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14,000 years of climatic and anthropogenic change in the Afromontane forest of São Tomé Island, Gulf of Guinea

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ABSTRACT

São Tomé (Gulf of Guinea, Central Africa) is a 854 km² tropical island that had a pivotal role in early European colonial expansion through the Atlantic between the 15th and 16th centuries. Historical sources suggest that native vegetation has been heavily impacted since human arrival (1470 CE) due to monoculture economies and the introduction of mammals and plants, some of which now have established wild populations. The Afromontane forest of São Tomé, located above 800 m.a.s.l., is particularly rich in endemic plant species and has remained relatively unaffected by direct human impacts. Here, we explore how environmental change influenced this forest through the study of a sedimentary sequence from the volcanic crater of Lagoa Amélia (1340 m a.s.l.), a palustrine system located at the boundary between submontane (800–1400 m a.s.l.) and mist forest (above 1400 m a.s.l.). We used fossil pollen, non-pollen palynomorphs, sedimentology and charcoal to determine forest dynamics from the Late Pleistocene to the present. From 14,000 to 12,500 cal yr BP the forest was dominated by taxa from higher altitudes, adapted to cooler and drier climates (e.g. *Afrocarpus mannii* trees and *Psychotria nubicola*). After 12,500 cal yr BP, a potential uphill migration was identified by an increase in taxa like the trees *Symphonia globulifera* and *Craterispermum cerinanthum*. From 11,200 cal yr BP through the rest of the Holocene taxa from lower altitudes became dominant (e.g. *Prunus africana*, *Polyscias*, and *Sabicea*), except at c. 8500 cal yr BP when rapid cooling led to forest opening. Charcoal showed that fires were frequent during the Late Pleistocene (14,000 to 11,200 cal yr BP), becoming rare during the Holocene until anthropogenic fires started at c. 2200 cal yr BP. Other recent anthropogenic impacts detected in Lagoa Amélia included the appearance of pollen of introduced plant species (e.g., *Cestrum*), and the increase in pollen of economically important species (*Elaeis guineensis*, *Zea mays*) and in fungal spores related to introduced herbivores. Our results reveal that climate changed the altitudinal distribution of the Afromontane forest in São Tomé during the Late Pleistocene, as observed on the African continent, and that this ecosystem was also strongly impacted by human arrival, through fire, farming, and introduced species.

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1. Introduction

Since the Pleistocene, the climate of Central Africa has been characterised by periods of cool and arid conditions (e.g. Last Glacial Period) alternated with humid phases (e.g. African Humid Period, c. 14,800 to c. 5500 BP) (deMenocal et al., 2000; Weldeab et al., 2005). These climate changes are known to have impacted biodiversity and human societies, causing significant ecosystem changes, such as the fragmentation of lowland tropical forests (Maley, 1989) and elevational shifts in vegetation belts (Lézine et al., 2019, 2023). Afromontane forests are often distributed in altitudinal bands between 800 and 3500 m a.s.l., and can be identified by characteristic taxa, such as conifer trees from the Podocarpaceae family. Palaeoenvironmental research has shown how

Afromontane forests responded to past climate changes and shifting fire regimes. For instance, sediments from Lake Bambili (Cameroon), showed how the upper Afromontane forest treeline currently located at c. 2800 m a.s.l., migrated downslope during glacial cooling and upslope during postglacial warming (Lézine et al., 2019). In addition, a record in Mount Kenya (Kenya) showed that during the Late Pleistocene-Holocene transition, Afromontane forests taxa, growing at c. 2000 m a.s.l., shifted to mixed montane forests due to increased forest fires (Rucina et al., 2009). These examples from continental Afromontane forests suggest diverse responses to climate change since the Late Pleistocene. However, it remains unclear if forests on African oceanic islands, such as São Tomé, in the Gulf of Guinea, exhibited similar dynamics or if, alternatively, they remained stable due to their insularity and the ocean acting

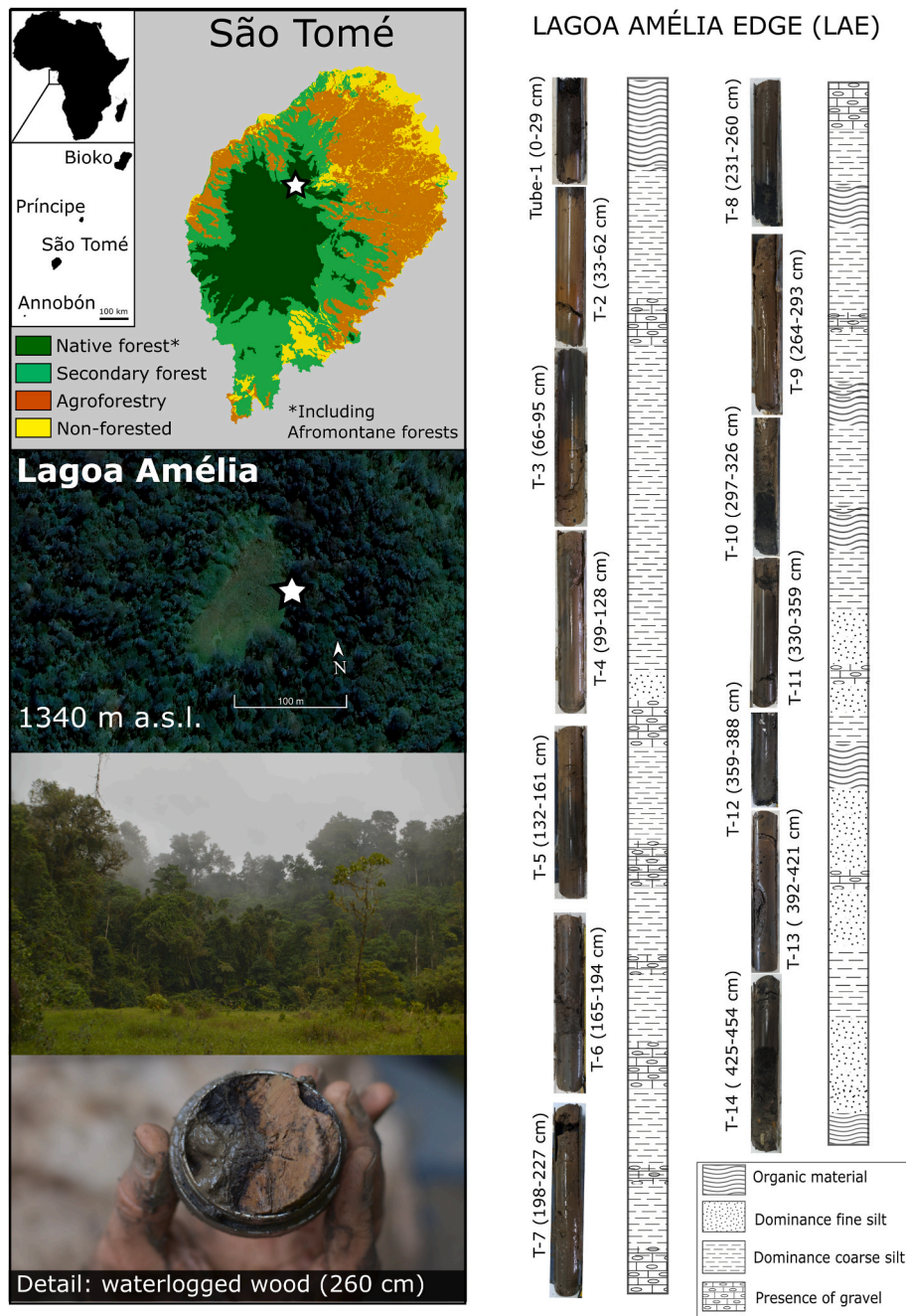


Fig. 1. Location of São Tomé Island and Lagoa Amélia (white star). Vegetation map modified after Soares (2017). Lagoa Amélia satellite image from Google Earth. Photos of the study site and sedimentary sequence with the detail of the waterlogged wood at 260 cm were taken by the team. Sediment description into first-order size classes after Blott and Pye (2012). 4 cm gap between core sections corresponds to sediment recovered in the percussion corer tip.

as a buffer to climatic shifts (Fernández-Palacios et al., 2011).

