic conditions, due to either a northward shift of the extratropical precipitation regime or a switch off in the SASM mechanism and/or a decrease in the amplitude of the ITCZ seasonal shift.

Paleoenvironmental reconstruction of core CO3 showed that the *Araucaria* forest was present during the last 130,000 years until approximately 50,000 years B.P. with a short re-expansion during the late glacial at ca. 17,000 yr B.P. *Araucaria* is a conifer relict from the Gondwana when cool and moist climatic conditions were favorable for its development (Enright and Hill, 1995; Kershaw and Wagstaff, 2001). When the South American continent progressively shifted northward to reach tropical latitudes, the climate became progressively warmer and *Araucaria* became less widespread in South America. Today two species can be found in South America as opposed to 17 in Australasia, and none in Africa. However, during glacial intervals when temperatures decreased in the Tropics, these conifers also had to face major dry episodes. *Araucaria* was well developed during the last interglacial and during the moistest episodes of the last glaciation, but the last dry glacial phase prevented this species from a new interglacial re-expansion in the region of São Paulo.

5.3. The Holocene

The Holocene started 12,000 years ago and represents our present interglacial. The precession signal is characterized by low summer insolation and has a major impact on the ecosystems of this area (Ledru et al., 1998b). Full development of the rainforest was observed after 9000 yr B.P. with a floristic composition similar to that of today. In the same way as during the previous rainforest expansion, during the glacial between 30 and 23 kyr B.P., *Weinmannia* was recorded and increased progressively throughout the period (Fig. 6) but both *Podocarpus* and *Hedyosmum* disappeared, attesting to warmer temperatures in the region. Two main forest regressions were characterized by the invasion of open vegetation. The first regression in the mid-Holocene, between 6000 and 4000 yr B.P., was characterized by a major reduction in the tree cover and a low mean S–W Index (Fig. 4). The second regression was observed during the past millenium. These regressions are in good agreement with global climate changes. Moisture rates decreased between ca. 9000 and 6000 yr B.P. at these latitudes. Migrations of populations (Schmitz et al., 1989), extinction of the megafauna (Vivo and Carmignotto, 2004), sterile archeological layers in Central Brazil (Araujo et al., 2005), low lake levels, e.g. Lake Titicaca (Argollo and Mourguiart, 2000), all attest to

drastic changes in environmental conditions. Observations of the last millenium revealed the interplay of climatic and anthropic impacts on tropical landscapes are still not easy to distinguish from one another (Crowley, 2000; Jomelli et al., 2008).

Although the forest expanded during the warm last interglacial, the same is not true for the last glacial where the two rainforest expansions were not linked to a global change in temperature (Jouzel et al., 1994; Petit et al., 1999; Johnsen et al., 2001) (Fig. 5). The regional increase in moisture rates during these periods probably resulted in feedback effects of ocean–atmosphere interactions and also affected tropical seasonality.

6. Conclusions

The Colônia pollen record shows a strong precession signal (~20,000 yr) providing evidence that changes in insolation are the main climatic factors driving rainforest expansion and contraction in the southern tropics. Tropical rainforest responds very rapidly to an increase in precipitation and/or to a change in seasonality. However, changes in the origin of precipitation, extratropical winter versus SASM summer precipitations do not match the precession cycle. When superimposed on the precession and on glacial cycles, regional effects of ocean–atmosphere forcings on tropical continental climate can be observed. For instance the beginning of the Holocene was characterized by the presence of the Atlantic rainforest responding to a summer precipitation regime, while the previous rainforest, 20,000 years previously, was the result of both winter and summer precipitation regimes that distributed the humidity all year round. Clouds and drizzle were probably very abundant between 30 and 23,000 years B.P. These convective patterns can be explained by a specific temperature gradient between the poles and the equator in both hemispheres regulated by the amount of ice in the Antarctic and in Greenland (Thompson et al., 2005). The winter extratropical precipitation regime was active until ca. 50,000 years B.P. as attested by the presence of the austral conifer *Araucaria*. In addition, the floristic composition of the forest was never the same during the precession cycles attesting to different climatic conditions in the crater at these times, and inferring the regional influence of the northern hemisphere/southern hemisphere on tropical hydrology.

Here, we show for the first time in the tropics that changes in the amplitude of insolation have a major impact on the composition of the forest. At ca. 80 kyr B.P. *Myrsine* was abruptly replaced by *Weinmannia* inferring specific physiological characteristics of these species that enabled such a clear response. This result needs to be further investigated before deciding which species will be capable of regenerating the rainforest in the future.

