

Late-glacial and Holocene vegetation, climate and fire dynamics in the Serra dos Órgãos, Rio de Janeiro State, southeastern Brazil

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Abstract

We present a high-resolution pollen and charcoal record of a 218 cm long sediment core from the Serra dos Órgãos, a subrange of the coastal Serra do Mar, located at 2130 m altitude in campos de altitude (high elevation grass- and shrubland) vegetation near Rio de Janeiro in southeastern Brazil to reconstruct past vegetation, climate and fire dynamics. Based on seven AMS ^{14}C ages, the record represents at least the last 10 450 ^{14}C yr BP (12 380 cal years BP). The uppermost region was naturally covered by campos de altitude throughout the recorded period. Diverse montane Atlantic rain forest (ARF) occurred close to the studied peat bog at the end of the Late-glacial period. There is evidence of small *Araucaria angustifolia* populations in the study area as late as the early Holocene, after which point the species apparently became locally extinct. Between 10 380 and 10 170 ^{14}C yr BP (12 310–11 810 cal yr BP), the extent of campos de altitude was markedly reduced as montane ARF shifted rapidly upward to higher elevations, reflecting a very wet and warm period (temperatures similar to or warmer than present day) at the end of the Younger Dryas (YD) chronozone. This is in opposition to the broadly documented YD cooling in the northern Hemisphere. Reduced cross-equatorial heat transport and movement of the Intertropical Convergence Zone over northeastern Brazil may explain the YD warming. Markedly extended campos de altitude vegetation indicates dry climatic conditions until about 4910 ^{14}C yr BP (5640 cal yr BP). Later, wetter conditions are indicated by reduced high elevation grassland and the extension of ARF into higher elevation. Fire frequency was high during the early Holocene but decreased markedly after about 7020 ^{14}C yr BP (7850 cal yr BP).

Keywords: Brazil, campos de altitude, fire history, late Quaternary, montane Atlantic rain forest, pollen, palaeoclimate, palaeoecology, tropical mountain, Younger Dryas chronozone

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Introduction

The neotropical mountain systems support the most biodiverse ecosystems on earth, yet we have little understanding of the factors that drive this high diversity. We are particularly ignorant of the role that history has played in the development of these hotspots of species endemism and richness (Churchill *et al.*, 1995; Broecker, 1997). This problem is particularly acute in the extra-Andean ranges of eastern Brazil, where rigorous palaeoecological work has only just begun. Although our knowledge is growing, we still lack a coherent vision of patterns of change in climatic conditions in

the Brazilian Highlands during glacial–interglacial cycling in the Late Cenozoic, and the response of vegetation to these cycles.

The mountains of southeast Brazil are found largely within two ENE-trending ranges – the coastal Serra do Mar and the more inland and higher Serra da Mantiqueira (Fig. 1). The lower and middle slopes of these mountains – the core of the Atlantic rain forest (ARF) – harbour some of the most diverse and biologically unique forest ecosystems on earth (Myers, 1988; Wilson, 1992; Davis *et al.*, 1997). The upper slopes of these ranges are swathed in montane cloud forest, giving way to páramo-like grass- and shrublands ('campos de altitude') on the higher summits (Safford, 1999a). The ARF is one of the most human-altered ecosystems in the tropics (Por, 1992; Dean, 1995). Within the ARF, only

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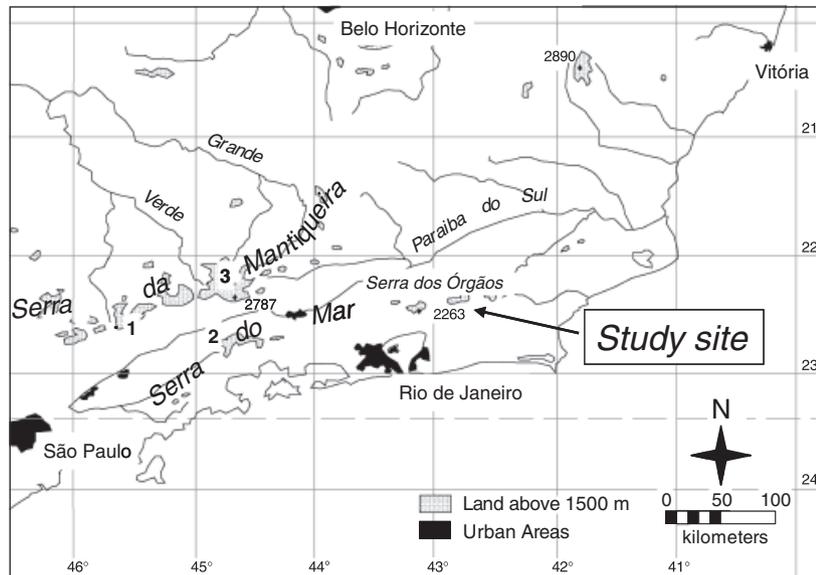


Fig. 1 Map showing the location of the Serra dos Órgãos in Rio de Janeiro State, southeastern Brazil. '1' indicates the location of Morro de Itapeva in the southern Serra da Mantiqueira; '2' indicates the location of the Serra da Bocaina.

habitats of mountain slopes and summits have survived European occupation relatively unscathed. Today, the last of these 'pristine' habitats are preserved in a number of small federal and state conservation units scattered across southern and eastern Brazil.

