


Synergy between climate and human land-use maintained open vegetation in southwest Madagascar over the last millennium

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Abstract

Madagascar experienced environmental change during the Late-Holocene, and the relative importance of climatic and anthropogenic drivers is still the subject of an ongoing debate. Using palaeoecological records from the southwest region at Lake Longiza, we provide additional records to elucidate the complex history of the island and to identify the changes that occurred in the tropical dry forest during the Late-Holocene. The data showed vegetation changes associated with climate variability until AD 900 as reflected by the variation in grass, dry-adapted taxa, deciduous trees, and isotope records. An increasing effect of human activities was recorded, indicated by increased coprophilous spore concentration, as a result of a shift from foraging to pastoralism leading to further opening of the ecosystem from AD 980. At the same time, the regional palaeoclimate record showed drier conditions from around AD 1000, which could have accentuated the changes in vegetation structure. More open vegetation was likely maintained by increased use of fire and herbivory around the area, as indicated by the multiple peaks in the charcoal and spore records. Since AD 1900, the pollen record from the southwest region showed that the ecosystem became increasingly open with an increased abundance of grass, pioneer taxa, and reduced diversity, which was linked to a simultaneous effect of climate and agropastoralism activities. Our study suggests that the dry conditions around AD 950 initiated the replacement of forest-dominant vegetation with grass-dominant communities over the last millennium, depicted as an open ecosystem at present. Subsequent changes in subsistence activities would have further maintained an open-structured ecosystem.

Keywords

fire history, herbivory activities, Late-Holocene, Madagascar, rainfall variability, vegetation dynamics

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Introduction

The island of Madagascar experienced massive environmental change associated with changes in species extinction, vegetation cover, and climate variability during the Late-Holocene (Crowley, 2010; Crowley et al., 2017; Godfrey et al., 2019; Razanatsoa, 2019). In terms of vegetation, palaeoecological records show an opening and/or loss of woody vegetation cover in the northwest, southwest, and southeast regions between 1500 and 950 calibrated years before present (cal years BP; AD 450–1000) (Matsumoto and Burney, 1994; Virah-Sawmy et al., 2010, 2016; Voarintsoa et al., 2017a). These changes coincided with the estimated period of early human presence across the island, ranging from 10,000 cal years BP to 1350 cal years BP (BC 8050–AD 600), based on archaeological artefacts, cut marks on animal bones, and introduced species (Anderson et al., 2018; Douglass et al., 2019; Hansford et al., 2018). In addition, between ca. 2500 and 500 cal years BP (ca. BC 550–AD 1500), the island experienced a substantial reduction in the number of large animals associated with habitat change at various palaeoecological sites (Burney et al., 2004; Crowley, 2010; Crowley et al., 2017). These events coincided during variable climatic conditions. Therefore, disentangling the effects of climatic variability (Virah-Sawmy et al., 2010) from anthropogenic activity (Burney, 1987a; Burney and Flannery, 2005; Crowley et al., 2017; Humbert, 1927; MacPhee and Burney,

1991; MacPhee et al., 1985; Muldoon, 2010; Wang et al., 2019) or a synergy between the two (Burney, 2003; Burney et al., 2004) on vegetation responses in Malagasy ecosystems is a complex challenge. Resolving the debates requires the use of high-resolution, multi-proxy palaeoecological studies. These are especially scarce in the drier, western regions where tropical dry forests and spiny thickets provide habitat for unique biodiversity and support the livelihoods of agropastoral and forager communities.

Western Madagascar, where the tropical dry forests (TDF) occur, is classified as a dry bioclimate region along a rainfall gradient with rainfall decreasing from the north towards the south of the island (Jury and Huang, 2004; Scroton et al., 2017; Tadross et al., 2008). Tropical dry forests typically include deciduous or

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evergreen taxa in either open or closed canopy structures, which comprise different vegetation assemblages including savanna, riparian forest, coastlines, and mangroves (Pennington et al., 2006; Portillo-Quintero et al., 2015; Sánchez-Azofeifa et al., 2005). This ecosystem provides various services to humans such as food, pasture, building materials, and fuel (Fajardo et al., 2005; Portillo-Quintero et al., 2015). Tropical dry forests are currently considered as one of the most heavily utilized and disturbed ecosystems worldwide (Gillespie et al., 2012; Hoekstra et al., 2004; Portillo-Quintero et al., 2015). In the southwest Madagascar, extensive agriculture exists, especially in areas with richer alluvium and clayey soils around the Morondava basin (Fauroux, 2001; Waeber et al., 2015). Agriculturalists often use “*hatsake*,” a method which consists of clearing forest and burning the biomass (Waeber et al., 2015) for crop cultivation (Scales, 2012). Furthermore, as a result of climate change, the region’s last forager communities have added seasonal agriculture to their livelihood using this method (Razanatsoa et al., 2021b). Such adaptation strategies and practices may have had an impact on the TDF over time, justifying the need for palaeoecological research in the area.

The existing palaeoecological records from these ecosystems showed an opening of the vegetation, which occurred in the last 1000 years (Matsumoto and Burney, 1994; Voarintsoa et al., 2017a) and includes the spiny thicket vegetation in the southern sub-arid region (Virah-Sawmy et al., 2016). Pollen data from a core sampled in the spiny thicket’s ecoregion around Andolonby, southwest Madagascar showed that fire-adapted species increased around 1000 cal years BP (ca. AD 950; Virah-Sawmy et al., 2016), after which they disappeared along with the other taxa characteristic of the vegetation. From 700 cal years BP (ca. AD 1250) to the present, the vegetation became dominated by dry-adapted taxa such as *Didiereaceae*, a taxon typical of spiny thicket vegetation, and associated with increasing aridity in the region (Burney, 1993; Virah-Sawmy et al., 2016). This evidence indicates the effect of climate on the vegetation. However, some of the evidence suggests that changes in land-use may have also contributed to the opening of the forests in these regions (Crowley et al., 2017; Voarintsoa et al., 2017a), while others have suggested a synergy between climate and land-use are the likely drivers of change (Burney, 2003; Burney et al., 2004).

Climatic drying in western Madagascar and marine regression in the western Indian Ocean reflected local desiccation during the last 2000 years (Camoïn et al., 2004; Vallet-Coulomb et al., 2006). Paleoclimate records from the northwest found that the climate was much drier and less variable between 4000 years ago up to around 1000 cal years BP (Wang et al., 2019) and after 1600 cal years BP (ca. AD 350; Voarintsoa et al., 2017b). A high-resolution 1700-year record of $\delta^{18}\text{O}$ speleothem at Anjohibe Cave in the northwest region was used to infer the variability of rainfall in the region during the Late-Holocene (Scroxton et al., 2017). Over the past 1700 years, the records show alternating three dry and wet phases in the tropical western Indian Ocean with each phase lasting about 500 years. These phases were associated with the displacement of the Intertropical Convergence Zone and global climate forcing (Scroxton et al., 2017). The correlation between the northwest regional record with other records across the Indian Ocean and the east African records (Scroxton et al., 2017) suggest that the climate of the northwest is strongly influenced by large-scale forcing and the speleothems isotope record from Anjohibe Cave can therefore be taken to represent regional trends in rainfall.

The longer-term record has recently been supplemented with high-resolution records from $\delta^{13}\text{C}$ in tree rings from the southwest, spanning the last 700 years (Razanatsoa, 2019). These records demonstrate a wetter period from AD 1300 until AD 1500, which coincides with the relatively wet period in the northwest record during the 500-year the dry phase (Scroxton et al., 2017). The tree

isotope records demonstrated a significant trend in decreasing rainfall over time (Razanatsoa, 2019), which also became more pronounced in the last millennia as recorded in pollen records from the region (Burney, 1993; Razanatsoa, 2019; Razanatsoa et al., 2021a; Virah-Sawmy et al., 2016). Although pollen evidence from the region generally supports climate as a long-term driver of vegetation change (Virah-Sawmy et al., 2016), evidence of climate change is equivocal and difficult to assess due to complex interactions with anthropogenic factors.

