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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. Frequent and 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.

Key words: Southeastern Brazil, campos de altitude (high elevation grassland), upper montane Atlantic Rain Forest, climate and fire history, Holocene.

INTRODUCTION

The Brazilian coastal highlands (Serra do Mar) extend for *c*. 1000 km along the Brazilian coastline from southern to northeastern Brazil, from the north of Santa Catarina State (26^{o} S) to the north of Rio de Janeiro State (21^{o} 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 *c*. 4000 km from 3° N latitude to almost 34° S (Ribeiro et al., 2009; Fundação SOS Mata Atlantica/ 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). 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; Behling and Safford, 2010; Ledru at al., 2005; Ledru et al. 2009; 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 North 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 about 5600 cal yr BP. Thereafter a trend toward warmer and wetter conditions resulted in expansion of montane forest and contraction of campos. The last *c.* 1000 years were the wettest period during the whole Holocene (Behling and Safford, 2010).

Centuries of exploitation reduced the Atlantic Forest to a patchwork of small fragments in a natural or semi-natural state, covering today only *c.* 10% of its pre-Columbian area (Fundação SOS Mata Atlantica/ INPE, 2017). While more intense occupation and deforestation occurred after European colonization, starting *c*. 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 around 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 mainly established 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 it ironically 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 the 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 since epiphytes and bamboos till large animals as jaguars (Martinelli and Bandeira, 1989, see also the Brazilian red books for flora and flora: Martinelli and Moraes, 2013 and ICMBio, 2018). As the climate becomes warmer and wetter, upward migration is expected and the reduction of available 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, 1997b, 2007; Behling et al., 2007; Behling and Safford, 2010; Behling et al., 2020; Ledru et al., 2005; Portes et al., 2018; Raczka et al., 2013; Scheel-Ybert, 2001; Veríssimo et al., 2012), 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. Our specific research questions were (1) how did climatic change and fire interact at this montane forest site to influence vegetation composition and dynamics during the Holocene?; and (2) how did Holocene vegetation dynamics differ 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 is located at 2003 m a.s.l., at latitude 22°27’53.49” S and longitude 43°2’27.04” W in the Serra dos Órgãos National Park (PARNASO), Rio de Janeiro State, southeastern Brazil (Fig. 1). The southeast facing site is characterized by 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), about *c*. 90 km from the Atlantic Ocean. 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).

