

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

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ABSTRACT. We analysed pollen and macro-charcoal from a sediment core representing the last 9840 cal yr BP, collected at 2003 m a.s.l. in a patch of upper montane Atlantic Rain Forest (UMARF) embedded in a campos de altitude (high-elevation grassland) matrix in the Serra dos Órgãos National Park, southeastern Brazil. From 9840 to 4480 cal yr BP, campos de altitude (CDA) was the dominant vegetation at the site, indicating that the climate was relatively cool and dry. However, pollen data document that UMARF was near the core site throughout the recorded Holocene. Relatively frequent high-magnitude fires occurred during the Early Holocene but became rarer in the Mid-Holocene after 4480 cal yr BP, when the climate became wetter. In the Mid-Holocene, UMARF and tree fern taxa became slightly more frequent at the site, but CDA vegetation continued to dominate most of the high-mountain landscape. A climatic change to wetter and warmer conditions during the last 1350 cal yr BP is evidenced by an increase in UMARF and even lowland forest taxa in our core, as well as the near complete absence of fire after this date.

KEYWORDS: southeastern Brazil, Holocene, campos de altitude (high-elevation grassland), upper montane Atlantic Rain Forest, climate and fire history

INTRODUCTION

The Brazilian coastal highlands (Serra do Mar) extend for ~1000 km along the southeastern Brazilian coastline from the state of Santa Catarina (26°S) to the north of Rio de Janeiro State (21°S) in the Atlantic Forest domain. The Atlantic Forest is one of the world's great tropical forest biomes, and once covered around 130 million ha of coastal and eastern Brazil, stretching ~4000 km from 3°N latitude to almost 34°S (Ribeiro et al., 2009; Fundação SOS Mata Atlântica/INPE, 2017). Due to the variability of environmental

conditions (geomorphology/topography, geology, climate, soils, ecosystems) together with a large elevational range, the Atlantic Forest is one of the most diverse biomes in the world and is considered among the most important and most imperilled biodiversity hotspots on earth (Myers et al., 2000). Before European settlement, the Serra do Mar was clothed in dense rainforest for much of its length, with drier cerrado (Brazilian savanna) formations inland, and elfin “cloud forests” and orographic grasslands (campos de altitude) at higher elevations, mostly above 1500–1800 m a.s.l. (Hueck, 1966; Dean, 1995; Câmara, 2003).

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At the highest elevations, cloud forests (here referred to as “upper montane Atlantic Rain Forest”, or UMARF) tend to occupy topographic concavities and other protected sites such as valleys and mild slopes, and campos de altitude (CDA) are more common on hilltops, plains and convex slopes, or where waterlogging occurs (Safford, 1999a).

Climatic changes during the late Quaternary greatly influenced the modern vegetation distribution. Present-day CDA is a vestigial vegetation type from colder and drier climates which reached its widest distribution during the Last Glacial and in particular the Last Glacial Maximum (25,000–17,000 yr BP), when forest vegetation was nearly completely absent in the higher mountains (Behling, 1997b; Behling and Safford, 2010). UMARF expansion began during the Late Glacial, indicating a shift to

moister conditions (Behling, 1997b; Ledru et al., 2005; Ledru et al. 2009; Behling and Safford, 2010; Veríssimo et al., 2012). A further increase in both temperature and precipitation in the Early to Mid-Holocene allowed the expansion of the Atlantic Rain Forest to higher elevations, markedly reducing the area occupied by CDA (Behling and Safford, 2010). Displacement of the Intertropical Convergence Zone (ITCZ) over northeastern Brazil might explain the Younger Dryas (YD) warming (second part of the YD period) documented in eastern Brazil, in contrast to the YD cooling in the Northern Hemisphere (Behling and Safford, 2010). A palaeoecological study carried out by Behling and Safford (2010) at 2130 m elevation in the Serra dos Órgãos (SDO core; Fig. 1c) recorded widespread CDA vegetation and drier climatic conditions until ~5600 cal yr BP. Thereafter a trend