Modern geologic landforms and biogeographic patterns in southern and eastern Brazil led researchers in the 1960s and 1970s to postulate significant dynamism in Late Cenozoic climates in the region (Bigarella *et al.*, 1965; Damuth & Fairbridge, 1970; Ab'Sáber, 1977), which contradicted traditional views of long-term stability in the (remnants of) tropical forest ecosystems that currently dominate the area. More recent palaeoecological and phytogeographic work has corroborated this dynamic vision, at least for the late Pleistocene and Holocene (e.g. Behling, 1997, 2007; Behling & Lichte, 1997; Behling *et al.*, 2004; Safford, 2007). Although it appears that certain parts of southern and eastern Brazil have supported forest for long, uninterrupted periods (e.g. Behling & Negrelle, 2001; Behling *et al.*, 2002; Ledru *et al.*, 2009), it is also clear that climates in the region have changed dramatically over time and many parts of the landscape have witnessed tremendous changes in their biota as a result.

Palaeoecological data remain relatively scarce for the southeastern Brazilian Highlands, but gaps in our knowledge have begun to fill over the last 10–15 years. Currently, the longest record from the southeastern mountains is a 35 000 yr BP pollen and charcoal record from the Morro de Itapeva (1850 m a.s.l.) in the southernmost Serra da Mantiqueira (Fig. 1). The Morro de Itapeva core documents expanded campos de altitude,

and the nearly complete absence of forest during the Last Glacial Maximum (35 000–17 000 yr BP), suggesting a markedly cooler and drier climate than today. Increased *Araucaria*, cloud forest and lower montane forest taxa in the pollen record during the Late-glacial (17 000–10 000 yr BP) indicate a subsequent shift to moister conditions. During the early Holocene, cloud forest developed close to the Morro de Itapeva site, reflecting a warm and moist climate on seaward slopes; at the same time, reduced levels of *Araucaria*, *Podocarpus* and other associated taxa suggest that the climate on the highland plateau was drier. In the late Holocene, frequencies of *Araucaria* and *Podocarpus* (etc) rise again, indicating a progressive increase in highland moisture towards modern levels. Charcoal records from the core show that fires were more frequent during the Late-glacial period (i.e. before arrival of humans) than during the Holocene (Behling, 1997).

Behling *et al.* (2007) recently extended the late Quaternary record from the southeast Brazilian mountains to the Serra do Bocaina, a subrange of the Serra do Mar about 120 km to the east of Morro de Itapeva. The two cores sampled (18 570–1280 yr BP) document broadly similar temporal patterns in climate and vegetation to the Morro de Itapeva site. Beyond documenting late Quaternary climate and vegetation dynamics in the Serra da Bocaina, Behling *et al.* (2007) also sought to discern terrestrial evidence for episodic warming of the tropical Atlantic during the Heinrich Event I (17 900–16 700 yr BP) and the Younger Dryas (YD) period (12 700–11 600 yr BP), which are hypothesized to relate to periodic slowing of thermohaline circulation in the

Atlantic (Rühlemann *et al.*, 1999). In the Serra da Bocaina cores, Behling *et al.* (2007) found no signal of sudden warming or increased precipitation for the Heinrich Event 1, but a significant erosion event documented by the cores brackets the YD period, and is probably linked to a period of high precipitation (Behling *et al.*, 2007).

In the current contribution, we geographically extend the palaeoecological record for the southeastern Brazilian Highlands to the Serra dos Órgãos, a further sub-range of the Serra do Mar found just north of Rio de Janeiro (Fig. 1). We document and discuss Late-glacial and Holocene vegetation and fire history for a 10 450 yr BP pollen and charcoal record from the study site. We also seek more concrete terrestrial evidence for sudden warming that is postulated to have occurred in the western tropical Atlantic during the YD period.

Modern environmental setting

Our study site is found in the Serra dos Órgãos ('Organ Mountains'), a sub-range of the Serra do Mar, approximately 50 km NNW of the city of Rio de Janeiro and the Atlantic Ocean, within the Serra dos Órgãos National Park (Fig. 1). Founded in 1939, the 11 800 ha Serra dos Órgãos National Park was one of the first federally protected conservation units in Latin America.