Moreover, the insolation cycle or glacial/interglacial cycle does not appear to impact on biological diversity which remained high in the Colônia crater both in the interglacial and the glacial. Instead, the biodiversity rates of the rainforest probably responded rapidly and abruptly to drastic changes in moisture rates (Fig. 4). Because of the variety of climates and elevations, thousands of plant and animal species could not occur anywhere but here. The Colônia pollen record shows that this great biodiversity was challenged several times in the past and that there were at least two drastic reductions in species during the past 130,000 years. Also marked differences between this area and the climatic patterns at higher northern and southern latitudes, e.g. high humidity during the glacial interval and an arid late glacial, imply patterns of climate evolution that are specific to some tropical environments. However, this study emphasizes the need for other independent regional dating controls to improve our chronology. The challenge facing us now is to core the next 440 m of peat that filled the Colônia crater and to review the previous glacial/interglacial cycles to cover the very-long-term evolution of a tropical rainforest.

Appendix A. List of all the taxa identified in the pollen record of Colônia core CO3

Arboreal Pollen
Araucaria (Araucariaceae)
Aegiphila (Verbenaceae)
Alchornea (Euphorbiaceae)
Alnus (Betulaceae)
Anacardium (Anacardiaceae)
Andira (Fabaceae)
Annonaceae
Apocynaceae
Apeiba (Tiliaceae)
Apuleia (Caesalpiniaceae)
Arecaceae C1
Arrabidea (Bignoniaceae)
Aspidosperma (Apocynaceae)
Astronium (Anacardiaceae)
Banara (Flacourtiaceae)
Bauhinia (Fabaceae)
Belangera (Cunoniaceae)
Bertiera (Rubiaceae)
Brosinum (Moraceae)
Caesalpiniaceae
Cassia (Fabaceae)
Cecropia (Cecropiaceae)
Cedrela (Meliaceae)
Celtis (Ulmaceae)
Chamaesyce (Euphorbiaceae)
Cissampelos (Menispermaceae)
Clethra (Clethraceae)
Clusia (Clusiaceae)
Cochlospermum (Cochlospermaceae)
Copaifera (Caesalpiniaceae)
Cordia (Boraginaceae)
Coussapoa (Moraceae)
Coutarea (Rubiaceae)
Croton (Euphorbiaceae)
Crudia (Caesalpiniaceae)
Cupania (Sapindaceae)
Cybianthus (Myrsinaceae)
Cybistax (Bignoniaceae)
Dalbergia (Fabaceae)
Daphnopsis (Thymeleaceae)
Desmodium (Fabaceae)
Dialium (Caesalpiniaceae)
Didymopanax (Araliaceae)
Dilleniaceae
Dinizia type (Mimosaceae)
Diospyros (Ebenaceae)
Doliocarpus (Dilleniaceae)

Dorstenia (Moraceae)
Drimys (Winteraceae)
Erythroxylum (Erythroxylaceae)
Eschweleira (Lecythidaceae)
Euphorbia (Euphorbiaceae)
Fabaceae
Fagara (Rutaceae)
Ficus (Moraceae)
Flacourtiaceae
Flacourtiaceae C4P4
Fusaea (Annonaceae)
Gallesia (Phytolaccaceae)
Geoffrea type (Fabaceae)
Guapira (Nyctaginaceae)
Guettarda (Rubiaceae)
Gouania type (Rubiaceae)
Hancornia (Apocynaceae)
Hedyosmum (Chloranthaceae)
Heliotropium (Boraginaceae)
Heteropteris (Malpighiaceae)
Humiriaceae
Hyeronima (Euphorbiaceae)
Hymenea (Caesalpiniaceae)
Ilex (Aquifoliaceae)
Jacaranda (Bignoniaceae)
Laplacea (Theaceae)
Licania (Chrysobalanaceae)
Linaceae
Lithraea (Anacardiaceae)
Loranthaceae
Mabea (Euphorbiaceae)
Machaerium (Fabaceae)
Mandevilla (Apocynaceae)
Maprounea (Euphorbiaceae)
Marcgravia (Marcgraviaceae)
Matayba (Sapindaceae)
Maytenus (Celastraceae)
Melastomataceae/Combretaceae
Melastomataceae/Combretaceae reticulé
Melastomataceae <20
Meliaceae/Sapotaceae
Menispermaceae
Mimosaceae (4de)
Mimosaceae
Mimosa scabrella type
Minquartia (Olacaceae)
Moraceae P2
Myrica (Myricaceae)
Myroxylon (Fabaceae)
Myrsine (Myrsinaceae)
Myrtaceae
Nectandra (Lauraceae)
Norantea (Marcgraviaceae)
Nothofagus (Fagaceae)
Nyctaginaceae
Ouratea (Ochnaceae)
Patagonula (Boraginaceae)
Paullinia (Sapindaceae)
Phyllantus (Euphorbiaceae)
Pisonia (Nyctaginaceae)
Plenckia (Celastraceae)
Podocarpus (Podocarpaceae)
Poiretia (Fabaceae)
Posoqueria (Rubiaceae)
Pouteria (Sapotaceae)
Protium (Proteaceae)