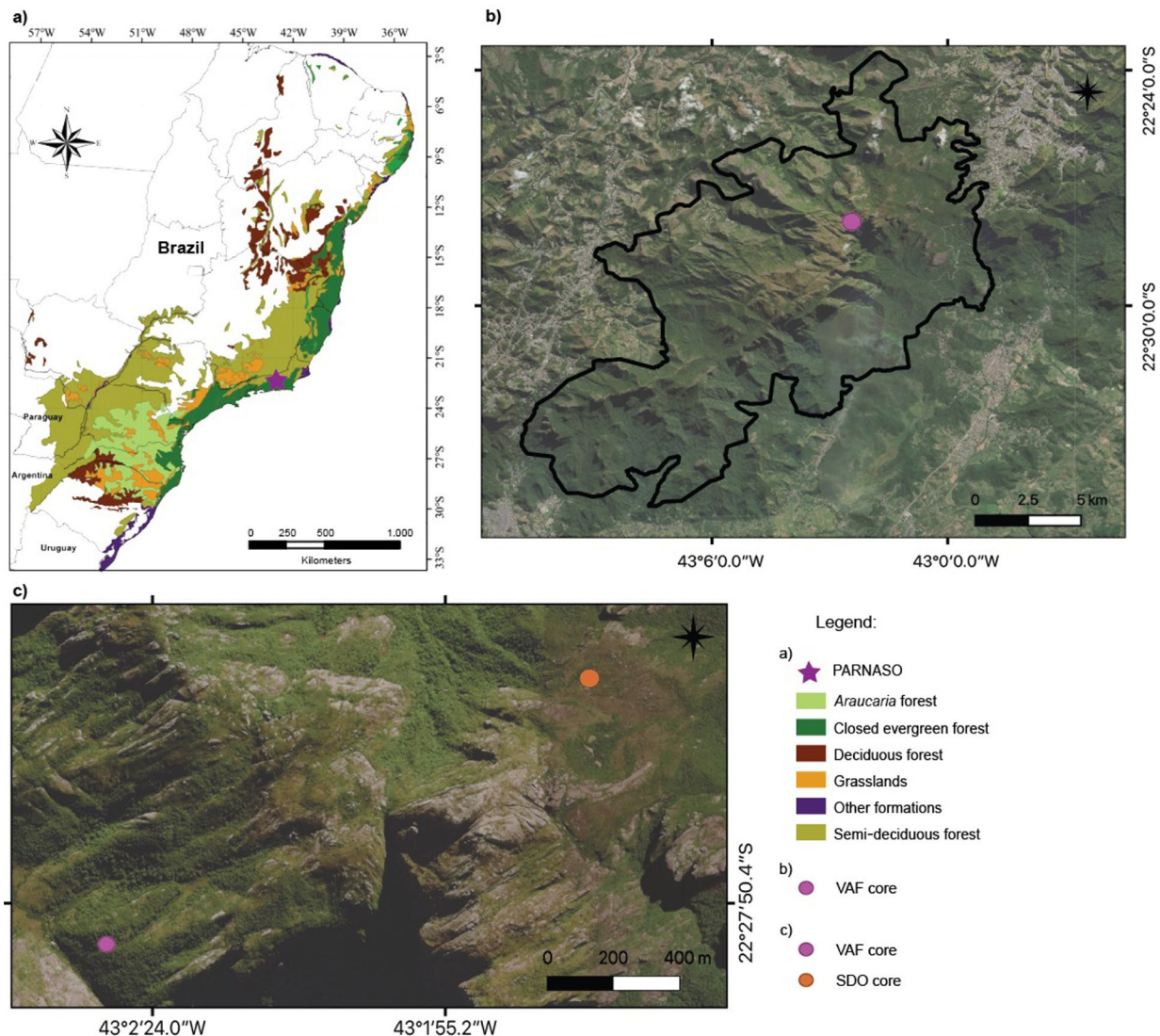


Fig. 1. Location of PARNASO and Vale das Antas Forest (VAF) core. (a) location of PARNASO (adapted from Fundação SOS Mata Atlântica/ INPE, 2017), (b) location of VAF core in PARNASO, and (c) distance and vegetation type of VAF core (in UMARF) and SDO core (in CDA) from Behling and Safford (2010)

toward warmer and wetter conditions resulted in expansion of montane forest and contraction of campos. The last ~1000 years were the wettest period during the entire Holocene (Behling and Safford, 2010).

Centuries of exploitation by humans reduced the Atlantic Forest to a patchwork of small fragments in a natural or semi-natural state, covering today only about 10% of its pre-Columbian area (Fundação SOS Mata Atlântica/ INPE, 2017). While more intense occupation and deforestation occurred after European colonization, starting at ~1500 AD, the history of human presence along the Brazilian coast started with the migration of Amerindians from the north, arriving in southeastern Brazil about 10,000 years ago (Figuti et al., 2004). Although mostly settled along the coast, these populations also occupied inland forests by ~1800 yr BP (Noelli, 2008). Evidence is strong that Amerindian practices of land use had important impacts on forest structure and composition before the arrival of Europeans (Portes et al., 2018). The first Portuguese settlements were established mainly in Rio de Janeiro State, beginning a period of more intense exploitation of the forest. Today, the southeast is the most populated region of Brazil, but ironically it supports some of the most important remnants of the Atlantic Forest, due to the steep topography and complex relief of montane areas in the region.

Most of the large forest remnants in southeastern Brazil are found in protected areas. One of the most important is Serra dos Órgãos National Park (PARNASO). Located in the northernmost part of the Serra do Mar, PARNASO protects montane rainforest stands and an important complex of UMARF and CDA on a high plateau that supports many rare and endangered species, from epiphytes and bamboos to large animals such as jaguars (Martinelli and Bandeira, 1989; see also the Brazilian red books for flora and fauna: Martinelli and Moraes, 2013 and ICMBio, 2018). As the climate becomes warmer and wetter, upward migration is expected and the reduction of habitat for high-mountain taxa is a strong possibility (Rull et al., 2009; Vegas-Vilarúbia et al., 2011). Understanding the temporal relationships between climate and vegetation is essential for conservation in the face of climate change, and palaeoecological studies can help to reveal which species and

ecosystems may need human intervention to persist (Behling and Pillar, 2007; Overbeck et al., 2015; Barnosky et al., 2017). Although the Brazilian highlands have been the object of palaeoecological investigations for more than two decades (e.g., Behling 1995, 1997a,b, 2007; Scheel-Ybert, 2001; Ledru et al., 2005; Behling et al., 2007, 2020; Behling and Safford, 2010; Veríssimo et al., 2012; Raczka et al., 2013; Portes et al., 2018), much more remains to be learned about how montane vegetation in this region is influenced by climate, fire and human impacts over the long term.

Here we report results from a multi-proxy study that analysed temporal vegetation dynamics in a forest patch currently occupied by UMARF and surrounded by CDA vegetation, located near the SDO core sampled by Behling and Safford (2010). Overall, our goal was to better understand temporal dynamics between forest and grassland vegetation in a highly heterogeneous landscape characterized by high biodiversity and high species turnover. Specifically, we wanted to determine (1) how climatic change and fire interacted at this montane forest site to influence vegetation composition and dynamics during the Holocene, and (2) how Holocene vegetation dynamics differed in this forest patch as compared to the CDA vegetation sampled in the nearby SDO core (Behling and Safford 2010).

ENVIRONMENTAL SETTINGS

The study site (2003 m a.s.l., 22°27'53.49"S, 43°2'27.04"W) is located in Serra dos Órgãos National Park (PARNASO), Rio de Janeiro State, southeastern Brazil (Fig. 1). The south-east-facing site is a 2.2 ha patch of upper montane Atlantic Rain Forest (UMARF) bordered by campos de altitude (CDA) in the Serra dos Órgãos, a subrange of the Serra do Mar (Brazilian coastal highlands), ~90 km from the Atlantic Ocean. The geologic substrate in the study area is Upper Proterozoic granite and granitoid gneiss, uplifted to its present elevation by Cenozoic tectonism associated with widening of the Atlantic Ocean (Riccomini et al., 1989). The Serra dos Órgãos follows a largely NE–SW orientation parallel to the coast. Soils at the study site are generally shallow, poorly developed, acidic and highly organic, with high amounts of litter (Falkenberg and Voltolini, 1995).

In the region the climate is controlled mostly by the South Atlantic Convergence Zone (SACZ), with most precipitation falling between November and April (Safford, 1999a; Vuille et al., 2012). The climate for the region generally has been defined as mesothermic, with mild and wet summers and moderate winters without a well-defined dry season (Nimer, 1977; ICMBio, 2008). The nearest long-term meteorological station is at Teresópolis (22°25.980'S, 42°58.980'W) at 1100 m a.s.l., where mean annual temperature is 17.6°C (July mean = 8.6°C, February mean = 27.2°C) and mean annual average precipitation is 1800 mm (Hijmans et al., 2005). Our field site is 900 m higher and there is considerable orographic enhancement of precipitation, resulting in a winter without a true dry season. PARNASO installed temperature data loggers near the study site in September 2012. Between September 17, 2012, and February 2, 2014, the mean overall temperature was 12.7°C, the maximum was 25.6°C and the minimum was 1°C (C. Cronemberger, PARNASO, pers. comm.). Temperatures in the nearby CDA in the Vale das Antas (slightly below our study site, in the valley bottom) showed a similar mean temperature (12.5°C) but the temperatures were more extreme due to the lack of trees and the valley bottom position (max = 27°C, min = -5.2°C). Safford (unpub. data) also measured winter temperatures in the Vale das Antas campos: in July 1997 a minimum of -9.8°C was measured, which is the lowest temperature recorded for the Serra dos Órgãos. From regressions against elevation, Safford (1999a,b; Behling and Safford, 2010) estimated precipitation at 2000 m elevation in the Serra dos Órgãos study site to be between 2500 and 3000 mm annually.