The debate around the precise causes of vegetation changes, whether anthropogenic or climatic remains unclear, especially in the drier western regions, where these TDF provide habitat for unique biodiversity and support the livelihoods of agropastoralist and forager communities. The mosaic nature of the vegetation in the region makes for a complex landscape template on which the imprint of anthropogenic activities is not fully understood. Providing additional high-resolution, multi-proxy palaeoecological records for this understudied ecosystem will shed light on the relative influence of drivers of change at the interface between the dry and sub-arid bioclimate region in southwest Madagascar. Investigating the long-term trends and patterns of vegetation change will further improve predictions of possible future change. In this study, we used independent proxies from a new record of climate using $\delta^{13}\text{C}$ tree rings (Razanatsoa, 2019) and $\delta^{18}\text{O}$ speleothem record (Scroxton et al., 2017) as a proxy for rainfall to investigate the impact of climate. We reconstructed vegetation change, fire history, and herbivory using pollen and sediment carbon isotopes, microscopic charcoal, and coprophilous dung spores, respectively, to contribute to the understanding of the environmental history of the island during the Late-Holocene and investigate the timing and impact of these drivers in southwest Madagascar. The study aimed to investigate, (i) the changes in vegetation structure, composition, and diversity in southwest Madagascar during the Late-Holocene, (ii) the history of fire and herbivory in the region, (iii) whether major changes in climate coincided with changes in vegetation, and (iv) the interactive influence of climate and anthropogenic factors in driving vegetation change.

Materials and methods

Study area

This research was conducted in the semi-arid southwest of Madagascar, which receives less than 800 mm of rainfall per year. Rainfall is irregular during the dry season, between March and November, and cyclical drought is common (Cornet, 1974; Middleton and Beinart, 2005). These dry periods can extend for several years and have become more prolonged and frequent in recent decades (Dewar and Wallis, 1999; Donque, 1972; Jury, 2003; Randriamahefasoa, 2013; Waeber et al., 2015). This trend was recently confirmed from a reconstruction of high-resolution rainfall over the last 700 years, showing the continued decreasing trend of rainfall at a decadal- to centennial-timescale (Razanatsoa, 2019). The region contains tropical dry forests including, but not limited to, dry deciduous forests (hereafter, “dry forest”) comprising multiple dry-adapted species, woody savanna, mangroves, and mosaics of riparian ecosystems and spiny thickets in the south.

Site details

We collected a sediment core at Lake Longiza within the dry forest area in the coastal plain in southwest Madagascar (−20.34666667°S, 44.40244444°E), which is a lake 3 km wide and approximately 4 m deep (at around 20 m above sea level). The diameter of the study site provided a large pollen source area (in the order of 10^2 – 10^3 m), which is suitable for a regional reconstruction of the vegetation (Sugita, 1994). Using a Russian corer, a 96 cm long core (named

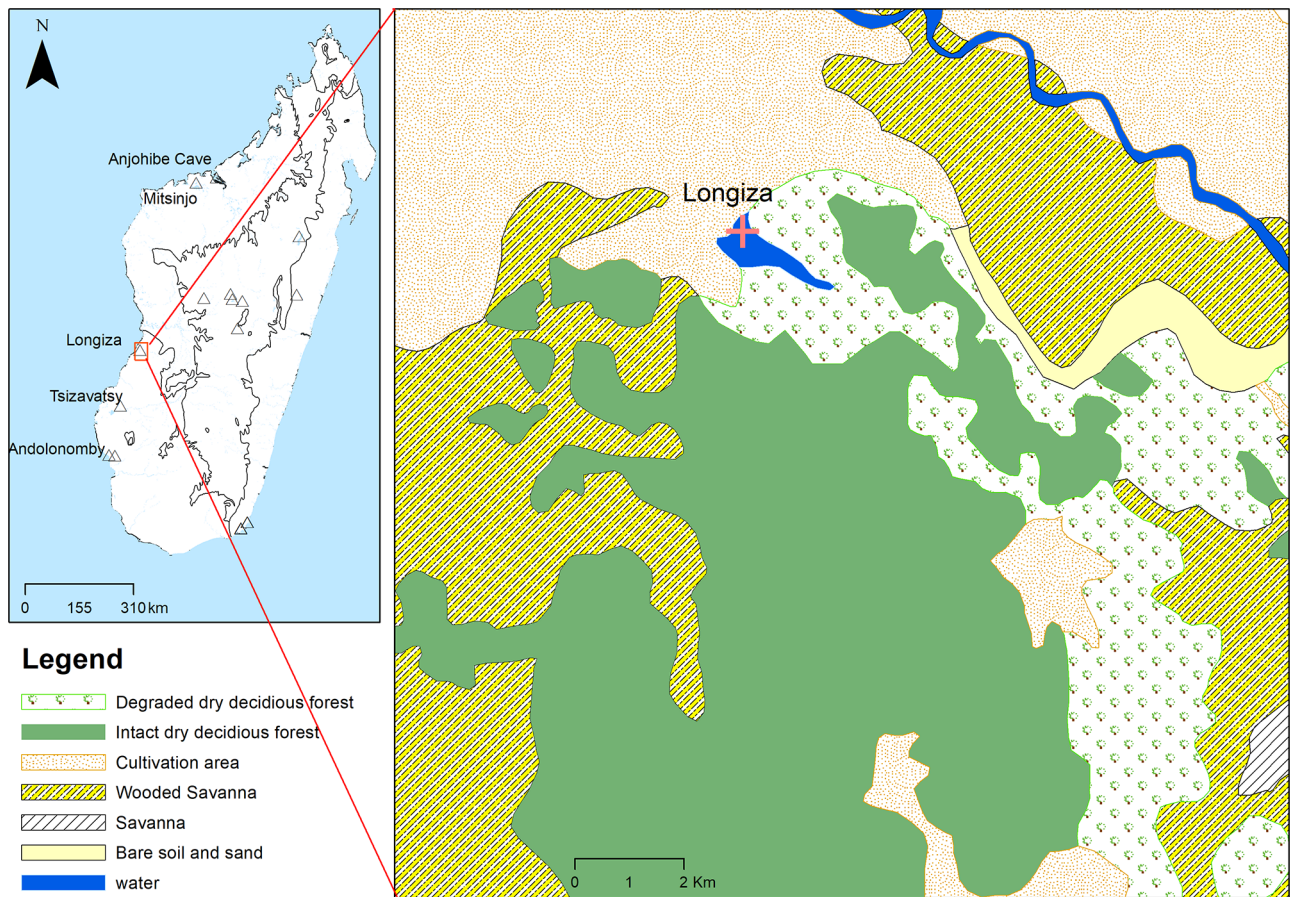


Figure 1. Location of the study site. Triangles indicate published palaeoecological sites in Madagascar with names of those located in the western region.

“LNG”) was extracted 150m from the edge of the lake (Aaby and Digerfeldt, 1986). The core contained material high in clay content and organic matter comprising several distinct layers of charcoal. Less than 5 km to the north of this lake is the Morondava River where forest and riparian vegetation exists on alluvium and fertile soils. Taxa such as *Podocarpus* spp., Myrtaceae, and *Pandanus* (cf. *P. xerophyta*) occur in the riparian vegetation of the streams (Farjon, 2010; Gray, 1953; Snow, 2008, 2010; Virah-Sawmy et al., 2016). Lake Longiza is surrounded by rice fields, with patches of intact dry forest, degraded dry forest, agricultural lands, and woody savanna in the wider landscape (Figure 1). The vegetation at the fringe of the lake contains taxa such as *Typha angustifolia* (Typhaceae), *Phragmites mauritianum* (Poaceae), *Oryza* spp. (Poaceae), *Musa paradisiaca*, *Ziziphus* spp. (Rhamnaceae), *Acacia* spp. (Fabaceae), *Adansonia grandidieri* (Malvaceae), *Androya decaryi* (Scrophulariaceae), and *Anacardium* spp. (Anacardiaceae). The dominant vegetation in this area is dry forests and includes many drought-tolerant species, such as those belonging to the family, Euphorbiaceae. This region is occupied by various ethnic communities of people with the majority conducting agropastoralism, and who practice swidden farming, called *hatsake*. The *hatsake* consists of the cutting down of trees and burning of the biomass (Waeber et al., 2015) to transform the ash as nutrients to the soil (Scales, 2012), which can be practiced on poor soils (Casse et al., 2004; Waeber et al., 2015). They also herd livestock, especially cattle and goats, which are often used as a hedge during lean periods (Dewar and Richard, 2012; Hänke and Barkmann, 2017; Kaufmann and Tsirahamba, 2006).