The oceanic islands of the Gulf of Guinea include Príncipe, São Tomé (together constitute the Democratic Republic of São Tomé and Príncipe), and Annobón (belonging to the Republic of Equatorial Guinea). These are part of the Cameroon volcanic line, which has a NE-SW disposition and extends to the continental island of Bioko (also belonging to Equatorial Guinea) and to Mount Cameroon in the African mainland, which is a 4040 m a.s.l. high active volcano, 50 km NE of Bioko. These islands are a biodiversity hotspot and have been called the “African Galápagos”. Among them, São Tomé (854 km²) is home to a remarkably high number of endemics, including c. 150 plant taxa and 40 land vertebrates (e.g., the shrew *Crocidura thomensis* and the bat *Chaerephon tomensis*) (Ceríaco et al., 2022a,b; Garcia et al., 2022; Stévant et al., 2022). Knowledge of the threatened flora and fauna of São Tomé has been growing in recent years (e.g., <https://cepf-stp-threat-flora.netlify.app/>). The Afromontane forest of São Tomé, distributed above 800 m a.s.l., is composed of the montane forest and the mist forest. These forest types (Fig. 1, represented in the vegetation map as ‘native forests’) have been threatened by a rapidly expanding human population (Heleno et al., 2022). São Tomé Island remained uninhabited until Portuguese settlement in the late 15th century (Garfield, 2015; Muñoz-Torrent et al., 2022). At the crossroads of many Portuguese colonial routes, and having fertile soil and diverse microclimates (Ceríaco et al., 2022a,b) São Tomé became an experimental ground for agriculture, receiving crops from around the tropics (Mensing et al., 2020). Our limited knowledge of historical land use changes suggests that native forests were extensively cleared, especially in the lowlands (de Lima et al., 2022). In 2006, around one-third of the island area was classified as Obô Natural Park (Direcção Geral do Ambiente, 2006), a protected area that covers most of the best-preserved Afromontane forest, where Lagoa Amélia, our study system, is located.

In this paper, we will assess whether the Afromontane forest of São Tomé responded to past environmental changes, as described in continental Afromontane forests (e.g. Lézine et al., 2013, 2019, 2023, Rucina et al., 2009), and how these have been affected by human colonization of the island. To this end, we used a battery of palaeoenvironmental methods and analysed a 14,000-year sedimentary sequence from Lagoa Amélia, a palustrine system crater at 1340 m a.s.l. At the boundary between montane and mist forests, this palustrine wetland represents a promising ecosystem to study the effects of different drivers of change through time.

2. Material and methods

2.1. Site location and fieldwork

In June 2021, we conducted fieldwork in Lagoa Amélia (1340 m a.s.l., 0°16'44.8"N, 6°36'30.3"E), a volcanic caldera that contains a palustrine wetland. Attempts to core the unconsolidated floating bog at the centre of Lagoa Amélia were unsuccessful. Alternatively, we extracted a 4.58 m deep sediment core from the edge of the lagoon, using a percussion corer (5 cm diameter). The sedimentary sequence was composed of 14 sections or drivers and it is called Lagoa Amélia edge (LAE) (Fig. 1).

The flora in the study site included the shrubs *Myrsine melanophloeos* and the endemics *Lea tinctoria* and *Heteradelphia paulowilhelmia*, but was dominated by herbs, such as grasses (e.g., *Panicum hochstetteri* and *Oplismenus hirtellus*), ferns (e.g., *Nephrolepis cordifolia* var. *pumicicola* and *Lepisorus excavates*), lycophytes (e.g., *Lycopodiella cernua*), begonias (e.g., the endemics *Begonia crateris* and *B. baccata*), and orchids (e.g., *Solenangis clavata*, and the endemics *Rhipidoglossum brevifolium* and *Dincklageella scandens*). Other flora included the climbers (e.g., *Anthocleista scandens*), the tree fern *Alsophila manniana*, and the tall native montane forest on the inner slopes of the crater. Lagoa Amélia is known as a biodiversity hotspot for ferns (Figueiredo et al., 2011).

2.2. The afromontane forests of São Tomé

The Afromontane forests include the montane (800–1400 m a.s.l.) and mist forests (1400–1800 m a.s.l.) (Exell, 1944; Figueiredo et al., 2011; Dauby et al., 2022). The montane forest is characterized by tree species such as *Prunus africana*, *Symphonia globulifera*, *Syzygium guineensis*, and the endemics *Croton stellulifer*, *Discoclaoxylon occidentale*, *Homalium henriquesii*, *Polyscias quintasii*, *Tabernaemontana stenosisiphon*, and *Trichilia grandifolia*, as well as understory species, such as *Oxyanthus speciosus*, *Piper umbellatum*, and the endemics *Alsophila welwitschii*, *Begonia subalpestris*, *Craterispermum cerinanthum*, and *Erythrococca molleri* (Oliveira, 1993; Figueiredo et al., 2011). The mist forest is characterized by the endemic conifer tree *Afrocarpus mannii*, and other trees such as *Melchiora mannii*, *Olea capensis*, *Peddiea thomensis*, *Psychotria guerkeana*, and *P. nubicola*, with an understory dominated by *Begonia* spp., *Pilea* spp., and *Tristema* spp., and the climber *Anthocleista scandens*. Above these vegetation belts (over 1800 m a.s.l.) there is a low forest, which includes scrublands (with the endemic shrub *Erica thomensis*), and grasslands (with herbs such as the endemic *Lobelia barnsii*) (Dauby et al., 2022). In contrast to the more humid montane forests and mist forests, this low forest has shallow soils and, at the peak of the dry season, can become dry enough to be vulnerable to fire (Monod, 1960).

2.3. Laboratory methods

Once transported to the Ecology Laboratory at the University of La Laguna (Canary Islands), we photographed the sediment core sections, described its colour and macroscopic characteristics, and carried out a sampling of 1 cm³ samples, isolating finds of interest, such as rock fragments and macro-remains (e.g., waterlogged woody material, Fig. 1). We carried out multiple analyses in a set of 49 samples: 1) fossil pollen and fern spores to track changes in regional vegetation; 2) non-pollen palynomorphs (NPPs), namely fungal spores to characterise changes in decomposers communities and coprophilous fungi that can identify the presence of herbivores (e.g., bovids, goats, etc.) (Cugny et al., 2010); 3) charcoal particles to study the occurrence of local (macro-charcoal particles over 150 µm) and regional fires (micro-charcoal particles under 150 µm). Finally, in another set of 45 samples we measured granulometry, sediment elemental composition, and organic content through loss on ignition (LOI), to study the dynamics of sediment deposition, erosion, and organic matter accumulation into the crater basin, respectively.

2.3.1. Palynomorph identification and counting and statistical analysis

For palynomorph sample preparation, we spiked the samples with exotic *Lycopodium* spores (batch 1031), sieved (using 150 µm and 10 µm meshes), floated with sodium polytungstate at 1.9 gravity, acetolysed, and mounted in silicon oil (Erdtman, 2011). Slides were inspected at ×400 magnification, counting microfossils until a sum of at least 300 pollen grains was reached, or over 150 in samples with low pollen concentration and/or poor preservation. For NPPs quantification, at least 300 fungal and fern spores were counted. To carry out fossil pollen identifications, we used a pollen reference collection assembled from plant samples stored at the São Tomé and Príncipe National Herbarium (STPH) and the Coimbra Herbarium (COI). The São Tomé pollen reference collection, currently located at the University of La Laguna's Ecology Laboratory, includes over 60 taxa, most distributed in Afromontane forests, and other taxa native to the island (see Table S4). We checked the taxonomy using the African Plant Database (APD, v3.4.0) and *MBG Tropicos* (v3.3.2). To complement the information from the pollen reference collection, we used regional literature from tropical Africa, such as pollen atlases (Gosling et al., 2013; Schueler and Hemp, 2016; Rasoloarijao et al., 2019) and NPPs research literature (e.g. Gelorini et al., 2011). We established the correspondence between pollen types and the species occurring in São Tomé (Table S2).

For analysis of pollen assemblage, all pollen grains were included in

the pollen sum, including potential wetland taxa since in some cases these could not be distinguished from terrestrial species (e.g. some pollen assigned to Cyperaceae). To divide the record into zones, we performed a CONISS stratigraphically constrained analysis using the packages Rioja and Vegan in RStudio (Oksanen et al., 2013). We calculated NPPs abundance as percentages over the pollen sum (Cugny et al., 2010). We also calculated microfossil concentrations relative to the known amount of exotic *Lycopodium* spores. We used the package Vegan to calculate detrended correspondence analysis (DCA) and used axis 1 as an indicator of pollen assemblage turnover through time (e.g. Bush et al., 2004; Blarquez et al., 2014; Castilla-Beltrán et al., 2021; Nogué et al., 2021). In addition, we carried out a rarefaction analysis based on pollen counts to calculate palynological richness using the package Hotelling and plotted the results with a linear regression using RStudio (Curran, 2018).