In the Serra dos Órgãos, CDA vegetation occurs above 1800–2000 m elevation, depending on substrate, topography, slope, aspect, and history of disturbance (Safford 1999a). CDA is most common on hilltops and convex slopes, and also dominates poorly drained valley bottoms (Safford, 1999a; see Fig. 1). Below 1800–2000 m elevation UMARF is the dominant vegetation, gradually replacing tall montane forest above ~1500 m a.s.l., while above these elevations UMARF becomes more and more restricted to protected sites.

The CDA is dominated by graminoids, in PARNASO especially by the giant bunchgrass *Cortaderia modesta*, montane bamboo (*Chusquea pinifolia*) and the large sedge

Machaerina ensifolia. Frequent herb genera include *Eryngium* (Apiaceae), *Paepalanthus*, *Plantago* and *Xyris* (Behling and Safford, 2010). Many sclerophyllous shrub taxa are found in the CDA, as well as smaller trees, often in some stage of succession toward (after fire or livestock incursion) or away from grassland (long-term lack of disturbance). More open habitats tend to support more woody taxa from Asteraceae (e.g., *Baccharis*, which is a good indicator of campos vegetation). Certain woody taxa from genera such as *Croton* and a number of genera from Myrtaceae (*Myrceugenia*, *Gomidesia*) and Ericaceae (*Gaylussacia*) are also more common in campos habitat. However, most woody taxa in the campos are forest taxa and their density is higher near forest borders. The UMARF is formed by twisted and dwarfed trees and shrubs distributed largely in one stratum normally less than 10 m high. Due to high air humidity and frequent fog, there is high abundance and diversity of epiphytes and mosses on tree trunks and branches, rocks and soil (Falkenberg and Voltolini, 1995; Safford, 1999a; Portes et al., 2001). Important tree genera include *Myrsine*, *Weinmannia*, *Clethra*, *Daphnopsis*, *Roupala*, *Symplocos*, *Tibouchina*, *Ilex*, *Ocotea* and a number of genera from Myrtaceae (Behling and Safford, 2010; Gomes, 2015). Tree ferns of various species are common, as well as epiphytes such as bromeliads and orchids. The grassland–forest ecotone, where scattered trees/open forest cover and understory species co-dominate, is marked by very high habitat heterogeneity. Many herbaceous species from Rubiaceae are especially common in these situations, likewise shrubs of Myrtaceae and Melastomataceae.

Our study site consists of an island of UMARF surrounded by CDA vegetation, located in a protected site facing southeast at 2003 m a.s.l. (Fig. 1), ~1.5 km from the higher-located SDO core site at 2130 m a.s.l. (Behling and Safford, 2010).

MATERIAL AND METHODS

SEDIMENT CORE SAMPLING AND DATING

In February 2015, a peat deposit was cored and a core 88 cm long was collected in an undisturbed area of UMARF on the lower slopes of the Vale das Antas (“Tapir Valley”) and herein called VAF (Vale das Antas Forest). From a base of bedrock, the 88 cm-long core was extruded onsite in two sections using a Russian Corer, wrapped in plastic film, and stored under

cool (~4°C) and dark conditions. Six organic bulk sediment samples were collected along the sediment for radiocarbon dating. Two samples were analysed at the Accelerator Mass Spectrometry (AMS) Laboratory at National Taiwan University (NTUAMS), and four samples at the AMS Poznan Radiocarbon Laboratory (LAMS) (Tab. 2). HCl tests on several core samples were negative and excluded the possibility of a carbon reservoir effect. The age-depth model was built with R-package Clam 2.2 (Blaauw, 2010) in R-Studio (R-Studio Team, 2016) using the Southern Hemisphere calibration curve SHCal13.14C and postbomb curve SH 1-2. Calib 7.1 was used for calculating median probability (Stuiver et al., 2019).

PALYNOLOGICAL ANALYSIS

In total, 44 subsamples (0.25 cm³) in 2 cm intervals were taken along the core for analysis of palynomorphs. Standard pollen techniques were used to process the samples, applying 40% hydrofluoric acid (HF) and acetolysis (Faegri and Iversen, 1989). The marker *Lycopodium clavatum* (20848±1546, batch 1031) was added to each subsample to determine the pollen concentration (grains cm⁻³) and pollen accumulation rate (grains cm⁻² yr⁻¹) (Stockmarr, 1971). The obtained residue was kept in distilled water and mounted on slides with glycerine for palynomorph analysis under a light microscope. A minimum of 300 pollen grains per sample were counted. Pollen and spores were identified based on the Brazil reference collection of the Department of Palynology and Climate Dynamics at the University of Goettingen, and with support of literature and electronic pollen keys (Behling, 1993; Melhem et al., 2003; Neotropical Fossil Pollen Search Tool developed by Dr. Hermann Behling and Dr. Chengyu Weng [unpublished]). Nomenclature is based on Flora do Brasil 2020 (<http://floradobrasil.jbrj.gov.br>).

Pollen and spore percentages were calculated from the pollen sum, including herbs, shrubs, trees and unknowns, and excluding ferns, mosses, fungal and non-pollen palynomorphs (NPPs). The groups were separated following Behling and Safford (2010) for further comparison: campos de altitude (CDA), upper montane Atlantic Rain Forest (UMARF), other Atlantic Rain Forest (OARF), lowland Atlantic Rain Forest (LARF), ferns (tree ferns and ferns), mosses, fungal spores and NPPs. The pollen diagram was constructed with C2 (Juggins, 2007); it portrays the most important taxa based on frequency and dominance. TILIA and TILIAGRAPH were applied to determine pollen assemblage zones based on stratigraphic constrained cluster analysis of the pollen sum by CONISS (Grimm, 1987).

MACRO-CHARCOAL ANALYSIS

For analysis of the past fire regime and its influence on vegetation, macro-charcoal particles (>150 µm) were counted in a total of 176 subsamples of 0.5 cm³ continuously extracted from the core at 0.5 cm resolution. Samples were prepared following the method of Stevenson and Haberle (2005, adapted from Rhodes, 1998), a procedure that greatly limits particle fragmentation. We added 6% H₂O₂ to remove organic material in the sediment and gently wet-sieved the samples, retaining

particles ≥ 150 µm. Concentrations were determined as particles per cm³. Fire regime characteristics were identified using CharAnalysis software (Higuera, 2009). The data were interpolated to the median temporal resolution (42 years) to obtain the charcoal accumulation rate (CHAR particles cm⁻² yr⁻¹). A window of 1000-year locally weighted regression was applied to separate background components (C_{background}) and peak components (C_{peaks}) (Higuera et al., 2010). A Gaussian mixture model was used to identify the C_{noise} distribution. The 99th percentile of the C_{noise} distribution was used to define thresholds. Poisson minimum-count was used to eliminate the peaks from statistically nonsignificant counts. We used a window of 1000 years to estimate the distribution of fire frequencies. Peak magnitude as an estimate of total charcoal deposition per fire event was used to reflect fuel consumption per fire and/or fire size (Higuera et al., 2010; Biagioni et al., 2015).