Geologic substrate in the Serra dos Órgãos coastal mountains is Upper Proterozoic granite and granitoid gneiss, uplifted to its present elevation by Cenozoic horst-graben-type tectonism associated with widening of the Atlantic Ocean (Machado Filho *et al.*, 1983; Riccomini *et al.*, 1989). The studied peatbog (22°27'30"S, 43°01'41"W) is formed in a shallow, elliptic basin (40 m wide × 100 m long) in a crystalline rock depression on the east shoulder of Pedra do Sino (Pt. 2263 m in Fig. 1) at 2130 m elevation. Mean annual temperature in the immediate study area is approximately 10.5°, absolute maxima and minima are about 25° and -10°, respectively. Mean annual precipitation is about 3000 mm, with a hibernal dry season (monthly precipitation < 50 mm) of 2–3 months (Safford, 1999a, b).

Vegetation surrounding the study site is of the campos de altitude ('high altitude grassland') type, which is found above treeline (1800–2200 m) throughout southeastern Brazil. It is dominated by tall bunchgrasses (especially *Cortaderia*), montane bamboo of the genus *Chusquea*, and a rich, heterogeneous mixture of sclerophyllous shrubs (especially *Baccharis*, *Escallonia*, and various Asteraceae, Ericaceae, Melastomataceae and Myrtaceae). Important forbs include *Eryngium*, *Paepalanthus*, *Plantago* and *Xyris*. Isolated copses of stunted trees, high elevation outliers of upper montane ARF ('cloud forest') are found in topographic concavities, on rock outcrops and in other protected sites. Important

tree genera within the upper montane ARF type (above 1500 m) include *Clethra*, *Roupala*, *Ilex*, *Rapanea/Myrsine*, *Symplocos*, *Weinmannia*, *Drimys* and *Maytenus*. Lower montane ARF is found between about 700 and 1500 m, dominated by tree species in the genera *Alchornea*, *Mollinedia*, *Myrcia*, *Sloanea* and *Cabralea*, shrubs in the genera *Psychotria* and *Leandra*, the palms *Euterpe* and *Geonoma*, and a variety of tree ferns (Rizzini, 1954; Lima & Guedes-Bruni, 1997; Safford, 1999a, 2001). Campos de altitude, upper montane ARF and than lower montane ARF are the main pollen and spore collecting source for the studied peat bog.

Materials and methods

The peat deposit was cored in its deepest part using a Russian corer. From bedrock, the total length of the core was 218 cm. Sections of 50 cm length were extruded on-site, wrapped in plastic and aluminium film and stored under cool (ca. + 4 °C) and dark conditions after return from the field and before sampling.

In total, seven peat samples containing charcoal (within 1 cm thick bulk subsamples) were taken for radiocarbon dating. Samples were dated through AMS at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, CA, USA. In three samples, charcoal was of sufficient quantity and quality to be directly dated. In three further samples, we dated bulk peat after thorough microsieving and washing in HCl (acidity in our samples was very high, pH 3.3–3.5, which immobilizes humic acids in the peat column). We tested the reliability of our bulk peat dates by randomly choosing one of the three bulk peat samples and running two concurrent tests using (1) the peat humic fraction derived from reprecipitation of base-wash residues, and (2) peat organics treated with both acid and base washes. Results are included in Table 2 (sample depth 123 cm). The final sample was dated from the humic fraction (Table 2).

For pollen analysis, 80 subsamples (0.5 cm³ each) were taken at 2 and 4 cm intervals along the 218 cm long core. All samples were processed with standard pollen analytical methods, using hydrofluoric (HF) and acetolysis (Faegri & Iversen, 1989). To determine the pollen concentration (grains cm⁻³) and pollen accumulation rate (grains cm⁻² yr⁻¹), one tablet of exotic *Lycopodium clavatum* spores was added to each sample. Pollen and spores were well preserved. A minimum of 300 pollen grains was counted for each sample. The total pollen sum includes herbs, shrubs and trees, and excludes aquatic taxa, fern, moss and fungal spores and the alga *Botryococcus*. Pollen identification relied on the first author's own reference collection (containing about 2000 Brazilian species) and pollen morphological descriptions in

Behling (1993). Pollen and spore data are presented in pollen diagrams as percentages of the total pollen sum. Carbonized particles (5–200 µm) were counted on pollen slides to calculate concentration (particles cm⁻³) and accumulation rate (particles cm⁻² yr⁻¹).