Chronology of the core

The chronology of the core was established based on nine accelerator mass spectrometry (AMS) radiocarbon dates of the bulk

sediment, which is the same fraction from which the proxies including fossil pollen were extracted (Table 2). All samples were pre-treated with acid for the removal of carbonate and sent to the iThemba LABS facility in Johannesburg, South Africa; Beta analytic Inc., Laboratory in Florida, USA and 14CHRONO labs in Belfast, UK. Age-depth models were performed using the package “rbacon” version 2.5.6 (Blaauw et al., 2021). Calibration was done using the Southern Hemisphere calibration curve “SHCal20” for older dates (Hogg et al., 2020) and the post-bomb curve “post-bomb_SH1-2.14C” for younger dates post 1950 (Hua et al., 2013). The chronology was established based on the age-depth model and used to identify sediment accumulation change over time. All calibrated ages within this paper were expressed in BC/AD for all cores in reference to BCE/CE.

Pollen, sediment carbon isotope, charcoal, and coprophilous fungal spore analyses

The lithology of the sediment was describe using the modified version of Troels-Smith (1955). Changes in the vegetation were evaluated using pollen and stable carbon isotope analysis on the sediment core. The sediment core was sampled every 2–8 cm. A minimum of 250 grains of terrestrial pollen (Quick et al., 2011; Scott and Woodborne, 2007) were counted for each level of the core depth for statistical analysis and to ensure 95% confidence intervals (Maher, 1972). Pollen grains were classified into ecological and vegetation association groups such as trees/shrubs and herbaceous, dry forest taxa including dry-adapted (xerophytic) taxa and riparian forest taxa. Sediment carbon isotopes ($\delta^{13}\text{C}$) were performed every 1–4 cm along the core. This indicates changes in the relative abundance of C_3 and C_4 plants in sediment deposits (Ehleringer and Rundel, 1988; McCarroll and Loader,

Table 1. Description of the LNG sediment core from Lake Longiza in southwest Madagascar based on Troels-Smith (1955).

Depth (cm)	Unit	Troels-Smith	Description	Munsel code	Color
0–16	LNG_strat-5	As3 Lf1 Th ⁺	Clayey and ferruginous deposit	10YR 4/2	Dark grayish brown
17–32	LNG_strat-4	As2 Dh1 Th1	Clayey samples with detritious and some discernible plants roots components	2.5Y 4/1	Dark gray
33–50	LNG_strat-3	As2 DII Th1	Clayey with some detritious of herbaceous and ligneous. Traces of charcoal	2.5Y 3/2	Very dark grayish brown
51–76	LNG_strat-2	As3 Gs1	Clayey and occasional coarse sand	2.5Y 4/2	Dark grayish brown
77–96	LNG_strat-1	As1 Ga2Gs1	Fine sand and clayey deposits with occasional occurrence of coarse sand.	2.5Y 4/1	Dark gray

2004; Tieszen, 1991) in consideration of the abundance of aquatic taxa. Sediment carbon isotope measurement was conducted on the bulk organic content of the sediment cores at the Stable Light Isotope Laboratory at the Archaeology Department, University of Cape Town. Pollen and coprophilous fungal spores were prepared in the laboratory following the protocols reviewed by Bennett and Willis (2001).

The history of fire in the surrounding vegetation of the lake was evaluated based on microcharcoal (<150 µm) and macrocharcoal (>150 µm) analyses at every 2–4 cm along the core. These are common proxies for the study of Quaternary fire history and provide data on contemporary fire regimes at regional/landscape and local scales (Blackford, 2000; Scott, 2000). Results are provided as an influx indicating the rate of fire during a given year. Apart from the macrocharcoal, no additional macrofossil analysis was performed on the core.

To evaluate herbivory at the study site, coprophilous fungus spores were analyzed following the method described by Etienne and Jouffroy-Bapicot (2014). A total of 300 spores and *Lycopodium* counts, under 1000× magnification with the addition of immersion oil, were analyzed. Coprophilous fungi grow on the excrement (dung) of large herbivores and their preservation in sediments indicates the presence of animals in the past. Though the spore assemblage does not distinguish between wild and domestic large herbivores, domestic herbivory is often inferred when the abundance of coprophilous spores occurs in association with crop pollen and/or other anthropogenic indicators (Goethals and Verschuren, 2020). The summed abundances of taxa such as *Sporormiella*, *Sordaria*, *Podospora*, and *Chaetomium* are suggested to be a more robust fungal-spore indicator for the presence of domestic large herbivores in an African context, rather than *Sporormiella* alone (Goethals and Verschuren, 2020) and they are widely used to infer pastoral activity near lakes (Cugny et al., 2010; Doyen and Etienne, 2017; Gelorini et al., 2012; Guillemot et al., 2015; López-Sáez and López-Merino, 2007; Razanatsoa et al., 2021b; Van Geel et al., 2003). In the present study, the concentrations of *Sporormiella*, *Gelasinospora*, *Coniochaeta*, *Podospora*, and *Sordaria*, were measured. These are some of the most reliable indicators of large herbivore presence alone or in combination (Baker et al., 2013; Ekblom and Gillson, 2010; Gelorini et al., 2012). The combination of charcoal and coprophilous spores as proxies provides the opportunity to evaluate the increasing occurrence of (agro) pastoralism in the area.

Data analysis

All data analyses were conducted in R studio version 4.1.0 (R Core Team, 2021). The community ecology and sediment analyses were conducted using the packages “Vegan” (Legendre and Gallagher, 2001; Oksanen et al., 2017) and “Analogue” (Simpson and Birks, 2012). Pollen percentages were transformed using the function *decostand* through the method of *Hellinger* as it considers the presence of zero values in the data (Legendre and

Gallagher, 2001)). Temporal variation of vegetation over time was identified using clustering techniques, as commonly performed in palaeoecological analyses (see Gil-Romera et al., 2010). This technique allows for the identification of significant stratigraphic changes in the pollen assemblage (Legendre and Birks, 2012; MacPherson, 2017). Cluster analyses, based on the Euclidean distance, were run using the function *chclust* in the R package “Analogue”, as well as the method of constrained incremental sum-of-squares (CONISS) (Birks and Gordon, 1985). The Euclidean distance measures the similarity between the sediment samples analyzed in the core where samples with similar taxonomic composition and abundance were grouped first. CONISS, a stratigraphically constrained test that analyses groups of samples within their relative age and zones, was identified using the function *cutree* (Birks and Gordon, 1985; Grimm, 1987).