LOSS ON IGNITION

To estimate the organic matter and carbonate content in the sediment, 0.5 cm³ subsamples were continuously extracted from the sediment and immediately weighed. The samples were dried at 105°C for 24 h and combusted at 550°C during 4 h. Afterwards the samples were dried again and OM% was calculated following the method described in Heiri et al. (2001).

RESULTS

STRATIGRAPHY, CHRONOLOGY AND ACCUMULATION RATE

The 88 cm-long core consists mostly of black organic material on a rocky subsurface. A detailed description is given in Table 1.

Six AMS radiocarbon dates were used to construct the age-depth model (Tab. 2), spanning the period 9840 cal yr BP (calculated age for the lowermost sample at 88 cm) to the present. After testing other age models, the data were best represented using a 0.3 smoothing spline (Fig. 2). Using this technique, the lowest accumulation rate is at 63 cm (203 yr/cm), while the highest accumulation rate is at present (8 yr/cm). Using interpolation, from the age-depth model the accumulation rate is 170 yr/cm at 88–67 cm core depth, 197 yr/cm at 66–43 cm, 40 yr/cm at 42–40 cm, 52 yr/cm at 39–33 cm, 59 yr/cm at 32–19 cm, and 11 yr/cm from 31 cm to the surface. Median probability was calculated using Calib 7.1 (Tab. 2).

Loss-on-ignition analysis demonstrated that the sediment is organic, defined as having more than 12% organic carbon. Organic content is lowest in the bottom part of the core, ~30% at 88–60 cm depth, and at 60–0 cm the average for organic matter is ~38%.

Table 1. Stratigraphy of the Vale das Antas core

Depth (cm)	Description
0–20	Black organic material, rather compact and strongly decomposed, some rootless, roots and plant remains
20–41	Black organic material, compact and strongly decomposed, few root fragments
41–61	Black organic material, compact and strongly decomposed, few plant remains, slightly silty
61–84	Black organic material, compact and completely decomposed, fine sandy
84–88	Black organic material, compact and completely decomposed, few small yellow rocks
88–	Rocky subsurface

Table 2. AMS radiocarbon dates from the VAF core, with calibrated age ranges at 95% confidence intervals

Lab code	Depth (cm)	Material dated	Date (^{14}C age BP)	Calendar age (cal yr BP) 2σ	Median probability (cal yr BP)
Poz-106102	19	Organic bulk sediment	180 ± 30	164–282 (46.1%) 56–123 (25%) –3–33 (13.4%) 132–157 (10.1%) 39–40 (0.3%)	152
Poz-106103	33	Organic bulk sediment	1115 ± 30	927–996 (68.5%) 1013–1056 (26.4%)	969
Ntuams-2691	40	Organic bulk sediment	1511 ± 9	1315–1369 (95%)	1343
Poz-106105	43	Organic bulk sediment	1610 ± 30	1400–1531 (90.1%) 1378–1393 (4.7%)	1461
Poz-106106	67	Organic bulk sediment	5460 ± 110	5982–6406 (92.2%) 5941–5974 (2.8%)	6196
Ntuams-2015	86	Organic bulk sediment	8465 ± 44	9396–9529 (82.7%) 9308–9361 (11.3%) 9375–9382 (1%)	9455

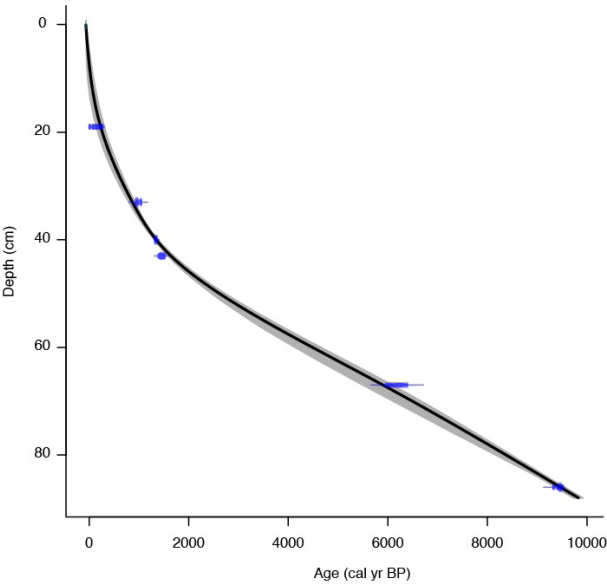


Fig. 2. Age-depth smoothing spline model for the Vale das Antas core

PALYNOLOGICAL RESULTS

The record is divided into three pollen zones based on constrained cluster analyses by CONISS: VAF-I, VAF-II and VAF-III. A total of 94 pollen and 37 spore taxa were identified in the 44 samples (supplementary material). 12 pollen types remain unidentified. The pollen percentage diagram (Fig. 3a) shows the dominant and most important taxa grouped

into CDA, UMARF, OARF, LMARF and ferns. The summary diagram (Fig. 3b) shows the total percentage sum for each group: CDA, UMARF, OARF, LARF, tree ferns and spores, and the sum of all Asteraceae types. Figure 3b also includes the depth curves of sedimentation rate (yr/cm), LOI (%), charcoal concentration (particles cm^{-3}), charcoal accumulation rate (particles $\text{cm}^{-2} \text{yr}^{-1}$), fire peaks and fire magnitude.

VAF-I (88–60 cm; 9840–4480 cal yr BP)
14 samples

This zone is characterized by the dominance of CDA pollen, averaging 61% and ranging from 49% to 69%. Poaceae is the most dominant taxon (46%, >32% to <55%), followed by different Asteraceae types which represent almost 10% of the pollen sum in this zone (>7.5% to <12%). However, *Baccharis* shows its lowest values in the core in this zone (~2%). Other taxa characteristic for the CDA assemblages in VAF-I are Apiaceae (~2%), Cyperaceae (1%) and Fabaceae (1%).