The software TILIA, TILIAGRAPH and CONISS were used for illustration of the pollen and spore data, calculations and cluster analysis (Grimm, 1987). The pollen diagrams include individual records of the most abundant pollen and spore taxa (Fig. 2), and records of the groups: lower, other and upper montane ARF, Campos de altitude (herbs), tree ferns and ferns (without *Isoetes*), mosses, *Botryococcus*, fungal spores, and concentration and accumulation rate of pollen and charcoal particles, and a cluster analysis dendrogram (Fig. 3). The separation of pollen into lower, upper and 'other' (i.e. indistinct taxa, which can occur in both upper and lower) montane ARF taxa is based on modern vegetation surveys in southeastern Brazil (e.g. Rizzini, 1954; Brade, 1956; Hueck, 1966; Lima & Guedes-Bruni, 1997; Safford, 1999c, 2001; Safford & Martinelli, 2000). The zonation of the pollen record is based on changes in the pollen assemblages and CONISS analysis.

Results

Stratigraphy

The 218 cm long Serra dos Órgãos core starts on a rocky subsurface and contains mostly dark brown or black organic material (peat) which is compact and strongly decomposed. A detailed description of both cores is given in Table 1.

Radiocarbon dates

Seven AMS radiocarbon dates (Table 2) provide chronological control for the Serra dos Órgãos pollen record and indicate deposits of Late-glacial and Holocene age. The calibration of the radiocarbon dates have been carried out after CALPAL (Weninger *et al.*, 2004). The base of the core has an age of 10 450 ± 50 ¹⁴C yr BP (12 380 ± 210 cal yr BP). The radiocarbon dates indicate that the sedimentation was continuous and without any recognizable interruptions. Based on the radiocarbon dates, the age range has been calculated for each pollen zone (Table 3). Owing to the relatively high accumulation rate in zone SDO-I, which is much higher than in the following zones, it is suggested that the duration of zone SDO-I is much greater than the 70 years indicated by the radiocarbon dates. The very high pollen accumulation rate in the lower part of the core (see later, Fig. 3) supports our suggestion.

Description of the Serra dos Órgãos pollen diagram

Pollen assemblages of the 80 counted samples are diverse. The pollen diagram displays the most frequent pollen and spore taxa of the 151 different types identified (Figs 2 and 3). About 23 pollen and spore types remain unknown. According to major changes in pollen assemblages and the CONISS analysis, seven local pollen zones (SDO-I–VII) were established (Table 3). Pollen concentration and pollen accumulation rate is relatively stable in the sediment deposits, excepting the high accumulation rates in zone SDO-I.

The Serra dos Órgãos pollen record is characterized throughout by relatively high sums of the lower, 'other' and upper montane ARF taxa and a frequent presence of herb pollen (Fig. 3). These arboreal and nonarboreal pollen groups show several fluctuations within the record.

Zone SDO-I (10 450–10 380 ¹⁴C yr BP, 12 380–12 310 cal yr BP) is marked by abundant montane pollen grains (34–41%), mostly originating from upper montane ARF taxa (9–14%) such as *Weinmannia*, the *Symplocos lanceolata* type, *Araucaria angustifolia* (1–2%) and *Podocarpus*; lower montane ARF taxa (8–12%) such as Moraceae/Urticaceae, *Alchornea*, the *Euterpe/Geonoma*-type; and other (indistinct) montane ARF taxa (10–19%) such as Melastomataceae, Myrtaceae, *Celtis*, and the *Trema* type. Campos de altitude (Herbs) pollen grains are also abundant (57–64%), especially from the Poaceae, Cyperaceae, Asteraceae subfamily Asteroideae, the *Baccharis* type and *Eryngium*. Tree fern spores, such as the *Cyathea schanschin* type and *Dicksonia sellowiana*, are relatively rare in this and in the following zones. Fern spores have their highest values in this and in the next zone, and are mostly comprised by the trilete psilate type. *Isoetes* spores are very abundant in zone SDO-I but uncommon in SDO-II. Moss spores, almost all of *Sphagnum*, are rare in both SDO-I and II, as are colonies of the alga *Botryococcus*. Fungal spores have moderate values, with higher values in SDO-II than SDO-I. The concentration of charcoal particles is low in zones SDO-I and SDO-II, but the charcoal particle accumulation rate in SDO-I is very high, and only matched again in the lowest part of SDO-IV.