2.3.2. Macro- and micro-charcoal analyses

For macro-charcoal analysis, we used a set of 49 1-cm³ sediment samples sieved using a 150 µm mesh and counted charcoal fragments under a low magnification microscope. Samples rich in organic matter were bleached using a low concentration of H₂O₂, to distinguish charcoal from other dark organic particles. For micro-charcoal analysis, we counted opaque, black angular pieces between 5 and 100 µm, alongside fern spores and *Lycopodium* spores in the pollen microscope slides (Finsinger and Tinner, 2005). We aimed for >100 elements between *Lycopodium* spores and micro-charcoal or stopped counting after reaching >300 *Lycopodium* spores in samples with minimal charcoal content. Micro-charcoal concentrations were estimated relative to the known concentration of exotic *Lycopodium* spores. Macro- and

micro-charcoal results are displayed as particles per cm³ (Fig. 2).

2.3.3. Sedimentological analyses

We dried and homogenized a set of 45 samples (1 every 10 cm) for elemental composition, granulometric analysis, and loss on ignition (LOI). For elemental composition analysis, we carried out 160-s measurements using a hand-held Fluorescence X-Ray using a Niton XL3T GOLDD mounted on a base. The semi-quantitative results are expressed as detected elements in percentages and ppm, presented as ratios for palaeoenvironmental interpretation, such as the Ti/Ca ratio, which can be interpreted as an indicator of detrital inputs into lake basins (Croudace and Rothwell, 2015). The remaining material of this non-destructive technique was used for granulometric analysis, using a Malvern Mastersizer-Hydro at the School of Geography and Environmental Science, University of Southampton, with soil analysis settings adjusted to non-spherical particles. 20-s measurements were averaged if the standard deviation was below 5%, which was achieved by adjusting the obscuration parameter. Results are expressed per fraction (Dx10, Dx15, Dx90) and as percentages of clay, silt and sand, including sub-categories such as fine and coarse sand. To estimate organic matter content, we ashed the dried material of the same set of samples at 550 °C for 4 h and calculated weight LOI using a high precision balance by weighing samples before and after (Heiri et al., 2001).

2.3.4. Radiocarbon dating and chronological modelling

To develop a chronological model, we dated 11 samples using AMS radiocarbon dating at three different laboratories: Queen's University Belfast, Scottish Universities Environmental Research Centre (SUERC), and BETA analytics (Table 1). We selected and sieved the sediment

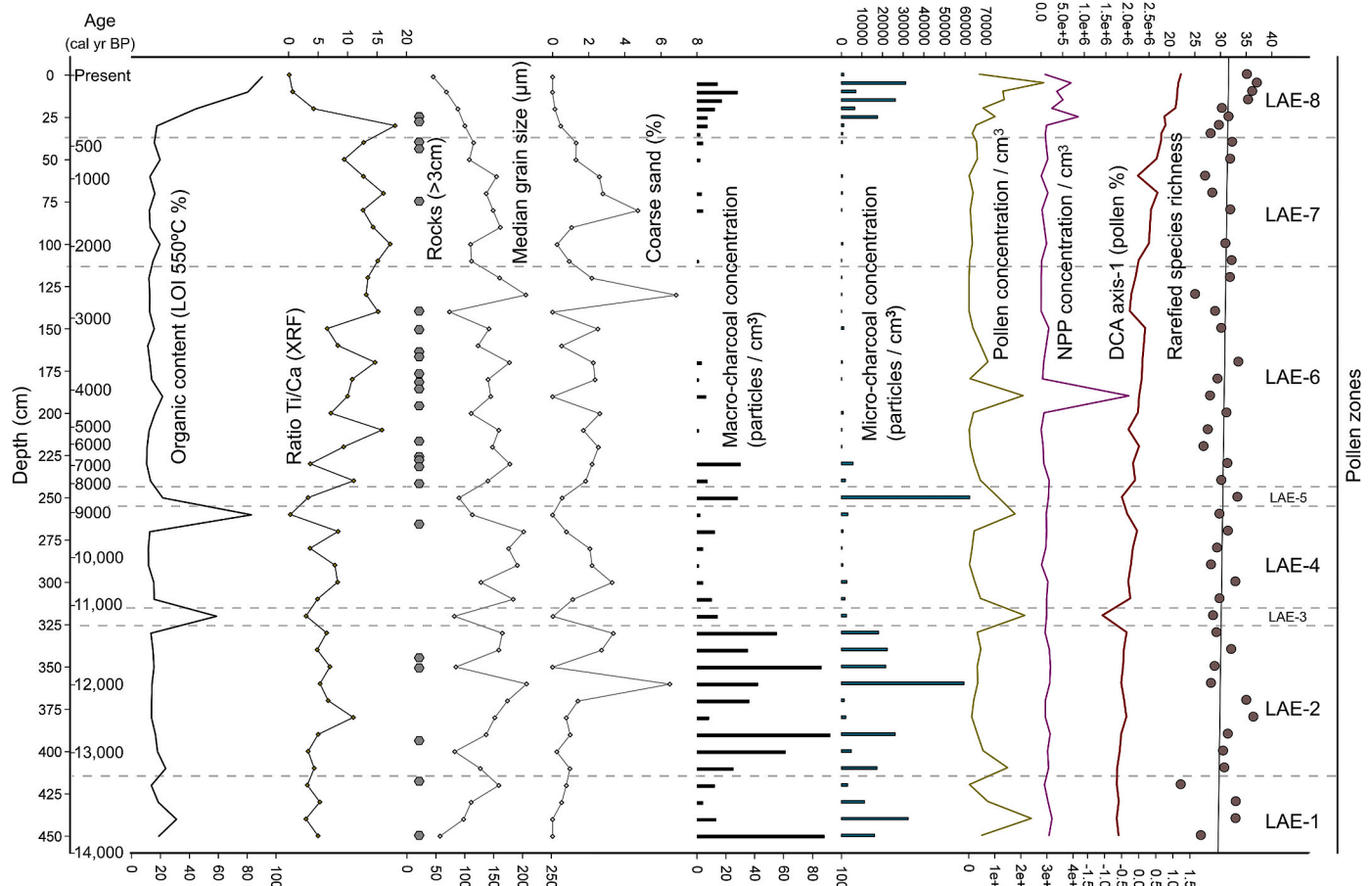


Fig. 2. Multi-proxy summary diagram showing sedimentological data (LOI, ratio Ti/Ca, granulometry), charcoal (micro- and macro-charcoal), fossil pollen and NPPs concentrations, DCA axis-1 results, rarefaction analysis, and pollen zones for Lagoa Amélia (LAE) core.

Table 1

Radiocarbon dating of Lagoa Amélia core (LAE). Data in bold was used to develop the age-depth model.

Code	Material	Depth (cm)	Radiocarbon age	Error	Calibrated yr BP (% 95.4)
UCIAMS-264635	Twig	20	264	35	450–151
Beta-651538	Wood cellulose	30	130	30	275–8
SUERC-104996	Bulk	60	7110	37	8014–7850
SUERC-104997	Bulk	140	7847	39	8930–8540
SUERC-105002	Bulk	200	3702	36	4151–3925
SUERC-104991	Wood cellulose	258	8188	40	9276–9018
SUERC-104992	Wood cellulose	292	9134	39	10481–10224
SUERC-104993	Wood cellulose	320	9769	42	11255–11113
SUERC-104994	Wood cellulose	385	8289	40	9428–9132
Beta-651539	Wood cellulose	411	11690	40	13607–13458
UBA-46606	Wood cellulose	450	11752	50	13752–13500

samples to isolate macrofossils that could yield precise dates. In the absence of seeds, we aim for wood cellulose and twigs. Due to bad macrofossil preservation, we dated bulk sediment samples for section 40–230 cm (Table 1).

We used the package RBAcon in RStudio to develop an age-depth model based on Bayesian statistics (Blaauw and Christen, 2011), using nine radiocarbon dates. Bulk dates from levels 140 and 60 cm (SUERC-104996 and SUERC-104997), were excluded from the age-depth model since the resulting ^{14}C dates were showing inversions likely due to the input of old or minerogenic carbon from the volcanic caldera walls in this section of the record (Björck and Wohlfarth, 2001). The RBAcon age-depth model results were used to calculate the sedimentation rate and the mean age (cal yr BP) of each sample.

3. Results

3.1. Paleoenvironmental description

The resulting age-depth model suggests that the Lagoa Amélia sedimentary sequence was deposited during the last 14,000 cal yr BP. Based on stratigraphically constrained CONISS analysis, the record was divided into 8 different zones (LAE-1 to LAE-8), including 2 zones with a single sample each (LAE-3 and LAE-5).