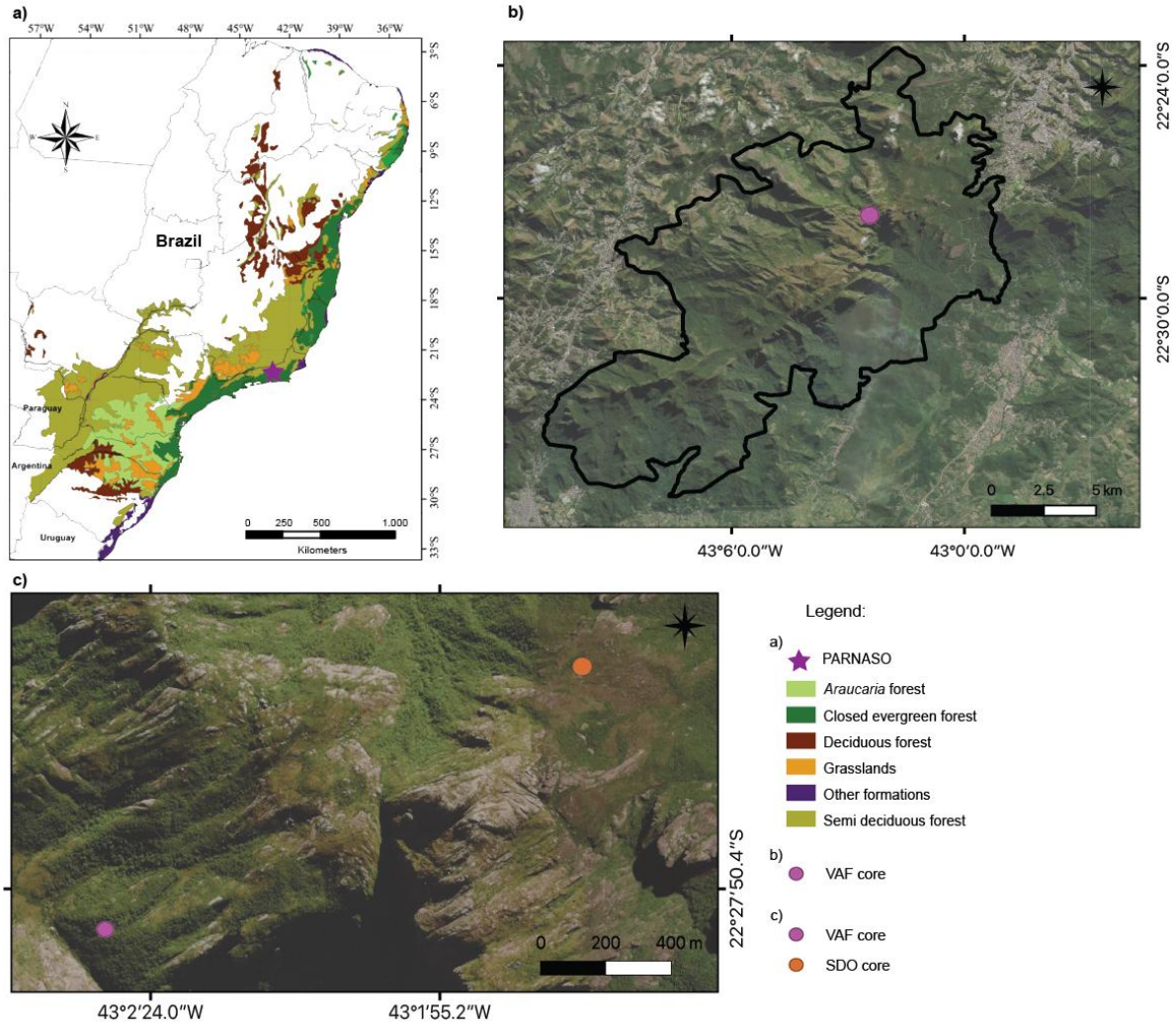

Fig. 1. Location of PARNASO and Vale das Antas Forest (VAF) core. a) national location of PARNASO (adapted from Fundação SOS Mata Atlântica/ INPE, 2017), b) location of VAF core in PARNASO and c) distance and vegetation type of VAF core (in UMARF) and SDO core (in CDA) from Behling and Safford (2010).

In the region, the climate is mostly controlled 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 has been generally 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 found at Teresópolis (22°25.980' S, 42°58.980' W) at 1100 m a.s.l., where mean annual temperature is 17.6 ^{o}C (July mean = 8.6 ^{o}C, February

mean = 27.2 ^{o}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 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 ^{o}C, the maximum was 25.6 ^{o}C and the minimum was 1 ^{o}C (C. Cronemberger, PARNASO, pers. comm.). Temperatures in the nearby CDA in the Vale das Antas (the study site is in forest slightly above the valley bottom) showed a similar mean temperature (12.5 ^{o}C), but temperatures were more extreme due to the lack of trees and the valley bottom position (max = 27 ^{o}C, min = -5.2 ^{o}C). Safford (unpub. data) also measured winter temperatures in the Vale das Antas campos, in July 1997 a minimum of -9.8 ^{o}C was measured, which is the lowest 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 which gradually replaces tall montane forest above about 1500 m a.s.l., while above these elevations UMRAF 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). A high number of sclerophyllous shrub taxa is found in the CDA, as well as smaller trees, often in some stage of succession moving 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 height. 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), around about 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 an 88 cm-long core was collected in an undisturbed area of UMARF in the Vale das Antas ("Tapir Valley") and herein called VAF (Vale das Antas Forest). From a base of bedrock, an 88 cm-long core divided in two sections of 50 cm length were extruded onsite using a Russian Corer, wrapped in plastic film and stored under cool (*c*. 4 ^{o}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) (Table 2). An HCl test on several core samples was negative and excludes the possibility of a carbon reservoir effect. The age-depth model was performed with R-package Clam 2.2 (Blaauw, 2010) in R-Studio (R-Studio Team, 2016) using the South Hemisphere calibration curve SHCal13.14C and postbomb curve SH 1-2. Calib 7.1 was used for calculating the median probability (Stuiver et al., 2019).