Zone SDO-II (10 380–10 170 ¹⁴C yr BP, 12 310–11 810 cal yr BP) is characterized by the strong representation of pollen from montane ARF taxa (41–59%). Lower and other montane ARF taxa increase significantly in this zone (from 12% to 25%, and from 13% to 23%, respectively), while the upper montane ARF taxa decrease slightly (from 14% to 11%). Pollen grains of Moraceae/Urticaceae, the *Euterpe/Geonoma* type, *Cecropia*, Myrtaceae, the *Trema* type, and *Weinmannia* show especially marked increases. Campos de altitude pollen decrease strongly (from 58% to 39%) mostly due to a decrease in

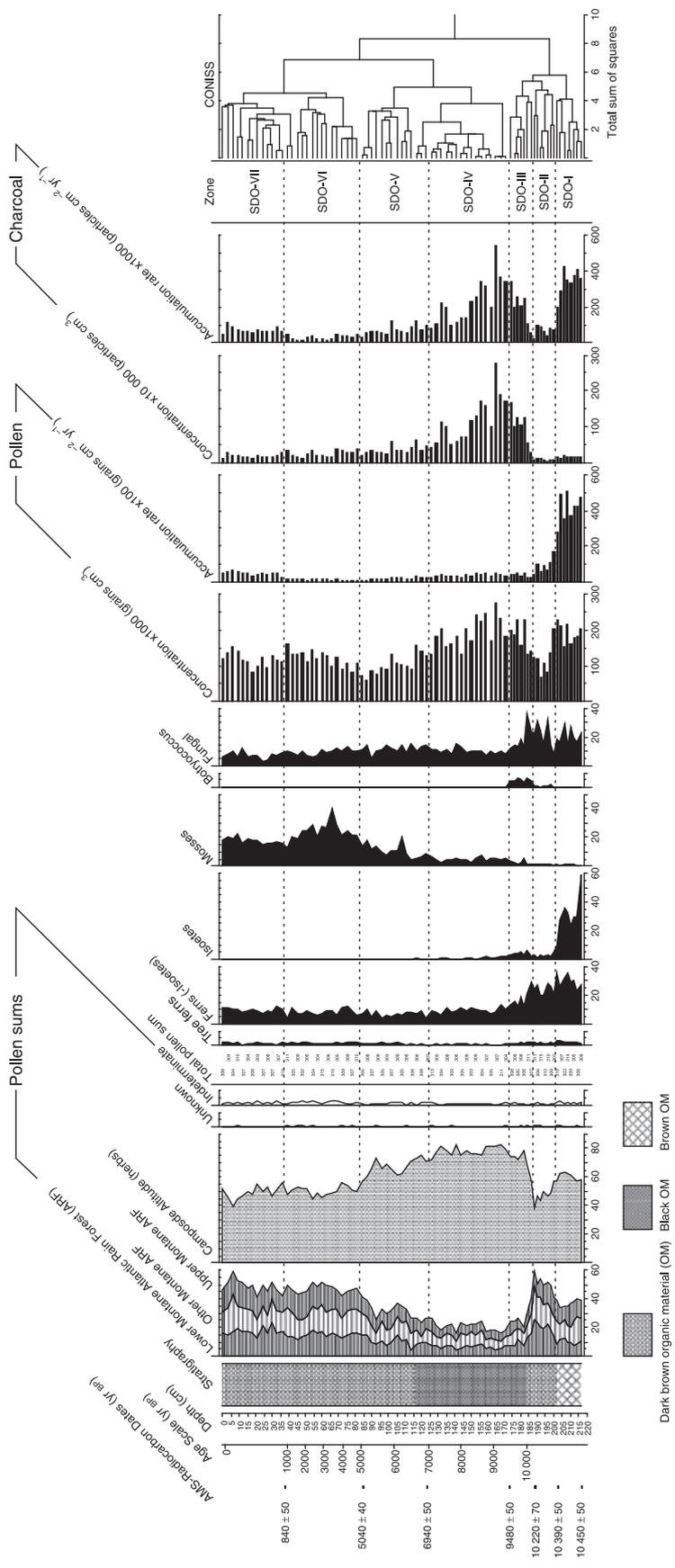


Fig. 3 Summary pollen diagram of the Serra dos Órgãos core, showing the AMS radiocarbon dates, stratigraphy, ecological groups, pollen sum numbers, pollen concentration and accumulation records, pollen zones, and the cluster analysis dendrogram.

Table 1 Stratigraphy of the Serra dos Órgãos core

Depth (cm)	Description
0–100	Dark brown organic material, compact and strongly decomposed, some plant remains, roots and rootlets
100–116	Dark brown – black organic material, transition to:
116–126	Black organic material, compact and strongly decomposed
126–184	Black organic material, very compact and completely decomposed, a little fine sand
184–202	Dark brown organic material, compact and completely decomposed, a few wood fragments
202–218	Brown organic material, compact and completely decomposed, fine sandy, a few wood fragments
218–	Rocky subsurface

Table 2 List of AMS radiocarbon dates of samples of the Serra dos Órgãos core

Lab. number	Depth (cm)	¹⁴ C yr BP	¹³ C/ ¹² C	Calibrated ages (cal yr BP)	Dated material
CAMS-66381	37	840 ± 50	–25	780 ± 70	Bulk peat
CAMS-66382	84	5040 ± 40	–25	5800 ± 70	Bulk peat
CAMS-66383	123	6940 ± 50	–25	7760 ± 60	Bulk peat
CAMS-56101	173	9480 ± 50	–25	10 830 ± 180	Charcoal
CAMS-56102	188	10 220 ± 70	–25	11 880 ± 200	Charcoal
CAMS-66384	202	10 390 ± 50	–25	12 340 ± 210	Charcoal
CAMS-73104	216	10 450 ± 50	–28	12 380 ± 210	Peat humic fraction