Pseudobombax (Bombacaceae)
Psidium (Myrtaceae)
Psychotria (Rubiaceae)
Qualea (Vochysiaceae)
Rhamnaceae
Roupala (Proteaceae)
Sapium (Euphorbiaceae)
Schizolobium (Caesalpiniaceae)
Sebastiana (Euphorbiaceae)
Senna (Caesalpiniaceae)
Serjania (Sapindaceae)
Simarouba (Simaroubaceae)
Solanum (Solanaceae)
Styrax (Styracaceae)
Symplocos-type reticulate
Symplocos (Symplocaceae)
Tabebuia (Bignoniaceae)
Talisia (Sapindaceae)
Tapirira (Anacardiaceae)
Terstroemia (Theaceae)
Thumbergia (Acanthaceae)
Tiliaceae
Tontelea (Hippocrateaceae)
Tournefortia (Boraginaceae)
Trema (Ulmaceae)
Trichilia (Meliaceae)
Vantanea (Humiriaceae)
Verbenaceae
Vismia (Clusiaceae)
Weinmannia (Cunoniaceae)
Xylopia (Annonaceae)
Xylosma (Flacourtiaceae)
Zornia (Fabaceae)

Non Arboreal Pollen
Acalypha (Euphorbiaceae)
Alternanthera (Amaranthaceae)
Amaryllis (Amaryllidaceae)
Apiaceae <20
Araceae
Artemisia (Asteraceae)
Asteraceae liguliflorae
Asteraceae tubuliflorae
Begonia (Begoniaceae)
Borreria (Rubiaceae)
Satureja (Lamiaceae)
Bromeliaceae
Caryophyllaceae
Cayaponia (Cucurbitaceae)
Chenopodiaceae
Cleome (Cleomaceae)
Commelinaceae
Coussourea
Cucurbitaceae
Cuphea (Lythraceae)
Ericaceae
Eriocaulon (Eriocaulaceae)
Eryngium (Apiaceae)
Evolvulus (Convolvulaceae)
Fuchsia (Onagraceae)
Gomphrena (Amaranthaceae)
Hyptis (Lamiaceae)
Justicia (Acanthaceae)
Lamiaceae
Loranthaceae
Malvaceae

Mikania (Asteraceae)
Philodendron (Araceae)
Piper (Piperaceae)
Polygala (Polygalaceae)
Puya-type (Bromeliaceae)
Poaceae
Polygonum (Polygonaceae)
Struthantus (Loranthaceae)
Trixis (Asteraceae)

Aquatics and terrestrial influenced by water level
Alismataceae
Cabomba
Cyperaceae
Drosera (Droseraceae)
Iridaceae
Juncaceae
Lentibularia (Lentibulariaceae)
Myriophyllum
Nymphoides
Onagraceae
Typha (Typhaceae)
Urticales
Xyris (Xyridaceae)
Anthoceros
Isoetes
Sphagnum

Ferns and bryophytes
Cyathea type 1
Cyathea type 2
Cyathea type 3
Cyathea esquaquensis
Cyathea ref. 296 Hooghiemstra 1984
Cyathea horrida (vdH)
Dicksonia
Ephedra
Grammites
Jamesonia-type
Lophosoria
Lycopodium
Meesea
Monolete
Mougeotia
Ophioglossum
Polypodium
Selaginella
Schizeaceae
Theliptirys
Trichomanes
Trilete

Algae
Botryococcus
Coelostrum
Pediastrum
Zygnema

Varia meaning unidentified taxa: 10 types

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