Palynological analysis

In total 44 subsamples (0.25 cm^3) in 2 cm intervals were taken along the core for analysing 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 residue obtained was kept in distilled water and mounted in slides with glycerine for palynomorph analysis under a light microscope. A minimum of 300 pollen grains was counted per sample. 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.jbjr.gov.br). Pollen and spore percentage were calculated from the pollen sum, including herbs, shrubs, trees, 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 performed with C2 (Juggins, 2007) and portrays the most important taxa based on frequency and dominance. TILIA and TILIAGRAPH were applied to determine pollen assemblage zones based on the stratigraphic constrained cluster analysis of the pollen sum by CONISS (Grimm, 1987).

Macro-charcoal analysis

For analysing 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 cm^3 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)) which is a procedure that greatly limits particle fragmentation. 6% H_2O_2 was added to remove organic material in the sediment and samples were gently wet-sieved, retaining particles ≥ 150 μm. Concentrations were determined as particles cm^{-3}. Fire regime characteristics were identified using the software CharAnalysis (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 ($C_{background}$) 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 insignificant 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 (Biagioni et al., 2015; Higuera et al., 2010).

Loss on ignition

To estimate the organic matter and carbonate content in the sediment, 0.5 cm^3 subsamples were continuously extracted from the sediment and immediately weighed. The samples were dried at 105 ^{o}C for 24 h, dried and combusted at 550 ^{o}C during 4 h. Afterward 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 mostly consists 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 (Table 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 from 88-67 cm core depth, 197 yr/cm from 66-43 cm, 40 yr/cm from 42-40 cm, 52 yr/cm between 39-33 cm, 59 yr/cm from 32-19 cm and 11 yr/cm from 31 to the surface. The median probability was calculated using the software Calib 7.1 (Table 2).

Loss-of-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, *c*. 30% from 88-60 cm depth, while from 60-0 cm depth the average of organic matter is *c*. 38%.

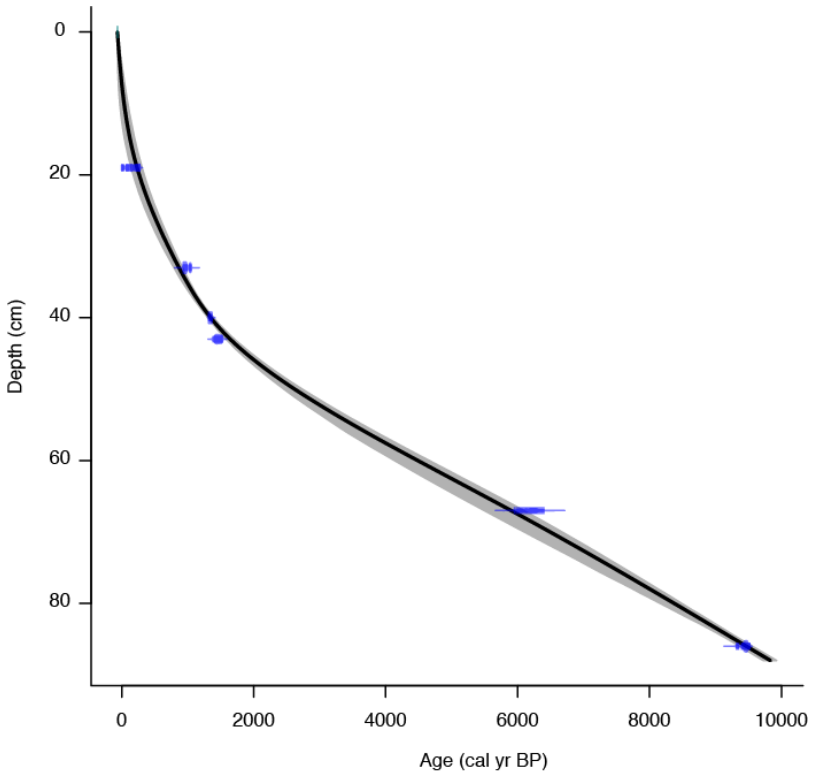

Fig. 2. Age-depth smoothing spline model for the Vale das Antas core.