Table 3 Pollen zones of the core Serra dos Órgãos, showing depth, the calculated radiocarbon age and the number of pollen samples of each pollen zone

Zone	Depth (cm)	Age range in ¹⁴ C yr BP and in cal yr BP	No. of samples
SDO-I	216–201	10 450–10 378	8
SDO-II	201–187	10 378–10 171	7
SDO-III	187–172.5	10 171–9454	7
SDO-IV	172.5–124.5	9454–7016	16
SDO-V	124.5–82.5	7016–4906	14
SDO-VI	82.5–37	4906–917	15
SDO-VII	37–0	917–49	13

Poaceae. Eriocaulaceae pollen have their highest values in this zone.

Zone SDO-III (10 170–9450 ¹⁴C yr BP, 11 810–10 800 cal yr BP) is marked by the strong decrease of pollen from lower (from 25% to 8%), other (23% to 7%) and upper (11% to 9%) montane ARF taxa (59% to 24%). Most of the arboreal taxa, particularly Moraceae/Urticaceae, the *Euterpe/Geonoma* type, Myrtaceae and the *Trema* type, decrease. Campos de altitude pollen greatly increase (from 39% to 74%), mostly due to a 20% increase in Poaceae pollen. *Sphagnum* spores are now slightly higher. The alga *Botryococcus* has its highest values in this zone and becomes very rare in the following zones. The concentration and accumulation rates of charcoal particles increase markedly from the beginning to the end of zone SDO-III.

Zone SDO-IV (9450–7010 ¹⁴C yr BP, 10 800–7850 cal yr BP) is characterized by a relatively steady balance in the

representation of montane ARF taxa and Campos de altitude taxa. Through zone SDO-IV, montane ARF increase slightly (from 18% to 26%), while Campos de altitude pollen decrease slightly (79–72%). Pollen grains from *A. angustifolia* disappear from the record at the beginning of this zone. Spores of the tree fern *D. sellowiana* remain very rare. Charcoal particles are abundant, their values decrease continuously to the end of zone SDO-IV.

Zone SDO-V (7010–4910 ¹⁴C yr BP, 7850–5640 cal yr BP) is similar to the previous zone, but in this zone the increase of montane ARF pollen and the decrease of Campos de altitude pollen is accelerated (from 27% to 41%, and from 71% to 57%, respectively). *Sphagnum* spores increase during this zone. Charcoal particles are markedly lower in zone SDO-V than in zones SDO-III or IV.

Zone SDO-VI (4910–920 ¹⁴C yr BP, 5640–880 cal yr BP) is marked by high values of the montane ARF pollen taxa

(48–50%) and similarly high values of Campos de altitude pollen taxa (50–48%). Spores of *Sphagnum* reach their peak abundance in this zone, and continue at high levels to the present day. Charcoal particles are at low abundances in the sediment deposits.

Zone SDO-VII (920–49 ¹⁴C yr BP, 880–49 cal yr BP) is characterized by high values (50–59%) of montane ARF pollen taxa and slightly lower values (48–40%) of Campos de altitude pollen sums. Among the arboreal taxa, the *Euterpe/Geonoma* type, *Cecropia* and *Symplocos tenuifolia* type have their highest percentages in this zone. The accumulation rates of charcoal particles are slightly higher in this zone than in zone SDO-VI.

Interpretation and discussion

The start of the accumulation of brown organic material at the base of the core during the Late-glacial suggests a change from drier to wetter climatic conditions in the study basin. Before that period the climate was probably too dry and peat could not accumulate in the basin. The deposition of frequent *Isoetes* spores (Zone SDO-I), followed by Eriocaulaceae pollen (Zone SDO-II), and then colonies of the algae *Botryococcus* (Zone SDO-III), indicates that conditions in the basin at the end of the Late-glacial were very wet. The basin was at least seasonally filled with shallow water before a peat bog began to develop at the beginning of the Holocene. The temporal development of the peat-bog is well documented by the gradual increase of *Sphagnum* spores in the deposits.