3.1.1. LAE-1, 450–415 cm (14,000–13,500 cal yr BP)

Zone LAE-1 showed medium levels of organic matter content (avg. 18% LOI), and low values of the Ti/Ca elemental ratio. Stones were very rare, median grain size increased throughout the zone from 57 to 159 μm , and coarse sand was absent or present in very low percentages (maximum of 0.75%) (Fig. 2). Sedimentation was the slowest in the record (of c. 10 yr per cm^3) (Fig. S1).

Pollen was well preserved, with high concentration values (up to 240,000 grains/ cm^3) except for the 420 cm deep sample that showed low pollen concentration (c. 2600 grains/ cm^3). The assemblage displayed high percentages of *Afrocarpus mannii* (avg. 10%), *Olea capensis* (avg. 9%), *Craterispermum cerinanthum* (avg. 5%), *Celtis* spp. (avg. 6%), *Trema orientalis* (avg. 3%), Moraceae/Urticaceae (avg. 3%), as well as high values of Asteraceae (avg. 8%) and Poaceae (avg. 3.5%). *Alchornea*, Begoniaceae, Commelinaceae, *Homalium*, *Macaranga*, Piperaceae, *Uapaca*, and *Utricularia* pollen was also present, and pollen of *Elaeis guineensis* was found at level 440 cm (Fig. 3). Rarefied species richness

values were some of the lowest in the record compared to other pollen zones (avg. 28), and DCA axis-1 pollen scores oscillate thought the zone at values around -0.5 .

The fern spore assemblage was dominated by Cyatheaceae tree-fern spores (*Alsophila*, up to 230% relative to the pollen sum), as well as morphotype monoete psilate (up to 430% relative to the pollen sum), with variable levels of other fern spores (Woodsiaceae, Polypodiaceae, and Pteridaceae). There was a high diversity of fungal spores, including spores of coprophilous fungi, such as *Cercophora*, *Chaetomium*, *Coniochaeta*, *Delitzchia*, *Podospora*, *Sordaria*, *Sporormiella* and, the most abundant being *Podospora* (up to 6%/pollen sum). We recorded a high percentage of the saprophytic/parasitic fungi *Rosellinia* (avg. 10%/pollen sum) (Fig. 4).

There was a peak in macro-charcoal particle concentration at 450 cm depth (88 fragments/ cm^3). Micro-charcoal concentration was consistently high, varying between 3037 particles/ cm^3 at level 420 cm to 32,307 particles/ cm^3 at level 440 cm (Fig. 2).

3.1.2. LAE-2, 415–325 cm (13,500–11,350 cal yr BP)

Zone LAE-2 held medium levels of organic content (avg. 15% LOI), with few rocks and gravel, despite an increasing trend of median grain size (ranging from 82 to 207 μm), and peaks up to 6% of coarse sand at levels 370, 340, and 330 cm.

The pollen assemblage showed continuity from LAE-1, yet held lower pollen concentration values (avg. 50,000 grains/ cm^3). DCA axis-1 scores increased from -0.64 to -0.36 . We recorded a marked increase in *Symphonia globulifera* (with peaks of up to 13 and 16%), an increase in *Craterispermum cerinanthum*, and decreases in *Olea capensis*, *Celtis* and *Afrocarpus mannii* (down to 6%, 3% and 1% respectively). From level 380 cm–370 cm there was an increase in *Sabicea* spp. (avg. 6%), *Clematis hirsuta* (avg. 4%), and *Psychotria*-type (up to 15%). There was also a moderate increase in Commelinaceae, and a moderate decrease in Poaceae (both taxa up to 3%). At the end of the zone (360–330 cm), we recorded punctual increases in Apocynaceae and *Vigna*-type, as well as of *Plantago*. Ferns showed a similar assemblage to LAE-1, with peaks in *Alsophila manniana* and monoete psilate fern spores in sample 360 cm (370% and 670% over the pollen sum, respectively). Overall, this section records some of the highest rarefied species richness values of the record (e.g., 36 at level 380 cm).

Coprophilous fungi percentages also increased around levels 360–340 cm, and there were small peaks in *Tetraploa* fungal spores (up to 3%/pollen sum), as well as sustained decreases in *Rosellinia* and *Kretzschmaria* fungal spores, with peaks around 360–340 cm.

We detected an overall high level of macro- and micro-charcoal concentrations, with peaks in macro-charcoal at levels 390 cm and 350 cm reaching 92 and 86 particles/ cm^3 , respectively, and in micro-charcoal at level 360 cm (59,000 particles/ cm^3).

3.1.3. LAE-3, 320 cm (11,100–10,850 cal yr BP)

Zone LAE-3 (sample 320 cm) contained a high percentage of organic material (58% LOI), and no coarse sand, gravel, or rocks.

Pollen concentration was high (c. 214,000 grains/ cm^3), and DCA axis-1 value was -1.06 , the lowest value of the record. The pollen assemblage was strongly dominated by *Trema orientalis* (44%), while the rest of the assemblage remained stable, even though it was probably underrepresented due to the hyperabundance of *Trema*. We also recorded *Lobelia* and *Vigna*-type taxa, as well as a decrease in the proportion of fern spores.

Coprophilous fungi were present, showing an abundance of Sordariaceae spores, as well as high levels of *Rosellinia* (10%/pollen sum).

Charcoal concentrations were low, 14 macro-charcoal particles/ cm^3 , and 2500 micro-charcoal particles/ cm^3 .

3.1.4. LAE-4, 315–255 cm (10,850–9200 cal yr BP)

Zone LAE-4 was characterized by medium levels of organic content (avg. 13%), except for a pronounced peak at level 260 cm (82% LOI),

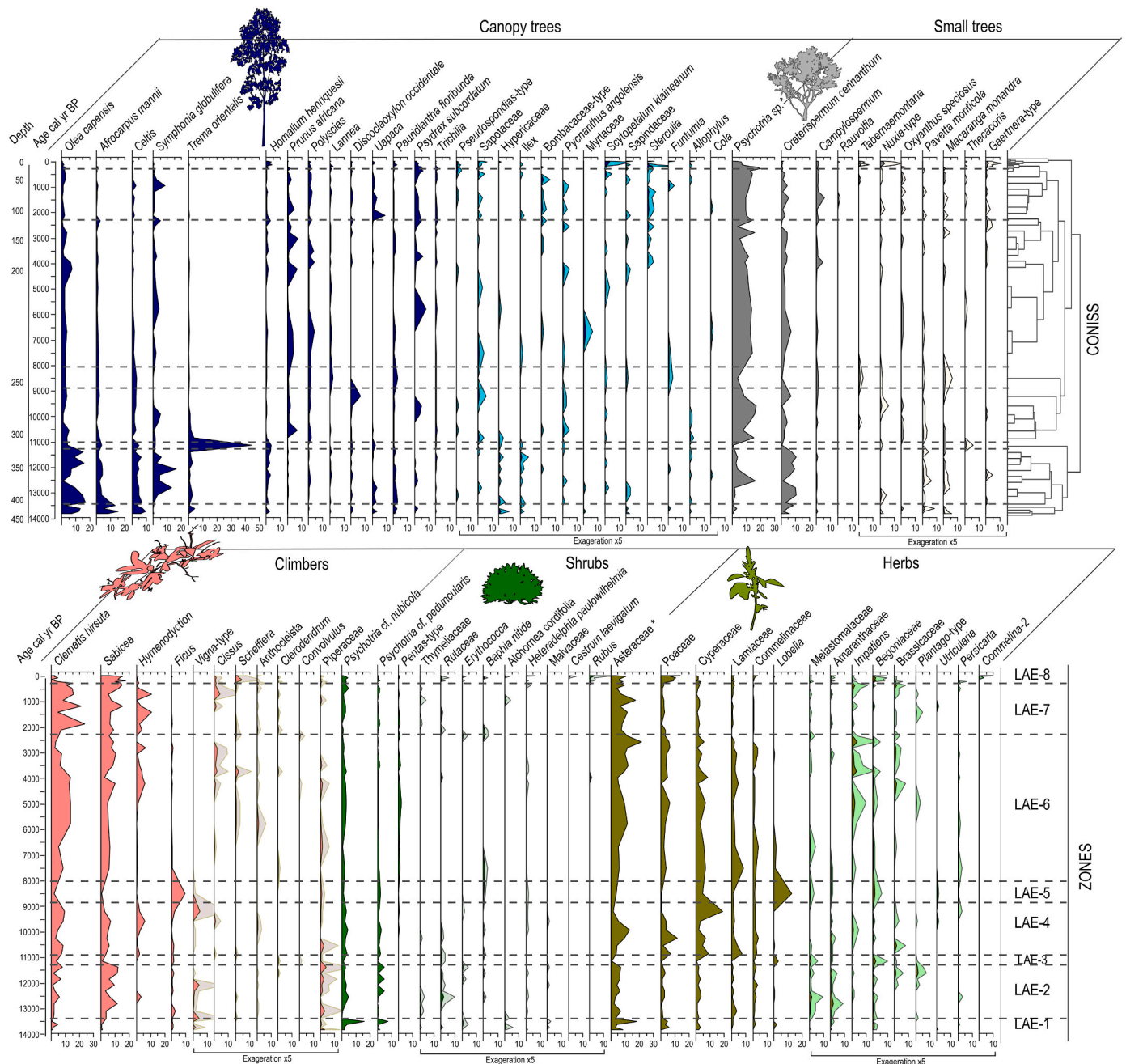


Fig. 3. Pollen diagram showing the percentage of taxa categorized as canopy trees, small trees, climbers, shrubs, and herbs, over 14,000 cal yr BP for Lagoa Amélia (LAE) core. The taxonomic selection is based on habit category (see Table S2), and the asterisk symbols denote taxa that can be assigned to two or more categories (e.g. Asteraceae, includes shrubs and herbs). For curves of rare taxa (<5%), we used exaggeration $\times 5$ (lighter colour). Taxa that did not reach a sum of 10 pollen grains in the record were excluded from the diagram.