The average sum of arboreal taxa represents 33% (25–44%) of the pollen spectra, and are dominated by UMARF, represented primarily by *Weinmannia* (10%, >5% to <17%) and *Myrsine* (6%, >3% to <8%). Most taxa of UMARF have their lowest values in this zone,

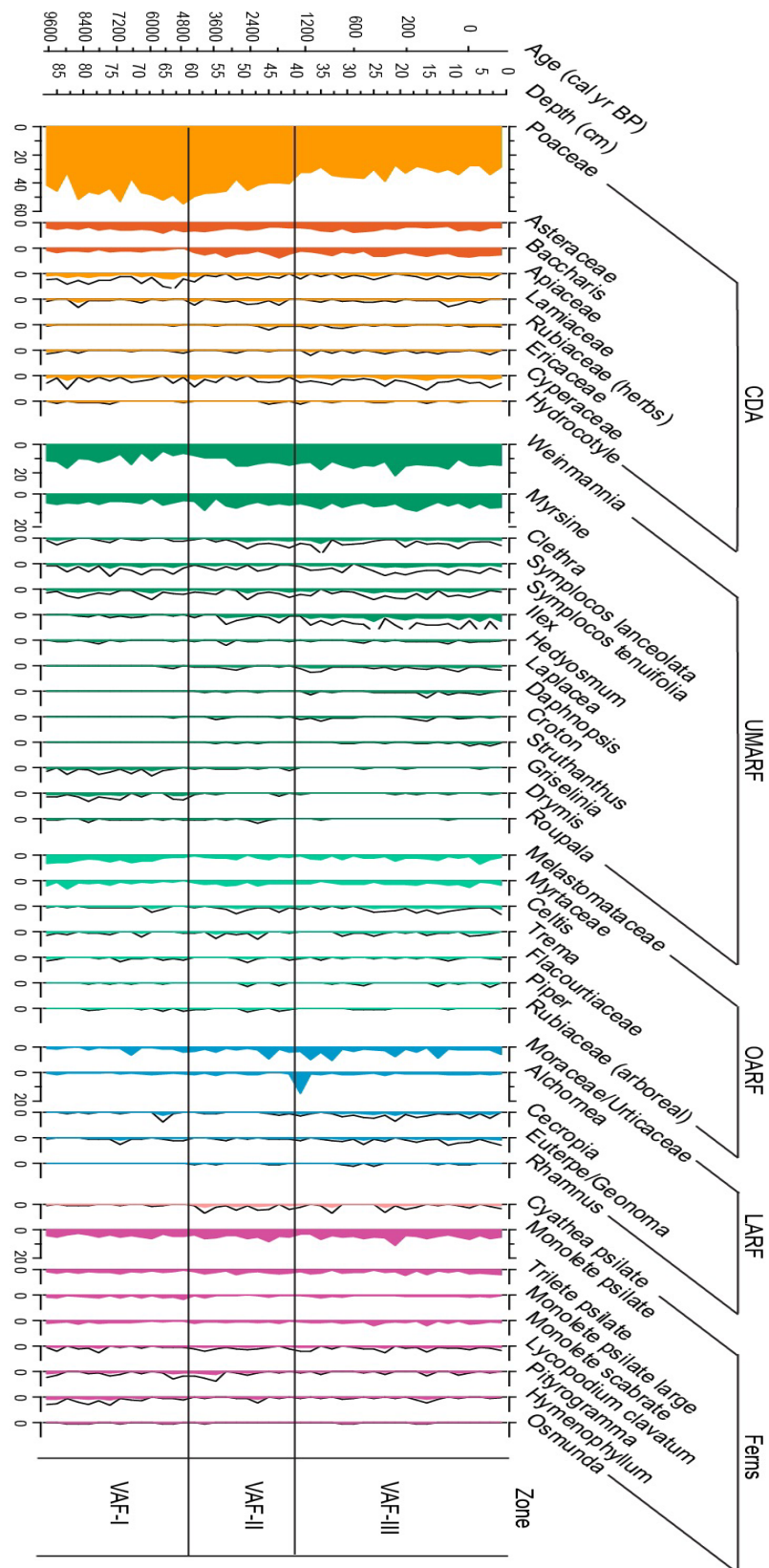


Fig. 3a. Pollen percentage diagram of the most important and most frequent taxa of the VAF core into each group

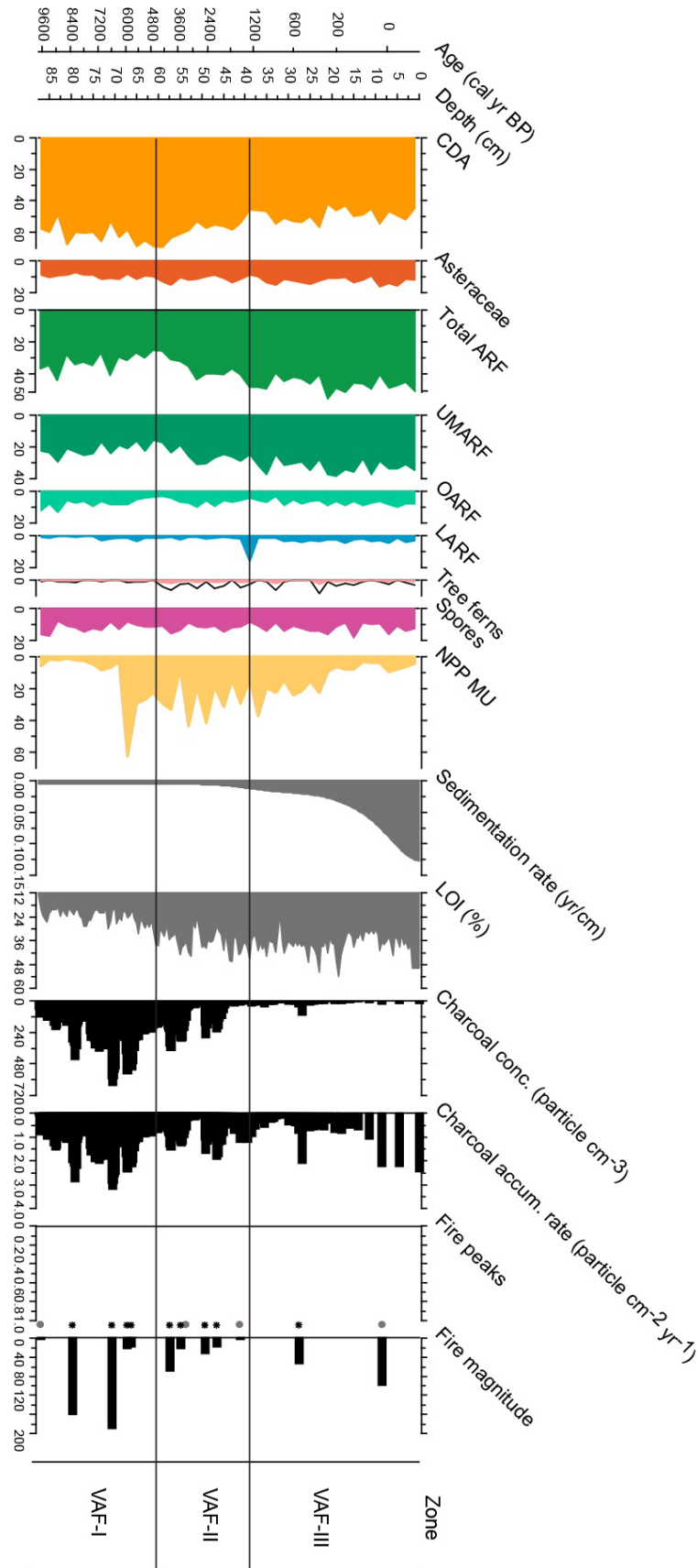


Fig. 3b. Summary diagram of the Vale das Antas Forest core, showing the ecological groups (%), sedimentation rate (yr/cm), loss on ignition (%), macro-charcoal concentration (particle cm⁻³) and accumulation rate (particle cm⁻²yr⁻¹), fire peaks and fire magnitude. A 5× exaggeration scale line is shown for low percentage values