Most of the identified pollen taxa in the Serra dos Órgãos core are insect pollinated, which have low pollen frequencies in the samples. Most frequent pollen grains in the core belong to wind pollinated taxa (see the percentage diagram). Both are reflecting the surrounding vegetation. Abundant grass and other herb pollen throughout the pollen record indicate that the uppermost regions of the Serra dos Órgãos have been naturally covered by campos de altitude-type vegetation since the Late-glacial period. Campos de altitude vegetation is extremely heterogeneous and diverse, but it is largely dominated by Poaceae. At the beginning of the record, i.e. at least since 10 450 ¹⁴C yr BP (12 380 cal yr BP), a species-diverse montane ARF was already well developed at higher elevations relatively close to the studied peat bog, but at a lower elevation than today as indicated by the higher amount of ARF pollen compared with the top sample of the core.

Between 10 380 and 10 170 ¹⁴C yr BP (12 310–11 810 cal yr BP), the pollen record documents a significant expansion of the montane ARF into higher elevations, reducing the area of the campos de altitude. During this period of about 500 cal yr, various taxa of the lower montane region, such as Moraceae/Urticaceae and

Euterpe/Geonoma, migrated upward to higher elevation, providing further evidence that climatic conditions were warm and wet at the end of the Late-glacial period. Tropical taxa of the montane ARF are quite sensitive to temperature changes. Temperatures during this period must have been similar to, or higher than today. Present day, the mean annual temperature at the study area is approximately 10.5 °C. Owing to the close proximity of the Serra dos Órgãos to the Atlantic Ocean, an increase of the Sea Surface Temperature (SST) in the Atlantic would be expected to have a strong influence on the climate in the coastal mountain region. The increase of the SST might be related to a reduced cross-equatorial heat transport, especially at the end of the YD chronozone (Rühlemann *et al.*, 1999).

Populations of the conifer *A. angustifolia* grew in the Serra dos Órgãos during the Late-glacial period and at the beginning of the Holocene. The absolute lack of these easily recognizable pollen grains after 9450 ¹⁴C yr BP (10 800 cal yr BP) suggests to us that *Araucaria* may have become locally extinct at that time. In contrast, Hueck (1953, 1966) believed that present-day *Araucaria* grew naturally as far north as the Rio Doce at about 18°N latitude (ca. 400 km NE of the study site), although only in 'rare and isolated stands'. Note that many *Araucaria* have been planted in southeastern Brazil and it is difficult to recognize natural stands. Today the most northerly 'forests' of *Araucaria* are found in the Serra da Bocaina, about 150 km WSW of the study site, and in the Serra do Itatiaia, the same distance west. We did find spores of the tree fern *D. sellowiana*, an important component of more southerly *Araucaria* forests. *D. sellowiana* still grows in the Serra dos Órgãos, although it is uncommon (Rizzini, 1954).

The relatively low concentration of charcoal particles indicates fires were not frequent at the end of the Late-glacial period. The high accumulation rate of charcoal particles in zone SDO-I compared with zone SDO-II is probably artificial, due to the brevity of the assigned time-period (see Radiocarbon dates, above). In reality, zone SDO-I is probably much longer than the calculated 70 years.

At the beginning of the Holocene (Zone SDO-III), the marked increase of Poaceae pollen suggests that campos de altitude vegetation expanded markedly in the Serra dos Órgãos and taxa associated with the montane ARF migrated downwards. These vegetation shifts were probably related to the onset of dry early Holocene conditions, which continued until about 4910 ¹⁴C yr BP (5640 cal yr BP). Dry climatic conditions with a long annual dry season during the early to mid Holocene period are also documented from several other sites in southeastern Brazil, such as Lago do Pires in the Atlantic lowland (Behling, 1995).

Fire became frequent in the campos de altitude of the Serra dos Órgãos during the early Holocene period, especially between 9450 and 7020 ^{14}C yr BP (10 800–7850 cal yr BP). The high frequency of fire is clearly connected with the drier climate signal, but whether the arrival of humans in southeastern Brazil played any role in this change in fire regime is open to question. The extreme isolation of the upper reaches of the Serra dos Órgãos, protected by high cliffs, steep slopes and thick forest, would seem to preclude the regular presence of humans at higher elevations. Indeed, Hueck (1966) states that before the arrival of Europeans there was no substantial Indian population in the mountains (where he got this information is unclear). This said, significant numbers of hunter-gatherers were in the ARF by 11 000 ^{14}C yr BP (Dean, 1995), the campos de altitude were of much greater areal extent than they are today, and they probably supported populations of game animals. The steadily increasing frequencies of *Cecropia* pollen in the Serra dos Órgãos core after 7020 ^{14}C yr BP (7850 cal yr BP) and especially after 920 ^{14}C yr BP (880 cal yr BP) may be a signal of increasing human activity in the area. Whatever the case, it is clear that the modern flora of the Campos de altitude is largely fire-adapted (Safford, 2001). We may never know if early humans played an important role in generating this selection pressure – certainly modern humans does. This topic remains a fertile ground for future studies.