Table 1. Stratigraphy of 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, little 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 VAF core, 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

Palynological results

The record is divided into three pollen zones based on the 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 percentage pollen 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. Fig. 3b also includes the depth curves of: sedimentation rate (yr/cm), LOI (%), charcoal concentration (particles cm^{-3}), charcoal accumulation rate (particles cm^{-2} yr^{-1}), fire peaks and fire magnitude.

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

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 (*c*. 2%). Other taxa characteristic for the CDA assemblages in VAF-I are Apiaceae (*c*. 2%), Cyperaceae (1%) and Fabaceae (1%).

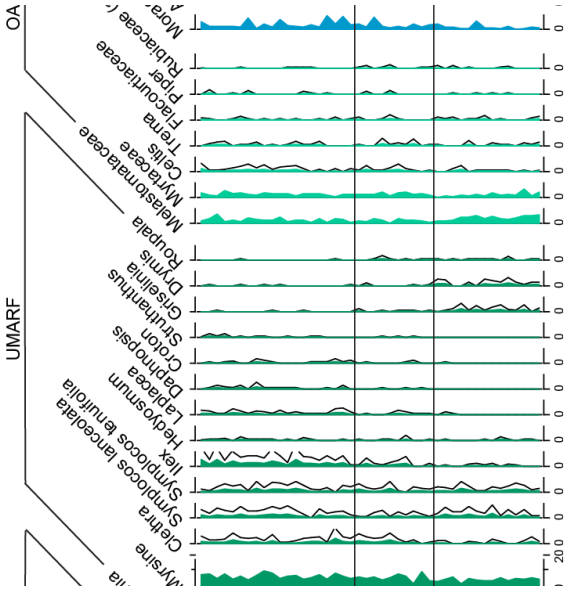

Fig. 3a. Pollen percentage diagram of the most important and most frequent taxa of VAF core into each group.

The average sum of arboreal taxa represents 33% (ranging from 25% to 44%)of the pollen spectra, and are dominated by UMARF, primarily represented by *Weinmannia* (10%, > 5% to < 17%) and *Myrsine* (6%, > 3% to < 8%). Most taxa of UMARF have their lowest values in this zone, however *Griselinia* and *Drimys* follow an opposite trend and are found at their highest densities in this zone, *c*. 1% each. In contrast to the UMARF group, the OARF pollen shows its highest values in this zone, averaging 8% and ranging from 4% to 13%, with Melastomataceae at *c*. 4% and Myrtaceae *c*. 2%. LMARF pollen are scarce in VAF-I and only average 3% of the pollen sum, ranging from 1% to 8%, primarily represented 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 about 12% (> 8% to < 17%).

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

The pollen CDA percentages slightly decrease to 59%, ranging from *c*. 70% at 50 cm to 54% at 41 cm core depth. Poaceae (43%, > 37% to < 49%) and Asteraceae types (*c*. 12%, > 9% to < 15%) continue as the main taxa, and *Baccharis* increases to *c*. 4%. The arboreal assemblage reaches *c*. 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* (*c*.7%, > 3% to < 11%). *Clethra*, *Symplocos lanceolata*, *S. tenuifolia* and *Ilex* represent *c*. 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 *c*. 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 primarily driven 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 about 47%(ranging from 39% to 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 *c*. 8% (> 6% to < 12%) respectively, other taxa also contribute to the increase in VAF-III. *Clethra*, *S. lanceolata*, *S. tenuifolia* occur with *c*. 1% each and *Ilex* reaches about 2%. OARF continues with *c*. 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%, varying from 3% to 20%), due to the expansion of Moraceae/Urticaceae (3.7%), *Alchornea* (2%,) *Cecropia* (1%) and *Euterpe/Geonoma* (0.7%). As in the previously zones, non-tree fern spores are at 12% (> 8.5% to < 16%), while tree ferns show slightly reduced values.