We conducted a rarefaction analysis of the data to estimate the palynological richness, an indicator of plant diversity (species richness) in the landscape. It assumes similar pollen sum counts for all samples (Birks and Line, 1992), which is based on a minimum sum of 250 pollen grains per sample excluding aquatics. This method has been used by other studies in palaeoecology (Colombaroli et al., 2009; Gil-Romera et al., 2010). However, because the number of taxa can be influenced by a few dominant species, detrended pollen richness was calculated by including the PIE evenness (probability of interspecific encounter) (Hurlbert, 1971). The PIE measures the probability that two randomly selected pollen grains will be of different taxa, which is not affected by the sample size or pollen diversity. PIE values range between 0 and 1, where 0 indicates that all pollen grains in a sample are the same and 1 indicates that they all differ. This was used to calculate the detrended pollen richness, which is the residual of the regression of the pollen rarefaction and the pollen evenness distributed around a mean of the pollen rarefaction (Colombaroli et al., 2009). In addition, compositional change (or beta diversity along a temporal gradient) was obtained from the first axis of the detrended canonical analysis (DCA axis 1) of the square-root transformed pollen percentages (Birks, 2006; Colombaroli et al., 2009). Results were then transformed using the Hill’s transformation to evaluate the change on a positive axis (Gavin et al., 2003).

All reconstructed proxies including pollen, charcoal, and coprophilous spores were then evaluated and compared with previously published records from the western region of Madagascar, including the $\delta^{13}\text{C}$ tree ring (Razanatsoa, 2019) and $\delta^{18}\text{O}$ speleothem (Scroxton et al., 2017).

Results

Sediment description

The lithology of the core “LNG,” based on a modified version of Troels-, contained five stratigraphic units and were labeled consecutively from the bottom to the top of the core (Table 1). These units were similar in color with varying shades of gray along the core and contained varying proportions of clay, sand,

Table 2. Radiocarbon dates of bulk sediment samples from the core recovered in Lake Longiza (southwest Madagascar). Uncalibrated and calibrated calendar years AD and BP provided.

Depth (cm)	Sample code	Lab ID	Uncalibrated radiocarbon dates (conventional dates – BP)	95% calibrated radiocarbon dates (cal years BP)	Probability (%)*	95% calibrated calendar dates (cal years AD)	Probability (%)*
25–26	LNG_25	IT-C-1588	113.60 ± 0.65PMC	–	–	1831–1873	25.7
30–31	LNG_31	BETA_498745	121.28 ± 0.45PMC	–	–	1833–1891	58
39–40	LNG_39	IT-C-1485	105.36 ± 0.60PMC	–	–	1879–1915	32.9
56–57	LNG_56	UBA_35670	611 ± 32	578–651	71.5	1299–1372	71.5
65–67	LNG_65	IT-C-1586	1310 ± 44	1176–1301	91	649–774	91
70–71	LNG_70	BETA_498746	1160 ± 30	974–1130	82.5	820–976	82.5
80–81	LNG_80	BETA_498747	610 ± 30	554–619	58.3	1333–1396	57.5
91–92	LNG_91	BETA_435567	2280 ± 30	2300–2349	51.6	–400–351	51.6
94–96	LNG_94	IT-C-1587	900 ± 33	732–834	60.2	1116–1218	60.2

*Indicate the highest range probability distribution of the calibrated dates from the measured radiocarbon dates.

and plant fragments (Table 1). The entire core contained a high content of clay, or *As* (*Argilla steatodes*), of grain sizes <0.002 mm (Table 1). LNG_strat-1 had the highest proportion of fine sand (50%), *Ga* (*Grana arenosa*), while 25% of LNG_strat-2 contained coarse sand, or *Gs* (*Grana minor*). Units LNG_strat-3 and LNG_strat-4 contained plant and animal material classified in coarse roots of herbaceous origin >5 mm, or *Th* (*Turfa herbacea*), *Dh* (*Detritus herbosus*) herbaceous fragments >2 mm, and *DI* (*Detritus lignosus*) woody fragments >2 mm. These plant materials were in the form of charcoal fragments in the unit LNG_strat-4. LNG_strat-5 differed from the rest of the core due to traces of ferruginous iron oxide particles, *Lf* (*Limus ferrugineus*) <0.1 mm, found at the upper level of the core which made up 25% of the samples.

Age-depth models and chronology

Radiocarbon dates of the LNG core are provided in Table 2 and the age-depth model used to establish the chronology is provided in Figure 2. The calibrated basal date of this core at 92 cm depth (BETA_435567; 2280 ± 30 ¹⁴C year BP) was BC 327–208 (2158–2277 cal years BP) followed by two other pre-bomb radiocarbon dates at 70 and 65 cm of AD 948–1017 (933–1002 cal years BP) and AD 675–876 (1074–1275 cal years BP), respectively. The post-bomb dates at 39, 30, and 25 cm were 105.36 ± 0.60% Modern Carbon (pMC), 121 ± 0.48 pMC, and 113.60 ± 0.65 pMC, respectively. These occurred toward the top of the core, which showed an increased rate in sedimentation. Eighty percent of the ages overlapped with the age-depth model. Two radiocarbon dates at 96 cm (IT-C-1587; 900 ± 33 ¹⁴C yr BP) and 80 cm (BETA_498747; 610 ± 30 ¹⁴C yr BP) were detected as outliers as they were stratigraphically inconsistent with the majority of the ¹⁴C dates. The age reversal caused by these outliers might be due to rootlet contamination in those sections. Rootlet penetration can leave small traces of modern carbon thereby contaminating the results even if the rootlets themselves have been removed. Sediment accumulation rates range from 0.03 mm year⁻¹ for the oldest section of the core from 380 cal years BC until 985 cal years AD (380 BC–AD 985) to ca. 0.25 mm year⁻¹ at the top of the core (Figure 2).

Pollen and isotope record from Lake Longiza

Based on the main shifts of vegetation recorded from the analysis of the pollen record, three significant zones of changes were recorded during the last 2000 years (Figure 3). These periods include from BC 200 to AD 1150, AD 1150 to 1950, and AD 1950 to 2010.

BC 200–AD 1100: Dry forest with a mosaic of Podocarpus (Podocarpaceae)–Myrtaceae riparian forest. This period between BC 200 and AD 1100 (LNG_1) was characterised by a dry forest with a mosaic of *Podocarpus*–*Myrtaceae* riparian forest with the abundance of dry forests taxa, such as *Acacia* (Fabaceae), with a mean relative abundance of 4 ± 2% and reaching its highest value around AD 830 (7%). The *Arecaceae* family also reached its maximum abundance (17%) at this time. Other abundant trees, such as *Gnidia* (Thymelaeaceae), *Ficus* (Moraceae), and *Trema* (Ulmaceae), had a mean frequency higher than 2% of the total pollen sum (TPS). The xerophytic component of the dry forest, including *Acalypha*, *Phyllanthus*, and *Securinega*, remained low during this period (on average <1%) except around AD 620 where the total abundance exceeded 2%. This period was also marked by the abundance of riverine trees, such as *Podocarpus* (4 ± 3%) and *Myrtaceae* (4 ± 1%). Of the herbaceous group, *Poaceae* covered 48 ± 6% of the TPS with a peak around AD 620 where its abundance reached 60%. All the other taxa remained relatively low during this period, except the *Urticaceae* type (3 ± 1%). Aquatic pollen abundance remained generally low with a mean abundance of 9 ± 4% and a maximum proportion of 15%. *Cyperaceae* (7 ± 4%) contributed most to this proportion of aquatics which peaked at 14% around AD 620. The results from the soil carbon isotope analysis showed a mean of –22 ± 2‰ with a more negative value (approximately –22‰) until around AD 620 where it became more positive (–21‰). This value continued to fluctuate from AD 880 (–24‰) until the end of this period (–19‰).