After 9000 ^{14}C yr BP, in the Serra dos Órgãos there was a slow but steady upward migration of taxa from the montane ARF until about 4910 ^{14}C yr BP (5640 cal yr BP), suggesting a long-term trend of slowly increasing climatic moisture. The area of campos de altitude decreased, as did the frequency of fire. By about 4910 ^{14}C yr BP taxa of the montane ARF had reached approximately modern elevation levels, heralding the onset of quasi-modern climatic conditions.

The slightly stronger presence of montane ARF and the decrease in campos de altitude pollen during the last 920 ^{14}C yr BP (880 cal yr BP) suggest a slight increase in moisture during this period. Other evidence for this interpretation includes minor increases in the pollen counts from palm trees (*Euterpe/Geonoma*) and from Myrtaceae. In the Serra dos Órgãos, the last about 1000 years appear to have been the most pluvial of the entire Holocene period. This corroborates the results of other palaeoecological studies from the region, including Lago do Pires, Minas Gerais (north of the study site; Behling, 1995), and several sites in southern Brazil (Behling, 2002; Behling *et al.*, 2004; Behling & Pillar, 2007).

Conclusions

Results of the about 10 450 ^{14}C yr BP (12 380 cal yr BP) old pollen and charcoal record from the Serra dos Órgãos

(2130 m elevation) indicate the existence of a naturally open landscape with high altitude grasslands (campos de altitude) at higher elevations throughout the recorded period. Diverse montane ARF occurred close to the studied peat bog at the end of the Late-glacial period. *A. angustifolia* occurred in small populations in the Serra dos Órgãos until the beginning of the Holocene, when it appears to have gone locally extinct. Today the nearest natural populations of *Araucaria* are found in the Serra do Mar about 150 km south of the study area in the Serra da Bocaina. At the end of the Late-glacial, between 10 380 and 10 170 ^{14}C yr BP (12 310–11 810 cal yr BP), the extent of campos de altitude was markedly reduced as montane ARF rapidly shifted upward to higher elevations. At the beginning of the Holocene, the montane ARF retreated downwards and the campos de altitude expanded. During the ensuing period, taxa of the montane ARF migrated steadily upward until, after about 4910 ^{14}C yr BP (5640 cal yr BP), elevations of major vegetation types closely corresponded to the present-day situation. There is evidence of a further, relatively minor upward movement of the ARF during the last 920 ^{14}C yr BP (880 cal yr BP). We hypothesize that future global warming will probably intensify the upward movement of the ARF and reduce the area of campos de altitude area in the Serra dos Órgãos and in other mountain ranges of southeastern Brazil.

Inferred climatic conditions for the Late-glacial period in southeastern Brazil are humid and cold, following a period of relatively dry climatic conditions during the last glacial maximum (LGM), inferred for the Morro de Itapeva record (Behling, 1997) and two marine records (Behling *et al.*, 2002).

The Serra dos Órgãos record documents that a very warm and wet period of a little more than two centuries in length occurred at the end of the YD chronozone. At their highest, temperatures during this episode were likely similar to, or higher than today. This strong and rapid warming signal at the end of the Late-glacial is in opposition to the YD cooling that has been documented in the northern hemisphere. Changes in the thermohaline circulation, with reduced heat transport from the southern Atlantic to the northern Atlantic provoking a warming of the western tropical Atlantic, may be the major cause for the rise in air temperatures we document (Rühlemann *et al.*, 1999). Additionally, movement of the Intertropical Convergence Zone (ITCZ) over northeastern Brazil may have also blocked northward-moving Antarctic cold fronts (Rühlemann *et al.*, 1999; Mulitza & Rühlemann, 2000). This pattern, which rarely occurs today, can produce very high rainfall in the Northeast (Arz *et al.*, 1998; Behling *et al.*, 2000; Jennerjahn *et al.*, 2004).

During the early Holocene the climate was dry, probably with a relatively long dry season. This result closely

corroborates other existing records from the southeastern Brazilian lowlands and highlands. Since 4910 ¹⁴C yr BP (5640 cal yr BP) the climate has become wetter, with shorter dry seasons. In the Serra dos Órgãos, the most pluvial period of the Holocene has been the last 920 ¹⁴C yr BP (880 cal yr BP), which also corroborates nearby records from the Atlantic lowland (Behling, 1995).

Fires were rare in the Serra dos Órgãos in the period immediately following the Late-glacial period, but became common during the early Holocene, as climatic conditions shifted from wet to dry and the campos de altitude expanded. Human input to the increased fire regime seems at least possible, if not likely, but is presently impossible to characterize. Fire frequency decreased markedly after about 7020 ¹⁴C yr BP (7850 cal yr BP), and has remained at similar levels since. There has been a slight rise in charcoal accumulation rates during the last about 1000 years.

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