but *Griselinia* and *Drimys* follow an opposite trend and are found at their highest densities in this zone, ~1% each. In contrast to the UMARF group, OARF pollen shows its highest values in this zone, averaging 8% and ranging from 4% to 13%, with Melastomataceae at ~4% and Myrtaceae ~2%. LMARF pollen are scarce in VAF-I and average only 3% of the pollen sum, ranging from 1% to 8%, represented primarily by Moraceae/Urticaceae (1.5%) and *Alchornea* (1%). Tree ferns occur only as a few single spores. Other fern spores show a roughly continuously percentage in the zone at ~12% (>8% to <17%).

VAF-II (60–40 cm; 4480–1350 cal yr BP) 10 samples

The CDA pollen percentages slightly decrease to 59%, ranging from ~70% at 50 cm to 54% at 41 cm core depth. Poaceae (43%, >37% to <49%) and Asteraceae types (~12%, >9% to <15%) continue as the main taxa, and *Baccharis* increases to ~4%. The arboreal assemblage reaches ~37% (ranging from 26% to 44%) mostly due to the UMARF group (25%, >17% to <31%), characterized mainly by *Weinmannia* (12%, >8% to <15%) and *Myrsine* (~7%, >3% to <11%). *Clethra*, *Symplocos lanceolata*, *S. tenuifolia* and *Ilex* represent ~1% each. The OARF assemblage gradually decreases to 6.5% (>3% to <10%), with Melastomataceae pollen declining to less than 2% while Myrtaceae increases to 2.5%. LMARF increases slightly to 4.5% (>2% to <10%) in VAF-II, driven primarily by Moraceae/Urticaceae which reaches almost 3% (>15% to <8.5%). Relatively speaking, tree fern pollen increases greatly in this zone but only to ~1%, while other fern spores are stable at 12% (>9% to <16%).

VAF-III (40–0 cm; 1350 cal yr BP to present) 20 samples

In this zone, CDA pollen show a noticeable decrease to 49% (ranging from 42% to 57%) of the pollen sum. This is driven primarily by the decrease of Poaceae to 32% (>27% to <39%). Asteraceae oscillates but on average maintains the same sum as VAF-II (12%, >9% to <16%), while Cyperaceae reaches its maximum average value of 1.5%. Arboreal pollen increases to ~47% (39–56%), led by UMARF pollen at 32% (>25% to <38%) and LMARF pollen at 7.5%. Although *Weinmannia* and *Myrsine* remain the most important taxa in the UMARF group,

increasing to 15% (>11% to <22%) and ~8% (>6% to <12%) respectively, other taxa also contribute to the increase in VAF-III. *Clethra*, *S. lanceolata* and *S. tenuifolia* occur at ~1% each and *Ilex* reaches ~2%. OARF continues with ~7% (ranging from 3% to 10%), and its main taxa (Melastomataceae and Myrtaceae) remain constant. A stronger change is observed in LMARF, which reaches its maximum (mean = 7.5%, 3–20%), due to the expansion of Moraceae/Urticaceae (3.7%), *Alchornea* (2%), *Cecropia* (1%) and *Euterpe/Geonoma* (0.7%). As in the previous zones, non-tree fern spores are at 12% (>8.5% to <16%), while tree ferns show slightly reduced values.

MACRO-CHARCOAL AND FIRE REGIME

CharAnalysis of macro-charcoal characterized the fire history for the past 9840 years (Fig. 3b). Average concentration for the entire sediment is 190 particles cm⁻³, decreasing from 250 particles cm⁻³ in zone VAF-I to 150 particles cm⁻³ in VAF-II and only 30 particles cm⁻³ in zone VAF-III. Local signal-to-noise exceeds 3.5, indicating good separation between peak and non-peak values. Of 13 fire peaks, 4 fire episodes failed to pass the Poisson minimum-count criterion, including the most recent peak at 9 cm depth (19 cal yr BP). The most recent significant peak is at 28 cm depth, (565 cal yr BP). The mean fire return interval (FRI, 95% probability), calculated with a 1000-yr window and only using fires that met the minimum-count criterion, is 998 yr (593–1449 yr). Using all 13 identified fire peaks and calculating the FRI across the entire record yields an FRI of 617 (446–827 yr). Under either measure, local fire events (fires within ~500 m of the core site) were rare over the period of our sample, but the nearly continuous presence of charcoal through the core demonstrates that fires were not uncommon regionally. Most fire peaks as well as the highest magnitude peaks occurred in zone VAF-I.

INTERPRETATION AND DISCUSSION

Overall, the stratigraphy and the organic matter content of the VAF core in Serra dos Órgãos National Park indicate that there was a change from drier to wetter climatic conditions in the region during the Holocene, demonstrated by the lower accumulation rate and

lower organic matter in the bottom part of the core. From the beginning of the pollen record, the general study area was dominated by CDA, rich in grass and shrubs, represented mostly by species of Poaceae, Asteraceae, Apiaceae and Cyperaceae. Forest cover at high elevations (>1800 m) in the Serra dos Órgãos and other mountains in southeastern Brazil is extremely heterogeneous and controlled largely by climotopographic and soil variables in combination with disturbance (Safford, 1999a,b, 2001). Other studies of palaeovegetation in the southeastern Brazilian mountains (Behling, 1997b; Behling et al. 2007; Behling and Safford, 2010; Veríssimo et al., 2012; Behling et al., 2020) show a trend of increasing forest cover – and decreasing campos cover – at high elevations since the Early Holocene, with acceleration of this trend during the Late Holocene, indicating that the regional climate during the Early Holocene was much drier than today and that CDA vegetation was much more widespread than today.

Our pollen data suggest that UMARF was not widely distributed at higher elevations (>1800 m) in the Serra dos Órgãos in VAF-I (9840–4480 cal yr BP), and that the more continuous local forest may not have developed until after 1350 cal yr BP (VAF-III). Before 4480 cal yr BP the study site was rich in genera of southern temperate-latitude ancestry such as *Weinmannia*, *Drimys* and *Griselinia*, implying a somewhat colder climate than today. UMARF taxa of tropical origin were also represented in the Early Holocene pollen, but their abundances were mostly low or very low before they began to rise substantially after 4480 cal yr BP. Examples of this pattern include *Clethra*, *Ilex*, *Laplacea*, *Daphnopsis*, *Croton* and the tree ferns. Some UMARF genera were already relatively common before 4480 cal yr BP but saw their abundances rise further thereafter. Examples are *Weinmannia* (2× increase) and *Myrsine* (50% increase). *Symplocos*, Melastomataceae and Myrtaceae (the latter two very common in both UMARF and OARF) showed relatively invariant abundances throughout the Holocene. The modern UMARF is characterized by species of temperate, Neotropical and tropical origin which occur in the majority of UMARF in southeastern and southern Brazil (e.g. Portes et al., 2001; Safford, 2007; Scheer and Mocochinski, 2009; Gomes, 2015; Moreira et al., 2018).