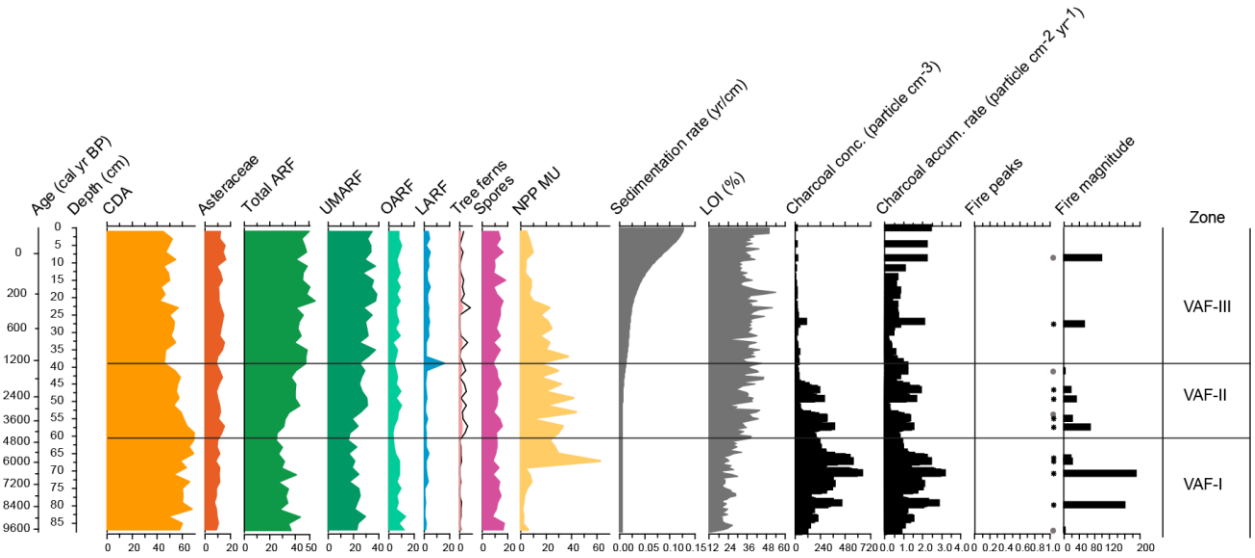

Fig. 3b. Summary diagram of the Vale das Antas Forest core, showing the ecological groups (%), sedimentation rate (yr/cm), loss of ignition (%), macro-charcoal concentration (particle cm^{-3}) and accumulation rate (particle $cm^{-2}yr^{-1}$), fire peaks and fire magnitude. A 5x exaggeration scale line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

Macro-charcoal and fire regime

The CharAnalysis of macro-charcoal characterize 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. The local signal-to-noise exceeds 3.5, indicating a good separation between peak and non-peak values. From 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 found 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 or so of the core site) were rare over the period of our sample, but the nearly continuous presence of charcoal through the core demonstrates fires were not regionally uncommon. Most fire peaks as well as the highest magnitude peaks occurred in zone VAF-I.

INTERPRETATION AND DISCUSSION

Overall, the stratigraphy and the organic content of the VAF core in the 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, mostly represented 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 climo-topographic and soils 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 in this trend during the Late Holocene, indicating that climates during the Early Holocene were much drier than today and 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 Zone I (9840-4480 cal yr BP), and that the more continuous local forest may not have developed until after 1350 cal yr BP (Zone 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 yr cal 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* (2x increase) and *Myrsine* (50% increase). *Symplocos,* Melastomataceae and Myrtaceae (the latter two very common in both UMARF and OARF) showed similar 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 current areas of CDA are under-represented in pollen assemblage due to the low pollen production and low accumulation rate of CDA taxa and also the over-representation of some arboreal taxa, especially pioneer or secondary species of montane forest upwards wind-transported. They propose the use of a restricted group of typical upper montane forest, which should be more sensitive to detect the local trend of forest changes (within the mosaic landscape) than the full groups of ARF. Therefore, following Portes et al. (2020), we aggregated pollen sums from *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* to represent UMARF and aggregated the same taxa used by Behling and Safford (2010) to represent the CDA. Fig. 4 shows the temporal trends in forest and in CDA from our VAF core and the SDO core sampled by Behling and Safford (2010) (which stretched back into the Late Pleistocene [12380 cal yr BP]), and superimposes the macro-charcoal concentration (particles cm^{-3}) from VAF core and the $\delta^{18}O$ 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 about 4500 yr BP, corroborating the higher charcoal concentration as well as the drier climate at that period. As climate became wetter after around 1400 cal yr BP, charcoal concentration decreases, the CDA:forest ratio drops to 50:50 and the group of upper montane ARF increases to around 30%. The SDO core shows similar patterns, with an accentuated increase in forest pollen after about 5000 cal yr BP, and the balance of campos vs. forest pollen dropping below 50:50 after around 1500 cal yr BP (Fig. 4). While VAF core was collected in a currently UMARF patch surrounded by CDA vegetation, SDO core was cored from a more widespread CDA vegetation. We hypothesize therefore that the patch of forest that currently occupies the VAF site has only been extant since sometime in the Late Holocene, although the pollen data make clear that upper montane forest taxa have been in the broader region throughout the Holocene.