AD 1150–1950: Open ecosystem with a mosaic of dry forest and Pandanus (Pandanaeae) riparian forest. This period between AD 1150 and 1950 (LNG_2) was marked by a decrease in dry forest (e.g. *Fabaceae*) and riverine forest taxa (e.g. *Podocarpus* and *Myrtaceae*) and an increase in *Poaceae*. Some dry forest taxa, such as *Arecaceae*, *Gnidia*, *Trema*, *Celtis*, and *Acacia*, remained abundant during this period with a mean frequency higher than 2% despite the decrease in proportion compared to the previous period. Decreases in *Podocarpus* (1 ± 1%) and *Myrtaceae* (3 ± 1%) were recorded for the riverine taxa in contrast with *Pandanus* which reached its maximum around AD 1900 (7%). All the riverine taxa had higher proportions at the beginning of this period, around AD 1150, but decreased over time until AD 1950. Similarly in the herbaceous group, taxa such as *Acanthaceae*, *Menispermaceae*, and *Urticaceae*, had a high relative abundance at the beginning but decreased over time. *Poaceae*, however, increased over time during this period from 51% around AD 1370 to 67% around AD 1950 with a mean abundance of 58 ± 8%. The proportion of aquatics increased to 10 ± 4% in

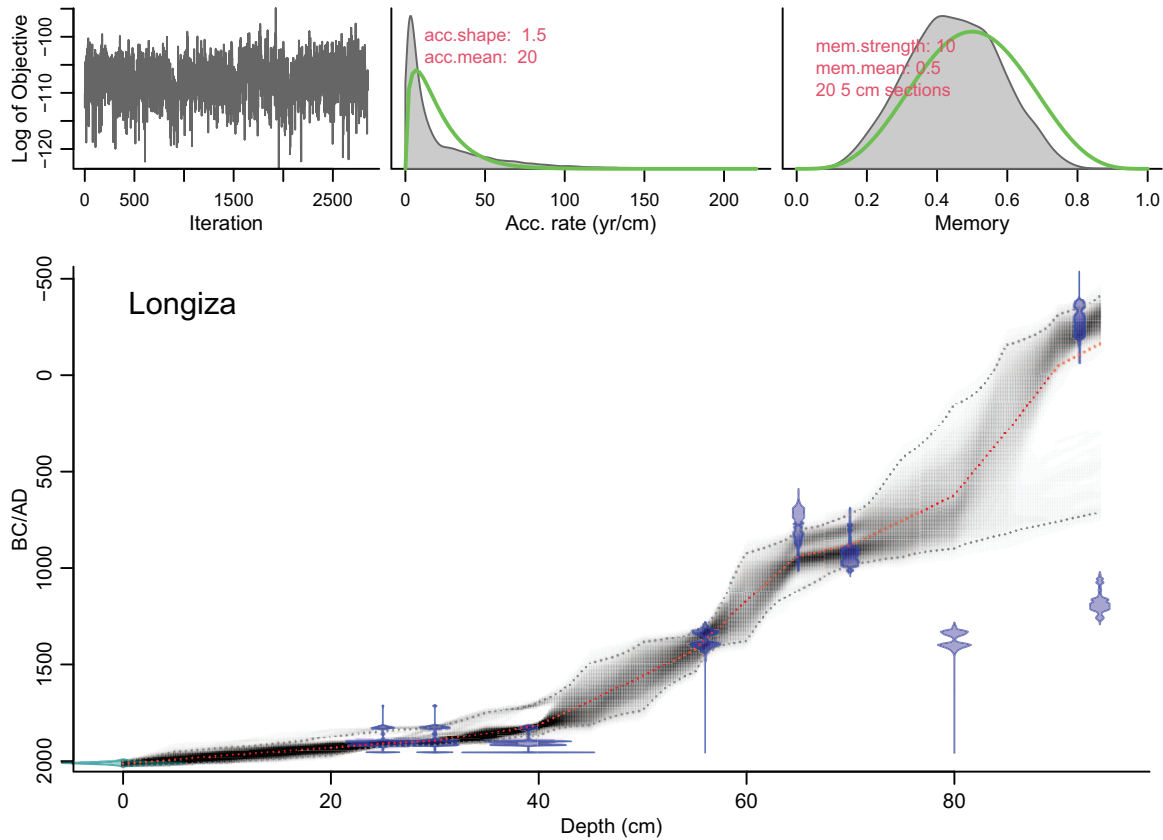


Figure 2. Age-depth models constructed for LNG core using BACON software (Blaauw and Christen, 2011) with the SHCal20 14C calibration curve (Hogg et al., 2020). Upper left: the MCMC iterations, showing a stationary distribution with little structure among iterations. Upper middle: prior (gray curve) and posterior (filled gray curve) distribution of accumulation rates. The mean accumulation rate was set to 20 yr/cm. Upper right: the prior and posterior probability distributions for memory (i.e. autocorrelation strength). Lower plot: the bacon age-depth model. Individual radiocarbon dates are shown in probability density functions of calibrated ages. Two radiocarbon dates were rejected by bacon as outliers. The gray area indicates the uncertainty envelope of the age model with dashed lines indicating 95% confidence intervals.

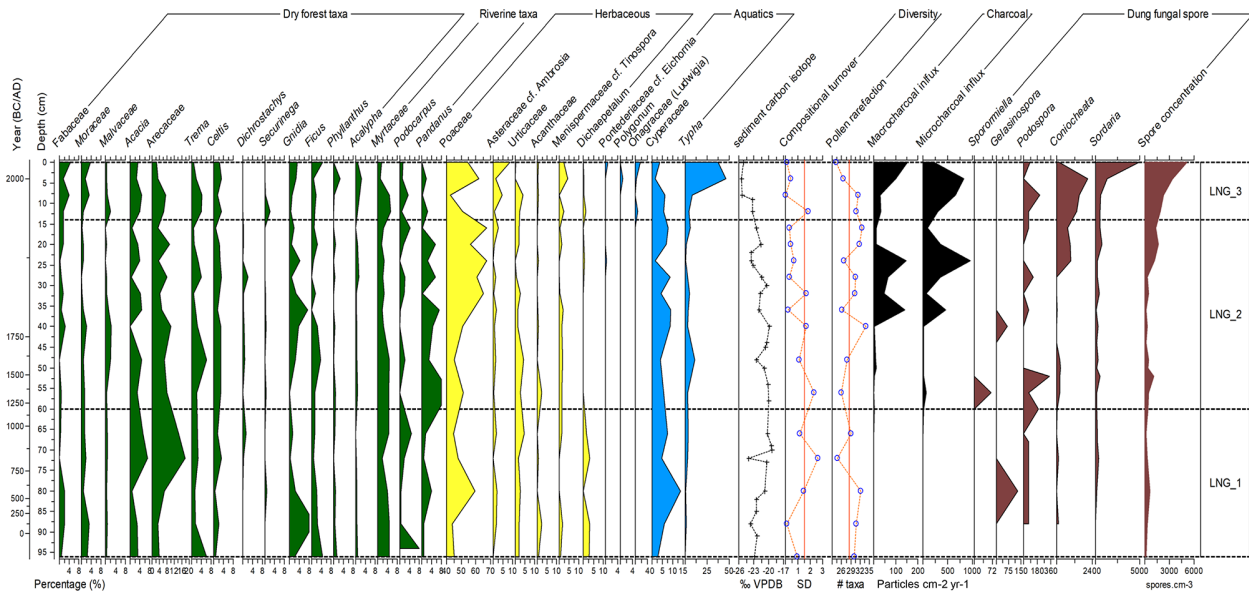


Figure 3. Simplified diagram from Lake Longiza. It contains pollen taxa with proportions higher than 2% grouped according to their associated vegetation and physiognomy, along with diversity measures, and $\delta^{13}C$ content of the sediment, microscopic charcoal influx, and coprophilous concentration. The measure of diversity indicating compositional turnover and pollen richness are evaluated through rarefaction analysis and detrended pollen richness. Ages are provided in calendar years (AD).

LNG_2 from AD 1150 to 1950 despite the decrease and variable rate of Cyperaceae abundance ($6 \pm 3\%$). This increasing abundance of aquatic plants was marked by the emerging presence and increase in *Typha*, which recorded its highest value at 11% around AD 1610, and the first appearance of Pontederiaceae in the record. During this period, the soil carbon isotope

at Lake Longiza was more positive ($\sim -19\%$ to -20%) until AD 1810 after which a gradual decrease of the isotope value from -21% to -23% was recorded.