with very variable values of median grain size (ranging from 113 to 202 μm), sand content (maximum 3% at level 300 cm) and Ti/Ca (ranging from 0.2 to 8.2%). The sedimentation rate gradually slowed down from 30 yr/cm^3 to c. 50 yr/cm^3 .

This zone showed a transition of DCA axis-1 pollen scores, from -0.25 to -0.05 . There was a decline (or absence) in dominant pollen types from zones LAE-1 and LAE-2 (e.g., *Afrocarpus*, *Olea*, *Craterispermum*, *Symphonia*), while *Psychotria*-type (up to 15%), *Hymenodyction* (up to 6%), *Psidium* (up to 4%), *Sabicea* (up to 6%), and *Clematis hirsuta* (up to 8%) showed increases. Asteraceae, Cyperaceae, Commelinaceae, and Poaceae also showed increases (up to 18%, 11% and 4% respectively). *Trema orientalis* pollen decreased until it disappeared from the assemblage. There were punctual increases in *Disocloaxylon*

occidentale (6% at level 260 cm). The fern spore assemblage was dominated by monolete psilate spores. There was a decrease in fungal spores, except for sample 260 cm, where coprophilous types were present, as well as abundant *Rosellinia* spores.

There were generally lower concentrations of macro-charcoal particles (below 15 particles/ cm^3) and micro-charcoal (c. 2000 particles/ cm^3) around 310–300 cm, decreasing in 290–270 cm, and then increasing to over 3000 at 260 cm).

3.1.5. LAE-5250 cm (c. 8500 cal yr BP)

Zone LAE-5 (sample 250 cm) showed medium levels of organic content (21% LOI), low median grain size (89 μm), and no rocks or coarse sand.

Scheffera-type, Rosaceae (cf. *Rubus*) and *Commelina*-2 showed a sustained presence, and *Elaeis guineensis* and *Zea mays* were also present. This section shows the highest values of rarefied species richness. As pollen concentration rose, the relative percentage of fern spores decreased.

The fungal spore assemblage was diverse, showing increases of *Rosellinia* (up to 54%/pollen sum), and abundant coprophilous fungi (e.g., *Cercophora* peaked at 11% at level 10 cm). There were also increases in the presence of *Sporochisma* (7%), *Meliola* (28%), *Sporidesmium*, and *Isthmospora spinosa* (up to 19%).

Micro-charcoal particles showed a moderate increase, up to 7000/cm³ at level 10 cm, where macro-charcoal concentrations also peaked, at 28 particles/cm³.

4. Discussion

4.1. Sedimentation process, chronological framework, and bog formation in Lagoa Amélia

The Lagoa Amélia Edge (LAE) sediment core studied here was deposited during the last 14,000 cal yr BP, following a complex process that led to clearly differentiated facies. Based on mineral, organic and sediment elemental composition (e.g., granulometry, XRF, LOI data), the sequence can be divided into sections dominated by fine and organic sediments, coarse sediment, and with presence of gravel (Figs. 1 and 2). Sedimentation rates indicate slower deposition on the bottom section of the record (458–250 cm), but changes in grain size and composition towards coarser material in the upper section of the record (250–30 cm) strongly suggest that sedimentation rates were shifting depending on the stability of the crater slopes (Fig. 2). This is in accordance with the Ti/Ca elemental ratio), which shows higher values in the upper section of the core, suggesting increased detrital inputs from the slopes that could have been caused by increased aridity potentially linked to more pronounced seasonality after c. 6000 cal yr BP.

The record also indicates local bog formation at five brief intervals: 14,000–13,900 cal yr BP, 12,700–12,600 cal yr BP, 11,200–10,800 cal yr BP, 9400–8400 cal yr BP, and 200 cal yr BP-present day. During these periods there was abundant preservation of organic matter (up to 90%), with high levels of pollen concentration and well-preserved wood fragments (Figs. 1 and 2), and an increased percentage of Poaceae and Cyperaceae pollen (Fig. 3), spores of saprophyte soil fungi (e.g. *Rosellinia*), and herb parasite fungi (e.g. *Tetraploa*) (Fig. 4). These plant and fungal communities are representative of locally abundant herbaceous taxa, suggesting that peat bogs were developing in the surface and edges of the crater lake. This situation is analogue to the present-day state of the lake, in which the floating bog is mostly constituted by herbaceous species (Fig. 1).

Being a sequence formed by a complex sedimentation process, the LAE age-depth model also deserves discussion. We excluded two radiocarbon dates (SUERC-104996 and SUERC-1049979) representing inversions. We interpret the inversions as old carbon from the crater walls being deposited in rapid erosive events (Björck and Wohlfarth, 2001; Grimm et al., 2009) (Fig. S1). This explanation aligns well with the acceleration of sedimentation detected at 140 and 60 cm. In addition, fast-paced deposition of mineral material is also the most likely cause of the ‘outlier’ radiocarbon dating results at level 200 cm (SUERC-105002, Fig. S1) that contrasts with an otherwise linear model. Finally, the date at 385 cm (SUERC-104994) yielded a younger age than expected, of which the most likely explanation is the intrusion of roots from vegetation growing at the edge of the lake.

4.2. Late Pleistocene to holocene transition: from mist to montane forest

Has the montane forest of São Tomé been stable during the global climatic changes occurring during the past 14,000 years, or has it shifted like continental Afromontane forests (Table 2)? The Lagoa Amélia

Table 2

Summary table of African mainland palaeoecological records cited in the text that show Afromontane responses to climate change in the Late Pleistocene and Holocene periods, including four records from Cameroon and four records of central and eastern Africa (see Table S3 for full details, including marine records).

Record	Reference	Pleistocene-Holocene change
Bambili twin crater system (NW Cameroon) ~2300 m a.s.l.	Lézine et al. (2019)	Increases in <i>Podocarpus</i> , <i>Olea</i> , <i>Celtis</i> , <i>Alchornea</i> , and <i>Clematis</i> pollen represent an uphill treeline expansion during the Pleistocene-Holocene transition. During the Heinrich 1 event (c. 16,000 yr BP) there was a severe drought, and the expansion paused, even reversing. The upslope movement resumed around 15,000 years ago, reaching the modern-day tree line elevation by the onset of the Holocene around 11,000 years ago.
Mbi crater lake (Cameroon) 2015 m a.s.l.	Lézine et al. (2023)	Early stages of tree expansion at Mbi started around 14,500 cal yr BP. Another phase of forest development occurred between 13,500 and 12,500 cal yr BP. However, this expansion was interrupted by a dry event (Younger Dryas). The transitions between the Bölling/Allerød and Younger Dryas events were more clearly observed at Mbi compared to Lake Bambili. During the onset of the Holocene (11,500–10,800 cal yr BP), there was a decrease in Poaceae and an increase in forest pollen, including <i>Schefflera</i> , <i>Alchornea</i> , <i>Olea</i> , <i>Nuxia</i> , and <i>Podocarpus</i> .
Lake Mbalang (Cameroon) m a.s.l. (1110)	Vincens et al., (2010)	The transition from a forested environment to an open savannah took place due to long-term aridification following the African Humid Period. The transition began around 6100 BP, when the percentages of pollen from <i>Podocarpus</i> , <i>Olea capensis</i> , and <i>Alchornea</i> started to decrease. The modern savannah environment (increase in Poaceae pollen) became established around 3000 BP. There was a brief phase of forest regeneration between 5200 and 4200 cal yr BP.
Lake Barombi Mbo (Cameroon) 300 m a.s.l.	Maley and Brenac (1998)	The representation of <i>Olea capensis</i> pollen indicates a relatively cool climate until approximately 13,000 yr BP, c. 10,000–2800 yr BP, the climate became very wet, and the representation of Poaceae pollen sharply decreased, while forest trees reached their maximum extension between 9500 and 3000 yr BP.
Cores KH3 and KH4, Lake Tanganyika (Tanzania, DR Congo), 655 m a.s.l.	Ivory and Russell (2016)	Between 15,000 and 11,000 years ago, there was a significant decline in previously abundant Afromontane trees such as <i>Podocarpus</i> and <i>Juniperus procera</i> , while <i>Olea</i> reached its maximum value. This period also saw an increase in Poaceae and <i>Artemisia</i> pollen, marking the beginning of the transition from Afromontane forest to the dominance of herbs. From 11,000 to 7200 years ago, <i>Olea</i> decreased while most lowland tree taxa reached their maximum