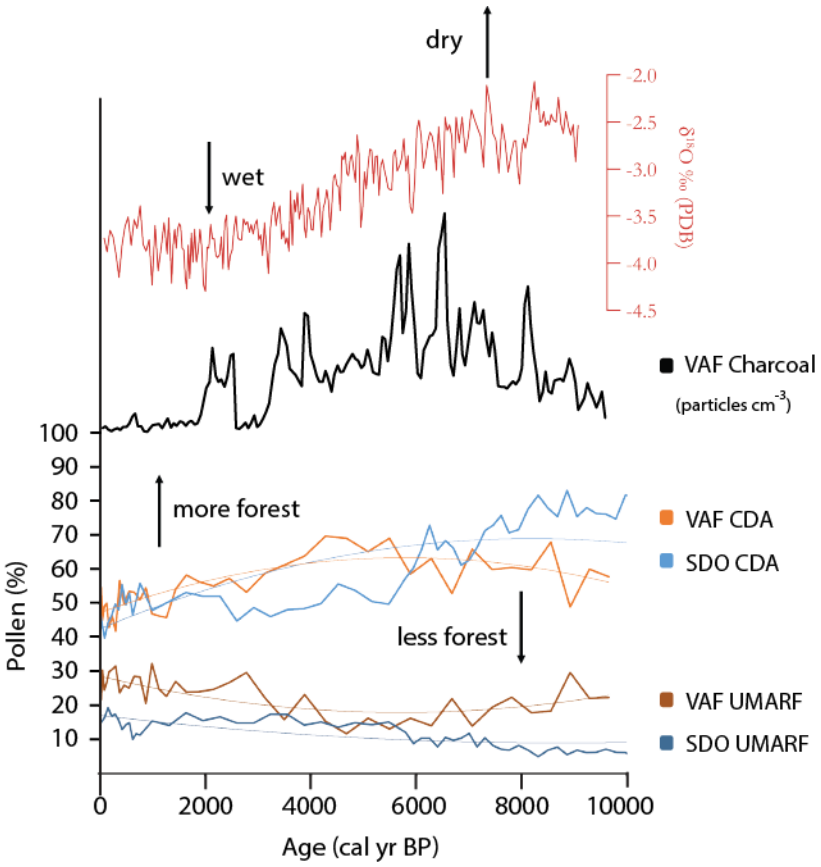

Fig. 4. Comparison of the sum (%) of *Weinmannia*, *Myrsine*, Myrtaceae and *Clethra* taxa representing UMARF from VAF core (VAF UMARF), the sum of *Weinmannia*, *Myrsine*,

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

The VAF core also documents temporal floristic variation that points to important 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 frequencies and magnitudes of fire; (4) relatively low pollen densities for *Baccharis*, which is a faithful campos indicator but under warmer temperatures; and (5) the elevated presence of cool climate indicators of southern temperate ancestry like *Drimys* and *Griselinia*. In addition, the nearby SDO core records *Araucaria* pollen until about 10,800 cal yr BP, further pointing to cooler Early Holocene temperatures. UMARF vegetation in the Early and Mid-Holocene seems to have been somewhat composed of a more southern-temperate flora.