AD 1950–2010: Mosaic of xerophytic-degraded dry forest with Myrtaceae. This period from AD 1950 until 2010 (LNG_3) was

characterized by an increase in dry forest taxa, especially those associated with an adaptation to drought (also called xerophytic taxa), and herbaceous taxa. Xerophytes were relatively abundant with a mean of $3 \pm 2\%$ in this period. Taxa such as *Securinega*, *Acalypha*, and *Phyllanthus* reached their maximum (2, 2, and 3%, respectively) around AD 2000. Some taxa that characterise dry forest (e.g. Fabaceae) showed an increasing rate of $3 \pm 1\%$ and reached their maximum at the present time (AD 2010, 4%). In addition, other trees such as Moraceae ($2 \pm 1\%$), including *Ficus* ($2 \pm 1\%$) and *Celtis* ($3 \pm 1\%$), had higher relative abundances during this period. However, other trees showed a decrease in proportion compared to the previous period. For example, the *Gnidia* type decreased from $3 \pm 2\%$ to $2 \pm 1\%$ and Arecaceae decreased from $7 \pm 2\%$ to $5 \pm 2\%$ at the present (AD 2010). Myrtaceae (3%) increased during this period while those previously classified as riverine (e.g. *Podocarpus* and *Pandanus*) decreased and became traces. For the herbaceous group, Poaceae decreased to $52 \pm 8\%$ in comparison with the previous period ($58 \pm 8\%$) but taxa such as Asteraceae cf. *Ambrosia* type became abundant with a mean of $4 \pm 3\%$ and peaked at the surface sample representing the present period (9%). This also applies to the Menispermaceae type which increased and reached its maximum in this zone ($2 \pm 2\%$). This period had the highest proportion of aquatics in the last 2000 years ($29 \pm 20\%$). This high rate is associated with a substantial increase in *Typha* surrounding the wetland reaching its highest value of 46% at AD 2000. The appearance of other aquatic taxa was recorded during this period, such as *Polygonium* and Onagraceae type (cf. *Ludwigia*), however, Cyperaceae remained relatively low ($4 \pm 2\%$). A significant decrease in the isotope value during the period was also recorded from -24 to -25% .

Pollen rarefaction, detrended pollen richness, and compositional turnover

Pollen rarefaction and detrended pollen richness showed the variation of pollen diversity within LNG over time, which was associated with compositional turnover (beta diversity) in the area (Figure 3). A maximum and minimum pollen richness of 33 and 23 pollen types was recorded around AD 1810 and AD 2010, respectively. The mean value across the entire core was 28 ± 2 pollen types. Three maximum turnovers of taxa around Lake Longiza were recorded in each zone associated with a reduction in pollen richness. The first zone showed the maximum change in composition for the entire period recorded around AD 830 with a value of around 3 Standard Deviation (SD) which marked a decrease in richness from 31 to 24 pollen types. During this period, taxa such as *Acalypha*, *Gnidia*, *Phyllanthus*, *Securinega*, and Fabaceae became scarce. A short recovery of the richness was recorded around AD 920 after which another turnover of 2 SD was recorded around AD 1370 in the second zone. The last zone (LNG_3) was marked by a decrease in pollen richness and was reflected in the compositional turnover of 2 SD around AD 1950. By the end of this zone (the near present period), several taxa in the dry forest tree group, such as *Dichrostachys*, *Trema*, *Securinega*, Arecaceae, and Malvaceae, became present only in trace quantities. All taxa from the riverine trees group also decreased significantly or became scarce.

Charcoal and coprophilous spore records from Lake Longiza in the last 2000 years

A total of $139,112 \text{ cm}^2$ of microcharcoal and 2752 particles of macrocharcoal with a mean of $632 \pm 563 \text{ cm}^2 \text{ cm}^{-3}$ and $120 \pm 111 \text{ particles cm}^{-3}$, respectively, were counted. The highest value of microcharcoal was recorded around AD 1910 (approximately $1910.8 \text{ cm}^2 \text{ cm}^{-3}$) and the lowest was recorded at AD 830 ($87 \text{ cm}^2 \text{ cm}^{-3}$; Figure 3). In contrast, the highest value of

macrocharcoal was recorded around AD 1560 ($364 \text{ particles cm}^{-3}$) and the lowest around AD 1370 ($8 \text{ particles cm}^{-3}$). The abundance of macrocharcoal and microcharcoal was not correlated ($R=0.2$, $p=0.36$) indicating that charcoal breakdown was minimal during the pre-treatment process, suggesting that they originated from different sources. Coprophilous spores increased significantly since the beginning of the record leading to a concentration of about $6000 \text{ spores cm}^{-3}$ at the present period. For individual spore concentrations, *Sordaria* dominated throughout the length of the core with its maximum concentration occurring in AD 2000 ($1289 \text{ spores cm}^{-3}$) and in AD 2010 ($4894 \text{ spores cm}^{-3}$) and the lowest around AD 1850 ($65 \text{ spores cm}^{-3}$). *Coniochaeta* spores remained relatively low fluctuating over time but reached its maximum concentration of $2123 \text{ spores cm}^{-3}$ in AD 2000. All other spore types (*Podospora*, *Gelasinospora*, and *Sporormiella*) remained relatively low throughout the time covered by the core. *Sporormiella* spores were found only around AD 1370 with a concentration of $66 \text{ spores cm}^{-3}$. The correlation between microcharcoal and spore concentration was positively significant ($R=0.55$, $p < 0.05$), as was the relationship between macrocharcoal and spore concentration ($R=0.51$, $p < 0.05$).

Following the period of vegetation shift, the charcoal and spore record of the three main periods is as follows (Figure 3):

From 220 BC to AD 1150 (LNG_1) a very low charcoal influx was evident, containing $<2 \text{ particles yr}^{-1}$ of macrocharcoal and a mean of $3 \pm 2 \text{ cm}^2 \text{ yr}^{-1}$ of microcharcoal. The spore concentration was also relatively low, with its lowest concentration of 195 cm^{-3} occurring in AD 90. However, there was a slight peak in spore concentration of 598 cm^{-3} at AD 830. From AD 1150 to 1950 (LNG_2) charcoal influx and abundance increased. At the beginning of this period, there were small consecutive peaks of an influx of $11 \text{ cm}^2 \text{ yr}^{-1}$ and $2 \text{ particles yr}^{-1}$ around AD 1370 and AD 1560 in microcharcoal and macrocharcoal, respectively. This was followed by two large peaks around AD 1880 and AD 1900 in microcharcoal and macrocharcoal. Peaks in spore concentration were also recorded at similar periods in AD 1500 (1089 cm^{-3}) and increased in concentration from 328 cm^{-3} in AD 1900 to 1307 cm^{-3} in AD 1940. However, spore concentration remained relatively low during this period even though there are some small fluctuations within this zone. The minimum value for this zone is $129 \text{ spores cm}^{-3}$ which was recorded in AD 1710. The last period from AD 1960 to 2010 (LNG_3) presented the highest concentration of charcoal around the lake with a mean of $252 \pm 146 \text{ cm}^2 \text{ yr}^{-1}$ for microcharcoal and $39 \pm 30 \text{ particles yr}^{-1}$ for macrocharcoal, with a steep increase in spore concentration. The minimum spore value was recorded in AD 1960 ($1912 \text{ spores cm}^{-3}$) and the maximum spore was recorded in AD 2010 ($5139 \text{ spores cm}^{-3}$).