(continued on next page)

Table 2 (continued)

Record	Reference	Pleistocene-Holocene change
Virunga volcanoes (Rwanda) 3474 m a.s.l.	McGlynn et al. (2013)	percentages, including <i>Alchornea</i> , <i>Bridelia</i> , <i>Macaranga</i> , <i>Myrianthus holstii</i> , and <i>Uapaca</i> , signifying the final decline of all Afromontane taxa. Around 5000 cal yr BP, there was a decline in ericaceous vegetation and an expansion of Afroalpine vegetation, followed by an increase in taxa associated with lower montane forest, particularly <i>Podocarpus</i> . These changes in vegetation reflect increasing aridity during the Mid- to Late Holocene.
Lake Rukwa (Tanzania) 800 m a.s.l.	Vincens et al. (2010)	During the deglaciation period (16,500 to 12,300 yr BP), the climate transitioned to warmer conditions, leading to a retreat of Afromontane taxa at higher altitudes on the plateau. This was accompanied by the expansion of wooded formations in the region. Around 12,100 yr BP, the local woodland and bushland experienced maximum development and diversity, indicating an increase in rainfall. The record shows reduced levels of <i>Hagenia</i> , <i>Juniperus</i> , <i>Olea</i> , and <i>Podocarpus</i> around the time of the Younger Dryas.
Mount Kenya (Kenya) 2154 m a.s.l.	Rucina et al. (2009)	During the Late Pleistocene to Holocene transition, a variable fire regime drove the reorganization of the ecosystem composition in the montane forest. This shift reflects the onset of a warmer and moister climate from the onset of the Holocene, as mixed montane forests became more established.

palaeoenvironmental record (LAE) reveals that the montane forest of São Tomé has shifted during the Late Pleistocene and the onset of the Holocene (c. 13,000 and 11,200 cal yr BP), both in altitudinal distribution and in species composition, in response to distinct environmental stressors. Between 14,000 and c. 12,500 cal yr BP the forest around Lagoa Amélia was dominated by *Afrocarpus mannii*, *Olea capensis*, *Psychotria nubicola*, and *Celtis* (Figs. 3 and 5). These trees are currently found in montane forest, *A. mannii* and *P. nubicola* being restricted to higher elevations, namely to mist forest on ridges (Dauby et al., 2022). High concentrations of macro- and micro-charcoal during the Late Pleistocene (Figs. 2 and 5) must evidence frequent fires around Lagoa Amélia and cannot be explained by volcanism, since the last eruptions in São Tomé occurred c. 1.5 Ma (Lopes, 2020).

A first shift in forest composition 13,000 cal yr BP, consisted of an increase in *Symphonia globulifera*, a tree currently associated with montane forest (800–1400 m a.s.l.) even though it can also be found on ridges at lower altitudes (Dauby et al., 2022). Another species that also showed higher frequencies at this time was the small tree *Craeterispermum cerinanthum*, another typical montane species (Figueiredo et al., 2011) that can also be found at lower altitudes (Fig. 3). Both species became abundant at Lagoa Amélia when palynological richness (values up to 36), and vegetation turnover were high, and fires were still frequent, suggesting fast species replacement. From 13,000 onwards, the regional climate warmed moderately and became relatively dry (Weldeab et al., 2005; Collins et al., 2017). LAE sedimentological data showed increases in the Ti/Ca ratio c. 12,500 cal yr BP, indicating detrital input to the crater lake, which could evidence the synchronicity with regional hydrological changes during this dry period (Weldeab

et al., 2005). In addition, the record also shows local bog formation occurring on the edges of the palustrine area, namely c. 14,000, 12,600, and 11,200 cal yr BP, which could be related to dry conditions due to the potential intermittent desiccation or at least to low water levels.

The documented changes during the Late Pleistocene in São Tomé Afromontane forests are best understood in comparison to mainland African records. In western Cameroon, montane forest taxa such as *Olea capensis*, currently inhabiting high elevations in areas with relatively low temperatures, were especially abundant at lower altitudes during the cool and dry glacial periods between 28,000 and 13,000 cal yr BP (Maley and Brenac, 1998). Similarly, the abundance of *Olea capensis* and *Afrocarpus mannii* recorded at LAE suggests they were more abundant around the crater during the Late Pleistocene. The global deglaciation brought changes in the distribution and composition of Afromontane forests in tropical Africa: between 15,000 and 11,000 yr BP the Afromontane treelines in Northwest Cameroon migrated upslope to reach modern-day elevations around Lake Bambili (Lézine et al., 2019), and forests expanded in the area of Mbi crater lake after 14,500 cal yr BP (Lézine et al., 2023). However, the process of forest migration (expansion and contraction) was interrupted during periods of rapid climatic change, such as the Younger Dryas (Lézine et al., 2013). There is also evidence that fire regimes were changing, for instance, in Mount Kenya (study site at c. 2000 m a.s.l.), increased forest fires during the Late Pleistocene-Holocene took place along with forest shifts from montane to mixed montane forests (Rucina et al., 2009). Our data supports a similar process, in which Late Pleistocene dry conditions led to more frequent fires near Lagoa Amélia, likely due to lightning strikes during the dry season (Ceriáco et al., 2022a,b).

In sum, these shreds of evidence suggest that the dynamics of island Afromontane forests during the Late Pleistocene deglaciation might have been analogue to those in the continent since the Afromontane forests of São Tomé were shifting according to regional climate conditions during this period. Between 14,000 and 11,200 cal yr BP mist forest was likely distributed at lower elevations than in the present (1400 m a.s.l.) due to cooler and dryer climatic conditions. Forest fires held a role in these shifts and are linked to dryer regional conditions. Although we cannot rule out other types of processes, such as compositional changes not related to altitudinal shifts, our results suggest that dry tolerant taxa of the Afromontane forests were distributed at lower elevations during the Late Pleistocene, and gradually moved upwards as the climate warmed and fires frequency increased during the deglaciation period (Table 2).

4.3. São Tomé's afromontane forest during the holocene

The end of the Younger Dryas brought increased precipitation in Central Africa (Collins et al., 2017). Afterwards, the Holocene (c. 11,700 BP) was characterised by warmer and more humid environmental conditions (Weldeab et al., 2005), which is considered a main driver of the current distribution of Afromontane forests (White, 1993). In addition, the temperature during the Early Holocene also shifted between cooler and warmer conditions in the Eastern Equatorial Atlantic, where São Tomé is located, with sporadic cooling episodes, such as the one that took place between 9000 and 8000 cal yr BP (Weldeab et al., 2005).