Modern pollen rain data from the Serra dos Órgãos (Portes et al., 2020) suggest that areas

of CDA are under-represented in the total pollen assemblage due to (1) the low pollen production and low accumulation rate of CDA taxa, and (2) the over-representation of some arboreal taxa, especially pioneer or secondary species of montane forest that are wind-transported over large areas and elevational ranges. Portes et al. (2020) proposed that a restricted group of typical upper montane forest taxa provides a more trustworthy measure of actual montane forest presence at a site than the full ARF group. Therefore, following Portes et al. (2020), we aggregated pollen sums from *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* to represent UMARF and we aggregated the same taxa used by Behling and Safford (2010) to represent the CDA. Figure 4 shows the temporal trends in this group of taxa and in CDA from our VAF core and the SDO core sampled by Behling and Safford (2010) (which stretched back into the Late Pleistocene, 12,380 cal yr BP), and superimposes the macro-charcoal concentration (particles cm⁻³) from the VAF core and the $\delta^{18}\text{O}$ record from Bernal et al. (2016). Our data suggest that the study site was dominated by CDA vegetation for most of the Holocene, with more or less uniform CDA vegetation in the Early Holocene and a notable contraction in the Late Holocene after ~4500 yr BP (but apparently occurring earlier at the SDO core site), corroborating the higher charcoal concentration as well as the drier climate at that period. As the climate becomes wetter after ~1400 cal yr BP, the charcoal concentration decreases, the CDA:forest (sum of ARF subdivisions) ratio drops to 50:50, and the group of upper montane ARF increases to ~30%. The SDO core shows similar patterns, with an accentuated increase in forest pollen after ~5000 cal yr BP and the balance of campos vs. forest pollen dropping below 50:50 after ~1500 cal yr BP (Fig. 4). While the VAF core was collected in a currently UMARF patch surrounded by CDA vegetation, the SDO core was cored from more widespread CDA vegetation. We hypothesize therefore that the patch of forest that currently occupies the VAF site has been extant only since sometime in the Late Holocene, although the pollen data make it clear that upper montane forest taxa have been in the broader region throughout the Holocene.

The VAF core also documents temporal floristic variation that points to important

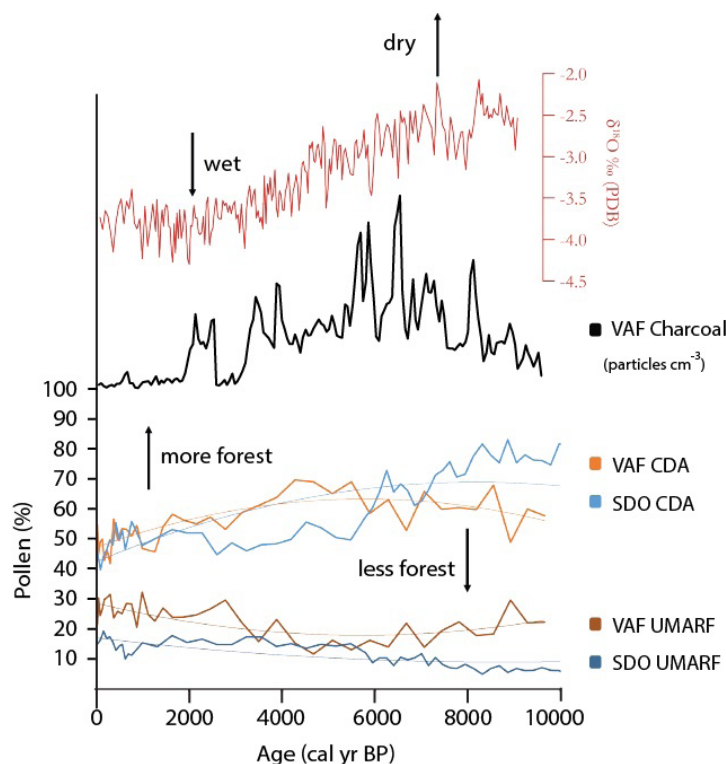


Fig. 4. Comparison of the sum (%) of *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* taxa representing UMARF from the VAF core (VAF UMARF), the sum of *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* taxa representing UMARF from the SDO core (SDO UMARF), the sum of the CDA group from the VAF core (VAF CDA) and the sum of the CDA group from the SDO core (SDO CDA), plotted with macro-charcoal concentration (particles cm^{-3}) from the VAF core and the $\delta^{18}\text{O}$ record from Botuverá Cave (Bernal et al., 2016) for the last 10,000 years. Trendline from 2nd-order polynomial

changes in climate over the course of the Holocene. We interpret the Early and Mid-Holocene as relatively cool and dry (but becoming gradually warmer and wetter over time), based on (1) the general lack of tree ferns, (2) low LOI values, (3) relatively high frequency and magnitude of fire, (4) relatively low pollen density for *Baccharis*, which is a reliable campos indicator but under warmer temperatures, and (5) the elevated presence of cool climate indicators of southern temperate ancestry such as *Drimys* and *Griselinia*. In addition, the nearby SDO core records *Araucaria* pollen until ~10,800 cal yr BP, further pointing to cooler Early Holocene temperatures. UMARF vegetation in the Early and Mid-Holocene seems to have included a more substantial component of southern-temperate taxa than it does today.

Zones VAF-II (4480–1350 cal yr BP) and VAF-III (1350 cal yr BP to present) represent the Late Holocene. After 4480 cal yr BP the organic matter in the soil increased in tandem with increases in the abundance of UMARF and OARF taxa. Taxa of tropical origin such as *Clethra*, *Symplocos*, *Celtis*, *Trema* and Flacourtiaceae expanded, as did the tree ferns. Associated with the rising elevation and expansion of

forest, fire magnitude and frequency declined, suggesting a shift to wetter conditions. A shift to even wetter conditions appears to have occurred at the beginning of VAF-III (~1350 cal yr BP), demonstrated by a strong and abrupt intensification of sediment accumulation, a decrease in charcoal concentration, and a reduction of CDA pollen to ~50% of the total. The sharp peak of *Alchornea* just after 1350 cal yr BP and the increase in other tropical LARF taxa (Moraceae/Urticaceae, *Cecropia*, and *Euterpe/Geonoma* type) are indicative of a rapid change toward a warmer and wetter climate in the Late Holocene. Since about 1200 cal yr BP the CDA/UMARF relationship has remained in an approximate balance in the study area. During this period, the last significant fire peak occurred at ~600 cal yr BP, possibly related to the VAF-III peak in CDA pollen and concurrent drop in UMARF pollen that occurred shortly thereafter.