Discussion

Vegetation change, fire history, and herbivory in southwest Madagascar during the last 2000 years

The 2000-year pollen record of the LNG sediment core extracted from Lake Longiza, presented taxa associated with dry forest, riparian forest, herbaceous taxa, and grass which were present throughout the whole period, suggesting the presence of a mosaic of vegetation in the area over time (Figure 4). This suggests the presence of patches of forest in a matrix of more open vegetation. This mosaic landscape reflects the biologically and physically heterogeneous nature of the modern landscape in southwest Madagascar (Callmander et al., 2013; Cornet and

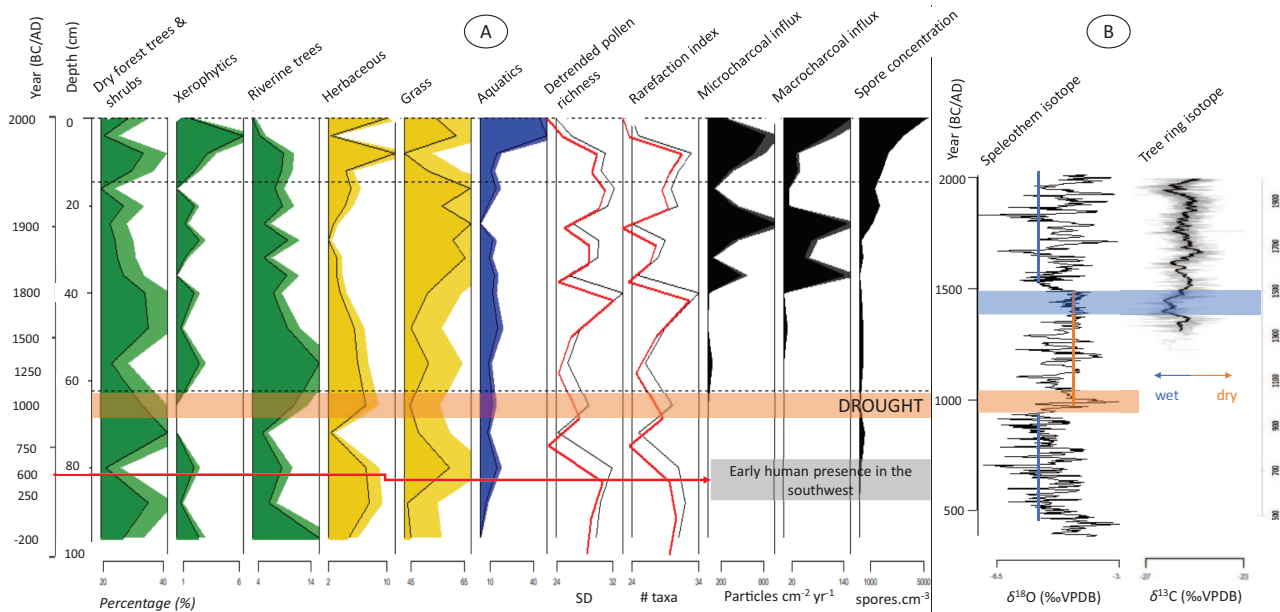


Figure 4. Environmental change in southwest Madagascar during the late Holocene with the recorded island-wide drought and suggested time of human presence in the region. (A) The left panel shows the cumulative changes in major ecological affiliations of the taxa from Lake Longiza pollen records with two times exaggeration along with the diversity, sediment carbon isotope, charcoal influx, and coprophilous spore concentrations generated through this study. (B) The right panel represents a published rainfall record from $\delta^{18}\text{O}$ speleothem at Anjohibe Cave in the northwest region covering the last 1700 years (Scroxton et al., 2017) with horizontal lines showing the 500-year dry (orange) and wet (blue) phases plotted and the tree ring $\delta^{13}\text{C}$ showing a succession of wet and dry periods over the last 700 years (Razanatsoa, 2019).

Guillaumet, 1976; Du Puy and Moat, 1996; Grubb, 2003; Moat and Smith, 2007; World Wildlife Fund [WWF], 2001) that facilitates a diverse array of taxa (Kindvall, 1996; Oliver et al., 2015; Watt, 1947). Such a record of vegetation alongside charcoal, dung fungal spores and existing regional climate records (Razanatsoa, 2019; Razanatsoa et al., 2021a; Scroxton et al., 2017) allows us to investigate the response of the tropical dry forest during the Late-Holocene to rainfall variability and land-use from fire and pastoralism.

From BC 200 Until AD 900: Climate as a driver of vegetation change. Based on palaeoclimatic records, as well as the low abundance of anthropogenic indicators, it seems likely that variability of rainfall is the main driver of vegetation change from the beginning of the record around BC 200 up until AD 900. The low rainfall during a long dry period recorded until AD 500 in the speleothems' oxygen isotope (Scroxton et al., 2017) probably led to the increase in the abundance of xerophytic taxa recorded around AD 620. Xerophytic taxa establish themselves predominantly during dry periods and are currently a major component of the dry forest in southwest Madagascar (Grubb, 2003; Sussman and Rakotozafy, 1994). There was also an increase in Poaceae confirmed by the less negative soil carbon isotope results, suggesting a C_4 -dominated landscape during a period with very low presence of charcoal and spores. This indicates that fire and herbivory activities were not dominant at this site during this period despite archaeological evidence of human presence and activities in the region starting around AD 650 (Anderson et al., 2018; Burney, 1987; Burney et al., 2004; Dewar et al., 2013; Douglass et al., 2018; Perez et al., 2005).

Evidence from other sites in the southwest suggested the expansion of xerophilous thickets and the contraction of woodland vegetation in the Late-Holocene, which coincided with the drying trend of the climate since the Mid-Holocene (Burney, 1993; Burns et al., 2016; Clarke et al., 2006; Vallet-Coulomb et al., 2006; Virah-Sawmy et al., 2016). This was also associated by an opening of ecosystems with increased

grass abundance, for example, as illustrated by a pollen record from the spiny thickets at Fiherenana-Manombo complex, which is a site located further south of Lake Longiza around AD 350 (Virah-Sawmy et al., 2016). These findings suggest that climate may have affected the vegetation structure during this period, and led to an increase in xerophytic taxa across the region.

After a wet period of about 400 years spanning from ~AD 500 to ~AD 900 (identified in the speleothem record, Scroxton et al., 2017), dry forest trees recovered slowly, and the landscape became dominated by C_3 plants at around ~AD 830 coinciding with a peak in trees and shrubs such as *Acacia*, *Ficus*, and *Areaceae* in the pollen record. This recovery of C_3 plants was similarly observed in the dry forest in the northwest region around AD 795 (1155 cal years BP) and AD 870 (1080 cal years BP) (Burns et al., 2016; Voarintsoa et al., 2017a). In these studies, the recovery in the northwest vegetation was attributed to the wet period from the relative position of the Intertropical Convergence Zone (ITCZ) (Scroxton et al., 2017; Voarintsoa et al., 2017a) which could have brought rainfall to the southwest region. During this period, there was a slight increase in charcoal and coprophilous spores around AD 830, which may suggest that the earliest presence of humans in the area surrounding the site practiced foraging activities. Other findings from the region have shown the earliest presence in southwest Madagascar occurred around AD 600 (Anderson et al., 2018). Such presence, however, has not affected the ecosystem surrounding Lake Longiza, similar to the changes recorded at Tsizavatsy which is located further south where the only forager communities in southwest Madagascar live. Palaeoecological data from their region suggested that foraging activities alone did not lead to massive changes in the vegetation (Razanatsoa et al., 2021a). Instead, it was the combination of these practices (such as pastoralism) and drying of the area that led to the opening of the ecosystem (Razanatsoa et al., 2021a; 2021b). The findings from Lake Longiza suggest the presence of earlier communities in the region practiced foraging activities starting around AD 600 until the end of the first millennium AD and that occurred while a

recovery of dry forest trees was recorded. This suggests that at least until AD 900, the vegetation responded solely to climate variation. Although human practices linked to foraging might have already existed in the area, they appear to have had a negligible effect on vegetation at this time.