During the onset of the Holocene (11,700 cal yr BP) the environmental conditions in Lagoa Amélia, were characterised by infrequent fires, likely due to high humidity, the consolidation of the cloud belt, and increased rainfall (Fig. 5). There is a period c. 11,200 cal yr BP (LAE 3, one sample), when the forest showed a sharp peak in the abundance of *Trema orientalis* trees, currently considered a pioneer species associated with disturbance (Fig. 3). After this peak, the forest changed through an increased abundance in canopy trees (e.g., *Prunus africana* and *Polyscias quintasii*), and diverse climbers (e.g., *Sabicea* spp., *Clematis hirsuta*). Importantly, most of these taxa are currently more abundant in submontane forest (800–1400 m a.s.l.), suggesting an uphill migration of this forest type after 11,200 cal yr BP. At the same time, the abundance of mist

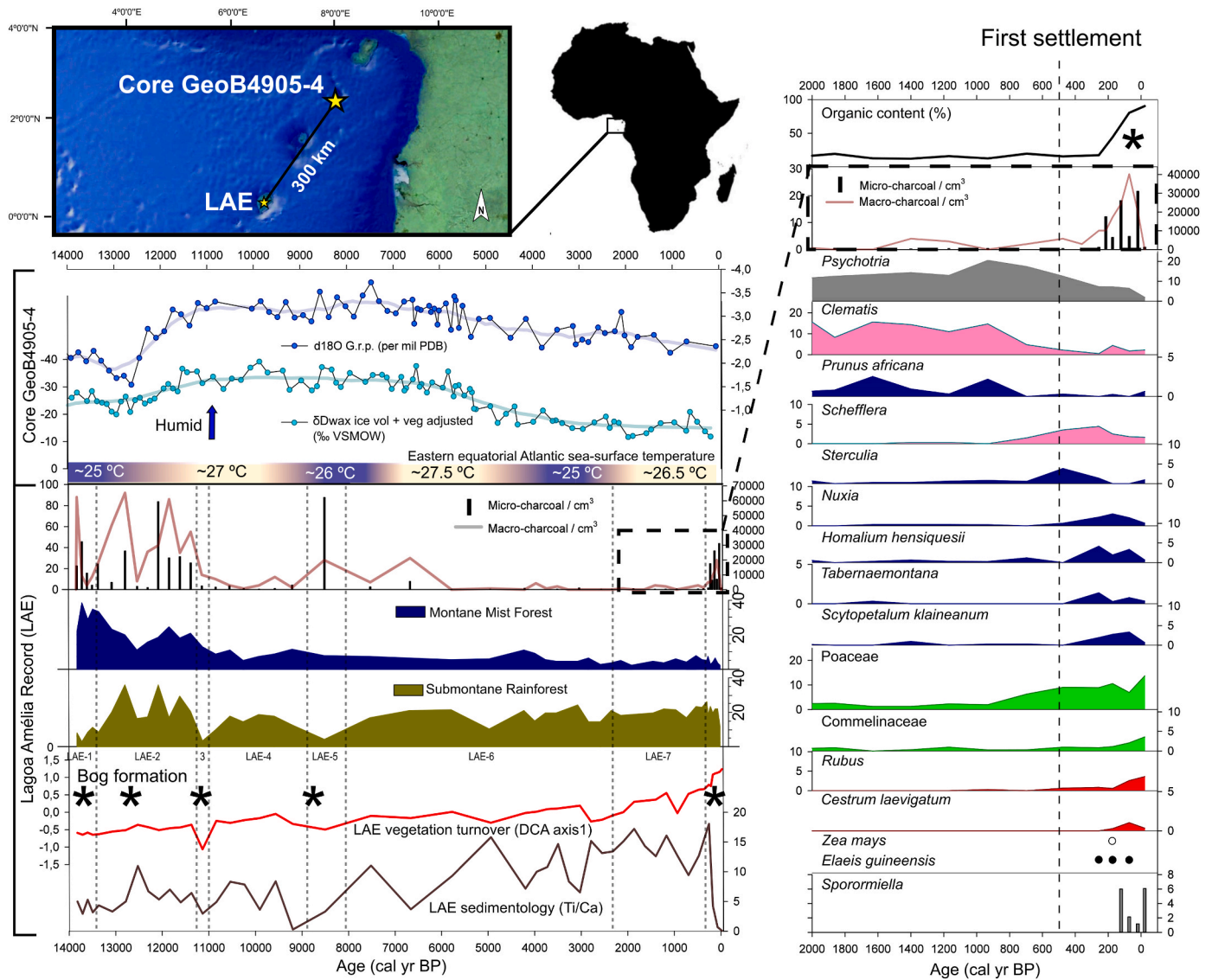


Fig. 5. Summary diagram of the main trends of ecological change in Lagoa Amélia, São Tomé. Left panel: 14,000 cal yr BP to present, showing regional climate trends from core GEOB4905-4 (Weldeab et al., 2005; Collins et al., 2017), fire regime (micro- and macro-charcoal), submontane and mist forests change and sedimentology. Individual pollen taxa included in the montane mist forest (dark blue): *Afrocarpus mannii*, *Celtis*, *Olea capensis*, and *Psychotria nubicola*. For the submontane forest (green): *Craterispermum cerinanthum*, *Polyscias quintasii*, *Prunus africana*, *Psydrax*, *Sabicea*, *Symphonia globulifera*, *Tabernaemontana*, and *Trichilia*. Right panel: focus on the period between 2000 cal yr BP and present, with multiple indicators of landscape change including vegetation change through selected taxa (dark blue trees, pink climbers, light green herbs, red introduced species, and dots economic species), organic matter, and dung-loving fungal spores (*Sporormiella*).

forest taxa, such as *Afrocarpus mannii*, declined at Lagoa Amélia, which might be explained by the uphill migration of mist forest taxa, already initiated at c. 13,000 cal yr BP. There are records of similar uphill migrations occurring in continental Africa during the Holocene. A record in Lake Tanganyika shows how *Olea* pollen, a tree typical of higher elevations, decreased in abundance between 11,000–7200 cal yr BP. In addition, lowland taxa expanded, which has been interpreted as the decline in cool-adapted Afromontane forest elements (Ivory and Russell, 2016; Table 2). Focusing on the early to mid-Holocene, the Lake Bambili record from NW Cameroon, indicates the highest Afromontane forest treeline over the last 90,000 yr due to increased moisture in the first half of the African Humid Period (Lézine et al., 2019, Table 2).

During the early Holocene, the single sample of LAE-5 (8500 cal yr BP) stood out as an outlier in terms of vegetation composition. It is characterized by a high percentage of *Lobelia* sp., a genus that in São Tomé includes only two native herbaceous species (*Lobelia barnsii*, *L. mollerii*) that are restricted to high elevations, where open vegetation is dominant. In addition, there is also a high abundance of *Ficus* (mostly

epiphyte trees or climbers), *Rosellinia* spores (saprophytic fungi), charcoal, and organic matter, indicating bog formation between c. 9000 and 8500 cal yr BP. This vegetation change with abundant herbaceous and climber plants coincided with known abrupt regional climate cooling that took place during the early Holocene (between 9000 and 8000 cal yr BP) when sea surface temperatures temporarily dropped in offshore Cameroon from c. 27 to c. 26 °C (Weldeab et al., 2005, Fig. 5). Although our interpretation relies on a single sample, this result is consistent with the Afromontane forests of São Tomé being sensitive to climate cooling during the early Holocene, which could have led to the forest becoming less dense.

At the end of the African Humid Period (c. 5500 cal yr deMenocal et al., 2000), aridity increased in the Gulf of Guinea, a process that could have impacted forests accross Central Africa (Weldeab et al., 2005). For instance, a record in Lake Mbalang (Cameroon) at 1110 m a.s.l. shows semi-deciduous/submontane forest retreat since 6100 cal yr BP followed by the establishment of savanna by 3000 cal yr BP (Vincens et al., 2010, Table 2). Also in Cameroon, it was described an episode of mixed

evergreen/semi-deciduous forest fragmentation around Lake Barombi Mbo (303 m a.s.l.) linked to increased seasonality from 6500 cal yr BP to the present (Lebamba et al., 2012). In contrast to these mainland examples, values of palynological richness and turnover in the pollen assemblage (Figs. 2 and 5) suggest that the forests around Lagoa Amélia remained mostly stable from the mid to late Holocene, suggesting that the end of the African Humid Period did not have significant effects on local submontane and mist forests.

4.4. Anthropogenic impacts on São Tomé afro-montane forests

Did human impact significantly change Afro-montane forest composition and dynamics in São Tomé? We assessed the influence of human settlement of the island (c. 500 BP to present) on highland forests that, due to their inaccessibility, have certainly experienced fewer impacts than lowland ecosystems (Eyzaguirre, 1986; de Lima et al., 2022). Nevertheless, Afro-montane forests might still exhibit significant impacts on forest composition, soil erosion, and fire regimes (Nogué et al., 2021) resulting from deforestation and introduced species. LAE documents human-driven impacts starting 360 cal yr BP until nowadays, including increases in macro- and micro-charcoal particles, introduced taxa, changes in local land use, and terrestrialization of the wetland found on the crater, through bog formation (Fig. 5).

Historical sources suggest that São Tomé was first settled by the Portuguese in the late 15th century (Muñoz-Torrent et al., 2022). However, the possibility that it was already inhabited cannot be entirely ruled out, namely because the island has not yet been extensively targeted by ancient archaeological research (Mitchell and Lunn-Rockcliffe, 2021, but see Cruz et al., 2023). Continental islands in the Gulf of Guinea, such as Bioko and Corisco, were inhabited by Bantu-speaking Africans before European arrival (Gelabert et al., 2019), but they are much closer to the mainland to which they were connected during the glaciations. Our data shows that pre-European landscape dynamics can be explained by vegetation responses to climatic shifts (see sections 4.1 and 4.2) and that there was no particular dominance of anthropophilic species. Late Pleistocene and early to mid-Holocene forest changes in São Tomé cannot be linked to long-distance transport by seafaring populations reaching the island, as the forest changes occurred too early. It is also important to consider that nearby African islands (e.g. Bioko), located much closer than São Tomé to the mainland, were only colonised around 2000 cal yr BP (Mitchell, 2022).