Other studies also suggest an intensification in Late Holocene precipitation. Moss spores in the nearby SDO core increased greatly in Late Holocene sediment (Behling and Safford, 2010). Palaeoclimate data from the last 10,000 years at Botuverá Cave (27°13'S, 49°09'W,

230 m a.s.l.; Bernal et al., 2016) registered an increase in rainfall starting about 4000 years ago (see Fig. 4), which coincides with the spread of forest vegetation and the declining occurrence and magnitude of fire in our core. Evidence for a relatively sudden increase in precipitation in VAF (see above) at around 1350 cal yr BP is also supported by studies of the SAMS (South American Monsoon System) over the last 2000 years, which show a strengthening monsoon during the Little Ice Age (LIA), resulting in a wetter period from ~1400 to 1800 AD (Vuille et al., 2012).

Charcoal in the VAF and SDO cores suggests that fires have occurred in the Serra dos Órgãos since at least the Late Pleistocene, that is, before the documented arrival of humans in southeastern Brazil around 10,000 years ago (Figuti et al., 2004). Longer records from other CDA sites in the southeastern Brazilian mountains show notably more fire even further back in time, such as the 35,000-year record from Morro do Itapeva in the southern Serra da Mantiqueira (Behling, 1997b) and the 18,600-year record from the Serra da Bocaina (Behling et al., 2007). However, fires in the immediate locality of the VAF core were infrequent during the Holocene. By using relatively large macro-charcoal (>150 µm) in our Char-Analysis, we restricted our assessment to fires that probably occurred within 500 m or so of the core site (Higuera et al., 2007). This permits a more site-specific understanding of the fire history and suggests that the Holocene fire return interval in this wet but seasonally dry landscape was long, ranging from around 600 to 1000 years (depending on our assumptions). It is also clear, however, that fires were, and usually still are, relatively small, and our analysis thus under-represents the fire regime of the broader landscape. Topographically the Serra dos Órgãos landscape is extremely abrupt and heterogeneous (the rise from Guapimirim to Pedra do Sino is 2210 m in less than 8 km, and some of the tallest rock walls in all of Brazil are found here), and the high mountain summits and plateau that support CDA are small, ringed by cliffs and humid forest, and cut by deep gorges (see Fig. 1). As a result, lightning ignitions that occur on topographic eminences with combustible fuels (graminoids or dry woody fuels) have little chance to spread far. Most lightning strikes in southeastern Brazil occur during the wet season, but lightning at

either the beginning or end of the wet season has the potential to cause fire (Safford, 2001). Today most ignitions are anthropogenic and occur during the dry season, when lightning ignitions are far more rare. Human-caused ignitions that occur during very warm and especially windy conditions can spread from mountain to mountain and even burn appreciable areas of forest. Control of such fires is a major conservation issue in the Brazilian National Park system.

Another reason our charcoal analyses almost certainly under-represent palaeofire frequency in the CDA is that macro-charcoal (>150 µm) is composed of charred woody fragments, but graminoids are the principal fuel for fire in the campos. Whitlock et al. (2004) noted that the best correspondence between real fire frequency and charcoal records is where woody vegetation is dense and continuous, a condition that is rare at the highest elevations of the Serra do Mar. Behling et al. (2020) found a similar site-specific fire return interval for the AN core from the Serra do Itatiaia (mean = 630 years through the Mid- and Late Holocene) and noted similar issues with the dominance of graminoid vegetation in the surrounding landscape. Obvious directions for further research are (1) to conduct macro-charcoal analyses of already published cores that predated the development of the analytical techniques (such cores exist from a number of high montane sites in southeast Brazil), (2) to obtain sediment core samples from more – and both elevationally and vegetationally more varied – locations in the southeastern Brazilian highlands, and (3) to develop new techniques to better assess fire frequencies and magnitudes using charcoal from herbaceous sources.

SUMMARY AND CONCLUSION

Like other studies of palaeovegetation in the southeastern Brazilian mountains (Behling and Safford, 2010; Behling et al., 2007; Scheel-Ybert, 2001; Veríssimo et al. 2012), the VAF record shows a clear trend from drier to wetter climatic conditions during the Holocene, and a clear trend of replacement of CDA vegetation by forest vegetation. The results indicate that the higher elevations of Serra dos Órgãos have been occupied by a mosaic of CDA and UMARF since the beginning of the record

(9840 cal yr BP), although the forest patch that occupies the VAF site probably has been extant only since ~1350 cal yr BP.

Both the VAF record (collected in a forest patch) and SDO record (cored in CDA vegetation) indicate that CDA was much more widespread in the Late Holocene than it is today, and both core sites also demonstrate a similar pattern of forest moving consistently upwards through much of the Holocene. This is especially the case for UMARF taxa but also for montane ARF. At around 1000 cal yr BP (1350 cal yr BP in VAF and 880 cal yr BP in SDO) the data indicate a marked shift toward a warmer and wetter climate, further favouring the expansion of forest vegetation. The variability in the timing of these climatic events between the two cores is likely related to differences in vegetation and relief as well as the error intrinsic to ^{14}C dating.

The macro-charcoal record in the VAF core corroborates changes seen in climate and vegetation. Fires were more frequent and of greater magnitude in the Early Holocene, decreased after ~4000 cal yr BP, and have been very rare in the Late Holocene. The nearby SDO core (Behling and Safford, 2010) showed similar patterns, with more frequent fire during the Early Holocene, especially from 10,800 to 7850 cal yr BP, and a decreasing trend until ~5640 cal yr BP, when charcoal concentrations and accumulation more or less levelled off.

Our results support the conclusions of previous studies (e.g., Behling, 1997b; Safford, 2001; Behling et al., 2007; Behling and Safford, 2010; Veríssimo et al., 2012) that fire has long been a natural disturbance factor in the campos de altitude. Nevertheless, before the arrival of humans at these mountain sites, fires mostly occurred during the wet season, and today anthropogenic ignitions occur primarily during the dry season in very warm and windy conditions; the fires can be enormous. Further research is needed to better define the natural fire regime in the Brazilian Highlands. Another conservation concern is the long-term increase in precipitation and temperature that has been underway for centuries and is rapidly accelerating as greenhouse gas emissions rise. Forest expansion into previously grassland-dominated sites threatens the habitat heterogeneity that underlies the high biodiversity and endemism of these montane sites (Safford, 2001; Portes et al., 2018). We recommend that

protected areas containing campos de altitude and upper montane rain forest should develop management strategies that incorporate observation, measurement, experimentation, and active management techniques that help to retain landscape heterogeneity (see Portes et al., 2018). The standard “hands-off” protectionism that has characterized national park management for the last century may be particularly poorly suited to conservation in an age of rapid global change (Cole and Yung, 2010; Safford et al., 2012).

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