Zones VAF-II (4480-1350 cal yr BP) and III (1350 cal yr BP to present) represent the Late Holocene. After 4480 cal yr BP organic matter in the soil increased in coincidence with increases in a number 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 expanse 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 (around 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 *c.* 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 at *c*. 600 cal yr BP occurred and may be related to the VAF-III peak in CDA pollen and concurrent drop in UMARF pollen that occurs shortly thereafter.

Other studies also suggest an intensification in Late Holocene precipitation. Moss spores in the nearby SDO core increased greatly in the Late Holocene sediment (Behling and Safford, 2010). Palaeoclimate data from the last 10,000 years at Botuverá Cave ($27^{o}13'S$, $49^{o}09'W$, 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 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 *c*. 1400-1800 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, i.e., before the documented arrival of humans in southeastern Brazil, which probably arrived in the region 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 years record from Morro do Itapeva in the southern Serra da Mantiqueira (Behling, 1997b), and the 18,600 years 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 CharAnalysis, we restricted our assessment to fires that occurred within probably 500 m or so of the core site (Higuera et al., 2007). This permits a more site-specific understanding of 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. The Serra dos Órgãos landscape is topographically 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 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 frequencies 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) note 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 to (1) conduct macro-charcoal analysis on 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) obtain sediment core samples from more – and both elevationally and vegetationally more varied – locations in the southeastern Brazilian highlands; and (3) 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 (i.e. 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 has probably been extant only since about 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 timing of these climatic events between the two cores are 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 around 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 about 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 and fire sizes 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 than 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 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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SUPPLEMENTARY MATERIAL

List of taxa identified in the VAF sediment.

Taxa	Subgroup	Group	Pollination
Asteraceae	Asteraceae	CDA	Entomophily
Ambrosia	Asteraceae	CDA	Entomophily
Baccharis	Asteraceae	CDA	Entomophily
Jungia	Asteraceae	CDA	Entomophily
Senecio	Asteraceae	CDA	Entomophily
Vernonia	Asteraceae	CDA	Entomophily
Alstromeria	Herbs & Shrubs	CDA	Entomophily
Amaranthaceae/Chenopodiaceae	Herbs & Shrubs	CDA	Entomophily
Apiaceae	Herbs & Shrubs	CDA	Entomophily
Borreria	Herbs & Shrubs	CDA	Entomophily
Ericaceae	Herbs & Shrubs	CDA	Entomophily
Eriocaulon	Herbs & Shrubs	CDA	Anemophily/Entomophily
Eryngium type 1	Herbs & Shrubs	CDA	Entomophily
Eryngium type2	Herbs & Shrubs	CDA	Entomophily
Fabaceae	Herbs & Shrubs	CDA	Entomophily/Aviphily
Hippeastrum	Herbs & Shrubs	CDA	Entomophily
Hypericum	Herbs & Shrubs	CDA	Entomophily
Hyptis	Herbs & Shrubs	CDA	Entomophily/Aviphily
Lamiaceae	Herbs & Shrubs	CDA	Entomophily/Aviphily
Malphigiaceae	Herbs & Shrubs	CDA	Entomophily
Malvaceae	Herbs & Shrubs	CDA	Entomophily
Poaceae	Herbs & Shrubs	CDA	Anemophily
Polygala	Herbs & Shrubs	CDA	Entomophily
Ranunculaceae	Herbs & Shrubs	CDA	Anemophily/Entomophily
Ripsalis	Herbs & Shrubs	CDA	Entomophily/Aviphily
Scrophulariaceae	Herbs & Shrubs	CDA	Entomophily
Spermacoce	Herbs & Shrubs	CDA	Entomophily
Valeriana	Herbs & Shrubs	CDA	Entomophily
Cyperaceae	Aquatics	CDA	Anemophily
Hydrocotyle	Aquatics	CDA	Entomophily
Liliaceae/Amaryllidaceae	Aquatics	CDA	Entomophily
Typha	Aquatics	CDA	Anemophily
Xyris	Aquatics	CDA	Anemophily
Allophylus	UMARF		Entomophily
Begonia	UMARF		Entomophily
Clethra	UMARF		Entomophily
Croton	UMARF		Entomophily
Daphnopsis	UMARF		Entomophily
Drymis	UMARF		Entomophily/Aviphily
Fuchsia	UMARF		Aviphily
Griselinia	UMARF		Entomophily
Hedyosmum	UMARF		Anemophily/Entomophily