The human settlement in São Tomé can be delineated into different phases of landscape change, depending on dominant land use strategies linked to rapidly developing Atlantic and global colonial economies (Muñoz-Torrent et al., 2022). When first discovered by Europeans in 1471 CE, São Tomé was described as being almost entirely covered by forest (Tenreiro, 1961), which matches our findings. The first phase of settlement took place from the late 15th to the middle of the 17th century, when a small population of Europeans and enslaved Africans established sugarcane (*Saccharum officinarum*) monocultures in the coastal lowlands (Eyzaguirre, 1986, Cruz et al., 2023). This first phase of settlement did not leave major traces in the montane forests near Lagoa Amélia. Indeed, the LAE record from this period (level 40 and 35 cm, dated c. 475 and 360 cal yr BP, respectively) shows continuity with samples of the Late Holocene, with no significant changes in charcoal concentration or pollen assemblage (Fig. 5).

Introduced species are a main driver of changes in insular ecosystems, including species extinctions (Essl et al., 2019; Fernández-Palacios et al., 2011; Walentowitz et al., 2023), and may have played a major role in the anthropization of forests in São Tomé. Historical sources document how sugarcane monocultures rapidly declined after the mid-17th century, and how numerous plant species kept being introduced while the Portuguese spread their sphere of influence (Ferrão, 1992), using this and other Atlantic islands (Madeira, Cabo Verde) as experimental locations to grow desirable species from across the globe that were less suitable for the temperate climate of mainland Portugal (Garfield, 2015;

Castilla-Beltrán et al., 2020). Since the mid-19th century, Portugal regained interest in São Tomé, establishing several crops notably coffee (*Coffea* sp.) and then cocoa (*Theobroma cacao*) (Muñoz-Torrent et al., 2022). The implementation of highly intensive agricultural systems promoted widespread deforestation, during which only the wettest and most rugged areas of São Tomé remained forested (Eyzaguirre, 1986; de Lima et al., 2022).

While this process took place primarily in the lowlands, these practices extended to the highlands, as reflected by the increases in macro- and micro-charcoal particle deposition in LAE, between 360 and 200 cal yr BP (Fig. 5). In addition, during this period, we identified several introduced plant taxa, namely *Cestrum laevigatum*, *Zea mays* (maize), and *Rubus* sp. *Rubus* pollen was most likely produced by the widespread and abundant introduced species *Rubus rosifolius*, although the native but currently rare *Rubus pinnatus* cannot be ruled out. African oil palm (*Elaeis guineensis*) pollen also became more abundant during this period. This palm is currently widespread in monoculture plantations, and mostly found at lower altitudes. However, it remains unknown whether *Elaeis guineensis* is native or introduced in São Tomé. Our pollen data show the presence of a few oil palm pollen during pre-European settlement (e.g. c. 13,700, 13,300, 7500, and 4900 cal yr BP, all <1%). This finding calls for future research to clarify the status of *Elaeis guineensis* in São Tomé (see van Leeuwen et al., 2008; Walentowitz et al., 2023), namely at lower altitudes, where it was more likely to occur before human arrival.

The impacts of introduced fauna on the montane forest are difficult to assess, as these ecosystems are currently not used for husbandry. However, fungal spores of dung-loving fungi (i.e. *Sporormiella*) can help us detect the presence of herbivores, such as it has been documented for ruminants in Canarian highland laurel forests in La Gomera (Nogué et al., 2013). Our results show that dung-loving fungi increased since 170 cal yr BP (Fig. 5), suggesting the occasional presence of introduced mammals, which might refer to livestock or to feral pigs. While herding is currently rare in the highlands, we cannot rule out the historical presence of livestock, like cows (*Bos taurus*), goats (*Capra hircus*), or donkeys (*Equus asinus*) and horses (*Equus caballus*), which used to be widely used for transportation (Henriques, 1917). Future studies using alternative proxies, such as *sedaDNA*, might help understand the role of introduced animals in forest change (Ficetola et al., 2018; Garcés-Pastor et al., 2022).

Our dataset, involving multiple lines of evidence, allowed us to test how complex culture-environment interactions may have influenced Afro-montane forests in Lagoa Amélia, leading to present-day forests (Mensing et al., 2020). We highlight two main processes detected in the LAE record after 200 cal yr BP. First, a trend in Afro-montane forest change: LAE reveals a decline in *Prunus africana*, and *Trichillia* tree pollen over the last 200 yr, suggesting changes in the extent or composition of the montane forest. Increased human activity at the lower boundaries of this forest could explain a retreat of the basal sections of the forest. We also detect potential changes in montane forest composition around Lagoa Amélia, including peaks in *Scytopetalum klaineanum* tree pollen, moderate increases in other tree taxa, such as *Homalium henriquesii*, *Nuxia*-type, *Sterculia*, and *Tabernaemontana stenosisiphon*, and increase in the abundance of pollen of climbers or trees of the genus *Schefflera* (Figs. 3 and 5). Increased turnover in the pollen assemblage (reflected in positive values in the DCA-1 axis, Fig. 5), and increased rarefied taxonomic diversity (Fig. 3) support the occurrence of forest change. Second, at a local scale, Lagoa Amélia became more terrestrialized, developing a highly vegetated palustrine system with a floating bog c. 200 cal yr BP. This is evidenced by a sharp rise in the percentage of organic content in the LAE sediment, while the grain size declined. The increase in pollen of herbaceous taxa, such as Poaceae and Commelinaceae, also reflects the changes in the plant matrix of the bog, namely the proliferation of herbaceous taxa that are scarce in the surrounding forest. Spores of saprophytic and parasitic fungi became abundant, including *Rosellinia*, *Meliola* (widespread parasitic fungi of

tropical trees), and its hyperparasite *Isthmospora spinosa* (which parasitizes fungi of the Meliaceae family, van Geel et al., 2011). This process could be driven by decreasing water levels, increased fire activity, and the influx of mammal excrements to the wetland, all contributing to increased nutrient-input and eutrophication, thus leading to the terrestrialization of Lagoa Amélia. Forest changes detected in this period could also be local phenomena linked to bog formation, including trees that colonized the edges of this new palustrine environment.

5. Conclusions and future directions

By comparing the responses of the São Tomé Afromontane forest to those recorded in the mainland during the Late Pleistocene, we show that both show similar responses to regional climate changes. The ‘Glacial Refuge Theory’, an influential hypothesis in African paleoecology since the 90s, postulates that dryer and cooler conditions in the Pleistocene caused the opening and fragmentation of tropical forests in the continent, pushing biodiversity to small pockets or refugia in the highlands (Maley, 1989). We believe São Tomé remained forested throughout the deglaciation, experiencing uphill migrations rather than forest fragmentation, as documented in the nearby Cameroon highlands (e.g. Lézine et al., 2019).

The location of Lagoa Amélia on the transition between the montane and mist forests allowed us to identify a decline in mist forest (currently found above 1400 m a.s.l.) between 14,000 and 11,200 cal yr BP, linked to a potentially uphill migration of vegetation belts, being replaced by taxa found at lower altitudes. Charcoal revealed that fires were common in the Late Pleistocene, but became rare in the early Holocene (c. 11,200 cal yr BP). Although the study site is located in a relatively inaccessible area, it showed the impacts of human activities both locally and in the lowlands, from 1470 CE to the present. Over the past 220 years, we have detected multiple signs of anthropogenic presence, including increased frequency of fires (charcoal), and the presence of introduced taxa (pollen and spores).

Our findings show that the natural history of island and mainland Afromontane forests may have more in common than previously assumed; challenging the idea that, in Gulf of Guinea islands such as São Tomé, these forests were buffered against the impacts of climate change due to the regulating capacity of the ocean. These forests might therefore be highly vulnerable to ongoing climate changes, worsening the threat level already assumed from more direct human impacts, like land use intensification and introduced species.

Author contributions

ACB, RFL, SN study design, ACB, RFL and LB fieldwork, ACB, EDCA and LdN samples preparation and palynomorph analysis, NS carried out sedimentological analyses, ACB, RFL, TS, SN and JMFP collaborated in the analysis and interpretation of the data, ACB, RFL and SN drafted the paper with significant contributions of all coauthors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2023.108381>.

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