From ~AD 900 until ~AD 1600: Vegetation change favored by dry periods and maintained by a shift to agropastoralism. After the climate effect was recorded on the vegetation until AD 900, there was a rapid transition into a more open landscape with reduced diversity at Lake Longiza. A shift in the vegetation was evident in the pollen records by the high prevalence of Poaceae, low prevalence of dry forest and riparian taxa, and a decrease in C₃ plants in the sediment isotope record. These changes coincided with the start of the dry periods recorded around AD 950–1000 (Scroton et al., 2017) leading to the opening of the ecosystem and reduction of dry forest taxa. However, despite the return into relatively wetter conditions in the region around AD 1300 (Razanatsoa, 2019; Scroton et al., 2017), the vegetation remained open. This coincided with the onset of massive charcoal influx and several spore concentration peaks recorded AD 1370 until AD 1570 which might suggest a shift in subsistence activities by the occupants in the region from foraging to agropastoralism, the latter which would involve burning and clearing of vegetation to improve forage quality and quantity. The practice of agropastoralism was suggested to have been introduced into the western region of Madagascar around AD 750 (1200 cal years BP) (Beaujard, 2012; Blench, 2008; Burney, 1987) and has possibly reached the surrounds of Lake Longiza a few centuries later. A shift in subsistence from foraging to more established agropastoralism activities and clearing for new lands potentially affected the vegetation leading to the opening and reduced abundance of dry forest.

Opening of the mosaic ecosystem was also recorded in other regions across Madagascar around the same period and were associated with human activities. From Andolononby, south of the study site, floral extinctions were recorded from ~AD 350 to 1250 (1600–700 cal years BP), simultaneously with a charcoal peak that was interpreted as the presence of agropastoralism using fire (Virah-Sawmy et al., 2016). In the northwest, the gradual change in vegetation around AD 870–1130 was suggested to be associated with shifting cultivation (Voarintsoa et al., 2017a) and a shift in subsistence (Godfrey et al., 2019). In the east, massive forest clearing occurred around AD 700–1100 (Agarwal et al., 2005). A similar gradual change in the structure of the ecosystem toward more open vegetation was recorded in the savanna woodland at Lake Tsizavatsy (Razanatsoa et al., 2021a). These suggest that although the climate initially affected the change in the vegetation as evidenced by an increase in grass and a decrease in riverine and dry forest tree taxa, it was maintained by human activities by the change in subsistence from foraging to pastoralism as indicated by the increase in herbivory and fire activities at least until AD 1600.

From ~AD 1800: Interacting effect of human activities and climate. The landscape appears to have been heavily impacted by human land-use and rainfall variability from the early 19th century. This is reflected in the high abundance of grass, pioneer species, and xerophytic taxa, as well as corresponding changes in the sediment carbon isotope ratio and increase in aquatics in the pollen record. From AD 1810, there is a massive influx of charcoal and spore reflecting high fire occurrence combined with increased herbivory in the record. Sudden peaks of charcoal in the sediment core have been interpreted as a past human land-use proxy (Burney, 1987; Dewar et al., 2013; Virah-Sawmy et al., 2016) while coprophilous fungus spores were associated with pastoral activities (Cugny et al., 2010; Doyen and Etienne,

2017; Gelorini et al., 2012; Guillemot et al., 2015; López-Sáez and López-Merino, 2007; Van Geel et al., 2003). The strong positive correlation between charcoal and dung fungal spore records from this core at Lake Longiza suggests that changes in the fire regime were influenced by anthropogenic, rather than climatic, drivers. The changes in the vegetation were particularly important around AD 1900. The high fire occurrence is possibly linked to the increase in agricultural activities especially through the practice of *hatsake* (swidden agriculture) during the international trade that occurred in the early 20th century (Fauroux, 2001). Since the area around Lake Longiza contains more fertile, alluvial soils with a higher carbon content, and higher water availability, this favored agricultural practice and human settlements (Raharimalala et al., 2010; Scales, 2011; Smith et al., 1997). Such a change in the ecosystem is reflected in the component of the pollen record where the ecosystem became dominated by taxa such as Myrtaceae possibly with taxa that are introduced such as cf. *Eucalyptus* and cf. *Psidium*, and Asteraceae (cf. *Ambrosia*) which are abundant in degraded vegetation in Madagascar today (Koechlin et al., 1974). Also, forest clearing and burning practices are widely used in the region and were suggested to be responsible for the decline and degradation of the riverine ecosystem along the Mangoky River (Vallet-Coulomb et al., 2006). Such practices explain the current state of the ecosystem with patches of rice fields and degraded forest and savanna woodland. These suggest an increasing human impact on the ecosystem associated with the expansion of agricultural and pastoralism around the Lake Longiza.

Palaeoecological records from the Lake Tsizavatsy, near the Mikea forager communities located further south of the Lake Longiza, presented a higher effect of desiccation and low changes in human activities (Razanatsoa et al., 2021a). This is because of the less fertile soils, the foraging livelihood of its occupants and the more arid climate recorded in the region (Razanatsoa, 2019). This site presented a high abundance of xerophytic taxa in the pollen record of the savanna woodland around AD 1910 which was also recorded at Lake Longiza. The increase in xerophytic taxa at these sites in the 20th century demonstrates a response of the ecosystem to the increasing dry periods and the shorter duration of wet periods associated with anthropogenic warming of the 20th century (Razanatsoa, 2019; Scroton et al., 2017; Thomas et al., 2004). Based on these records, we found that human land-use, through agropastoralist activities including shifting cultivation and pastoralism, and climate, through drying, reduced the tree abundance, and increased grasses and xerophytes of the vegetation in the region since the 20th century. This indicates the impact of both factors on the structure and composition of the community over time.

Conclusion

This paper provides new evidence on the environmental changes that occurred in Madagascar during the Late-Holocene and has shed light on the interacting effects of climate and human activities on the tropical dry forest of the southwest. Pollen and carbon isotope records from Lake Longiza indicate that the tropical dry forest in the southwest was a mosaic of dry and riparian forests during the last 2000 years which became increasingly open with decreasing species richness and a reduction of woodland/forest elements over time. An in-depth analysis of the drivers of these changes revealed consecutive or simultaneous effects between climate and human activities especially the shift in subsistence from foraging to pastoralism and agriculture.

From BC 200 to AD 900, rainfall variability was the main driver of vegetation change with alternating drier and wetter conditions causing variation in the abundance of dry-adapted taxa, grass, and deciduous trees, as reflected in the isotope record of the

sediment. The landscape around Longiza was dominated by C_4 grassland from AD 620 until AD 830, when wetter conditions led to an increase in the dominance of C_3 plants, associated with the slow recovery of dry forest trees.

A combined influence between climate and anthropogenic drivers was recorded from around AD 950. Dry conditions followed by the shift in subsistence from foraging to pastoralism around AD 1300 as indicated by the increase in spore concentration, led to the transition from dry forest dominated into a more open landscape marked by a high prevalence of Poaceae, a low prevalence of dry forest and riverine ecosystems, and the overall reduction in plant diversity, reflected in the pollen rarefaction analysis.

In the 19th and 20th centuries, the influence between climate and anthropogenic factors were recorded. A transformation of the landscape associated with charcoal peaks and increasing spore concentration suggests a burnt landscape the result of agropastoralism. However, an increase in dry-adapted taxa was recorded in the pollen records in the last 2000 years possibly associated with the drying of precipitation over the last millennia. These simultaneous effects of both rainfall and anthropogenic activities on the ecosystem since the 20th century was associated with reduced biodiversity as seen in the decrease in taxa richness.

Though the abundance of forest elements changed over time, none were lost, suggesting that thresholds of resilience have not been exceeded. However, the trend of declining diversity suggests that if current trends continue, there may be an internal re-organization, involving the loss of mosaic elements requiring higher water availability and an increase in disturbance-adapted taxa. Further investigation should focus on the ecological function and resilience of the tropical dry forest ecosystem to these drivers to help inform existing conservation strategies of areas in the south-west where drought frequency and increasing anthropogenic disturbance are increasing. Specifically, the conservation of vegetation heterogeneity, and hence landscape resilience, might require restoration or protection of wooded and forest elements that might otherwise be converted to grassland due to the combined effects of aridification and human activities.

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