Ilex	UMARF		Anemophily/Entomophily
Laplacea	UMARF		Entomophily
Mimosa scabrella	UMARF		Entomophily/Aviphily
Myrsine	UMARF		Anemophily
Ouratea	UMARF		Entomophily
Podocarpus	UMARF		Entomophily
Roupala	UMARF		Entomophily/Aviphily
Struthanthus	UMARF		Entomophily
Styrax	UMARF		Entomophily
Symplocos lanceolata	UMARF		Entomophily
Symplocos tenuifolia	UMARF		Entomophily
Weinmannia	UMARF		Entomophily/Aviphily
Alseis floribunda	OARF		Entomophily
Araliaceae	OARF		Entomophily
Bignoniaceae	OARF		Entomophily/Aviphily
Celtis	OARF		Anemophily
Coccocypselum	OARF		Entomophily
Dodonea	OARF		Anemophily
Euphorbiaceae	OARF		Entomophily
Flacourtiaceae	OARF		Entomophily/Aviphily
Lamanonia	OARF		Entomophily
Matayba	OARF		Entomophily
Melastomataceae	OARF		Entomophily
Meliaceae	OARF		Entomophily
Meliosma	OARF		Entomophily
Menispermaceae	OARF		Entomophily
Mimosaceae	OARF		Anemophily/Entomophily/Aviphily
Myrtaceae	OARF		Entomophily/Aviphily
Oreopanax	OARF		Entomophily
Pera	OARF		Entomophily
Piper	OARF		Anemophily/Entomophily
Prockia	OARF		Entomophily/Aviphily
Prunus type	OARF		Entomophily
Rubiaceae	OARF		Entomophily
Sapindaceae	OARF		Entomophily
Schefflera	OARF		Entomophily
Sebastiana brasiliensis	OARF		Anemophily
Sebastiana commersoniana	OARF		Anemophily
Solanum	OARF		Entomophily
Trema	OARF		Anemophily
Urvillea	OARF		Entomophily
Vochysia	OARF		Aviphily/Entomophily/Monkeys
Alchornea	LARF		Anemophily/Entomophily
Cecropia	LARF		Anemophily/Entomophily
Euterpe/Geonoma	LARF		Entomophily
Hyeronima	LARF		Entomophily
Moraceae/Urticaceae	LARF		Anemophily
Rhamnus type	LARF		Entomophily
Sapotaceae	LARF		Entomophily/Quiropterophily
Virola	LARF		Entomophily
Alsophila	Tree fern		Hydrophily
Cyathea psilate	Tree fern		Hydrophily
Cyathea reticulate	Tree fern		Hydrophily

Cyathea verrucate	Tree fern		Hydrophily
Dicksonia	Tree fern		Hydrophily
Lophosoria quadripinnata	Tree fern		Hydrophily
Nephelea	Tree fern		Hydrophily
Anemia phyllitides	Spore		Hydrophily
Hymenophyllum	Spore		Hydrophily
Lycopodium clavatum	Spore		Hydrophily
Lycopodium foveolate form type	Spore		Hydrophily
Monolete clavate	Spore		Hydrophily
Monolete echinate	Spore		Hydrophily
Monolete psilate	Spore		Hydrophily
Monolete psilate large	Spore		Hydrophily
Monolete scabrate	Spore		Hydrophily
Monolete striate	Spore		Hydrophily
Monolete with perispore	Spore		Hydrophily
Osmunda	Spore		Hydrophily
Phaeoceros	Spore		Hydrophily
Pityrogramma	Spore		Hydrophily
Polypodiaceae	Spore		Hydrophily
Pteridophyta type 4	Spore		Hydrophily
Pteridophyta type 7	Spore		Hydrophily
Pteris type	Spore		Hydrophily
Sellaginella excurrens type	Spore		Hydrophily
Sphagnum	Spore		Hydrophily
Trilete clavate	Spore		Hydrophily
Trilete psilate	Spore		Hydrophily
Trilete scabrate	Spore		Hydrophily
Trilete striate	Spore		Hydrophily
Trilete verrucate	Spore		Hydrophily
Trilete with perispore	Spore		Hydrophily

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