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Influence of Late Holocene Climate Change and Human Land Use on Terrestrial and Aquatic Ecosystems in Southwest Madagascar

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Madagascar's biota underwent substantial change following human colonization of the island in the Late Holocene. The timing of human arrival and its role in the extinction of megafauna have received considerable attention. However, the impacts of human activities on regional ecosystems remain poorly studied. Here, we focus on reconstructing changes in the composition of terrestrial and aquatic ecosystems to evaluate the impact of human land use and climate variability. We conducted a paleoenvironmental study, using a sediment record that spans the last ~1,145 years, collected from a lakebed in the Namonte Basin of southwest Madagascar. We examined physical (X-ray fluorescence and stratigraphy) and biotic indicators (pollen, diatoms and micro- and macro-charcoal particles) to infer terrestrial and aquatic ecosystem change. The fossil pollen data indicate that composition of grasslands and dry deciduous forest in the region remained relatively stable during an arid event associated with northward displacement of the Intertropical Convergence Zone (ITCZ) between ~1,145 and 555 calibrated calendar years before present (cal yr BP). Charcoal particles indicate that widespread fires occurred in the region, resulting from a combination of climate drivers and human agency during the entire span covered by the paleorecord. Following settlement by pastoral communities and the disappearance of endemic megafauna ~1,000 cal yr BP, grasslands expanded and the abundance of trees that rely on large animals for seed dispersal gradually declined. A reduction in the abundance of pollen taxa characteristic of dry forest coincided with an abrupt increase in charcoal particles between ~230 and 35 cal yr BP, when agro-pastoral communities immigrated into the region. Deforestation and soil erosion, indicated by a relatively rapid sedimentation rate and high K/Zr and Fe/Zr, intensified between 180 and 70 cal yr BP and caused a consequent increase in lake turbidity, resulting in more rapid turnover of the aquatic diatom community. Land use and ongoing climate change have continued to transform local terrestrial and freshwater ecosystems during the last ∼70 years. The current composition of terrestrial and aquatic ecosystems reflects the legacy of extinction of native biota, invasion of exotic species, and diminished use of traditional land management practices.

Keywords: agro-pastoralists, environmental change, dry deciduous forest, aquatic ecosystems, herbivore introductions, socio-ecological systems

INTRODUCTION

Remote islands of the southwestern Indian Ocean were among the last regions worldwide to be permanently colonized by humans. Human settlement and land use practices, which invariably involve non-native plants and animals, may contribute to loss of endemic biota and transformation of native ecosystems (Douglass and Zinke, 2015; Wang et al., 2019). On Madagascar, people hunted endemic fauna (Perez et al., 2005; Anderson et al., 2018), introduced domesticated animals and plants (Crowther et al., 2016; Hixon et al., 2021a), and promoted the expansion of grasslands (Burney, 1987b; Burns et al., 2016). The timing of human arrival and contribution of hunting to faunal extinctions on Madagascar have received considerable attention (Crowley, 2010; Feranec et al., 2011; Douglass et al., 2019a). The direct and indirect impacts of anthropogenic activities on the composition and function of terrestrial and aquatic ecosystems are a subject of ongoing research. Only recently have studies begun to focus on the long-term consequences of human activities on Madagascar's ecosystems (Virah-Sawmy et al., 2010, 2016; Burns et al., 2016). Integration of paleoecological, archaeological, and historical information provides a long-term perspective to assess the timing and socio-ecological consequences of human disturbance on such insular ecosystems (Douglass and Cooper, 2020).

The timing of the peopling of Madagascar has been widely debated (Crowley, 2010; Anderson et al., 2018; Hansford et al., 2018; Lawler, 2018; Douglass et al., 2019a; Mitchell, 2020; Hixon et al., 2021a). However, a growing body of archaeological research suggests that foraging communities had settled the island permanently by ∼1,500 cal yr BP, several centuries before a pulse of faunal extinctions that included giant lemurs, pygmy hippos, giant tortoises, and elephant birds (Douglass and Zinke, 2015; Douglass et al., 2019a). Human subsistence strategies later diversified, as evidenced by the coincident spread of southeast Asian crops and pastoralism, beginning by around 1,000 years ago (Crowther et al., 2016; Godfrey and Crowley, 2016; Hixon et al., 2021a). The emergence of agro-pastoral economies involved the introduction of animals such as zebu cattle (*Bos taurus indicus*), sheep (*Ovis aries*), and goats (*Capra hircus*), as well as cultigens like rice, greater yam, coconut, and Indian saffron during the last millennium (Burney et al., 2004; Kull et al., 2012; Beaujard, 2017).

Contemporary Malagasy people rely on a range of ecosystems. People typically use grasslands and succulent woodlands to fodder livestock and exploit forests for hunting and as sources of firewood, construction materials, and edible and medicinal plants (Bloesch, 1999; Kaufmann and Tsirahamba, 2006; Kull and Laris, 2009; Fritz-Vietta et al., 2017). Lakes and wetlands also constitute important sources of animal protein and drinking water, and anthropogenic disturbances have degraded these ecosystems and threatened aquatic biodiversity (Bamford et al., 2017). Although fire is the leading cause of past forest degradation and loss (Kull, 2000), paleoenvironmental data suggest that wildfires and fire-adapted vegetation were common even before the expansion of human populations on the island (Virah-Sawmy, 2009; Godfrey and Crowley, 2016). Today, Madagascar's biodiversity is increasingly threatened by intensifying land use practices (*e.g.,* deforestation, charcoal production, shifting cultivation, and industrial mining) and the climate crisis (Spencer et al., 2005; Hannah et al., 2008; Goodman et al., 2018). Interactions between land use and climate change have important socio-ecological impacts, including biodiversity loss, ecosystem degradation, pollution, disruption of traditional lifeways, and conflicts over natural resources (Scott et al., 2006; Virah-Sawmy et al., 2009; Harvey et al., 2014; Douglass and Cooper, 2020).

Climate change and human activities have also shaped Madagascar's vegetation. Paleoecological reconstructions have shown, for example, that *Erica-Myrica* heath/grasslands replaced *Uapaca* woodlands during the last 950 years in coastal southeast Madagascar due to marine surges, reduced precipitation, and anthropogenic fires (Virah-Sawmy et al., 2009). In contrast, the vegetation around Andolonomby/Ambolisatra in the coastal southwest transitioned from a palm-savanna to depauperate, xerophytic bush ∼700 cal yr BP, during a period of intensified burning and a possible drought event (Virah-Sawmy et al., 2016). Multiple studies have shown that (1) northwest Madagascar was wetter and relatively forested during the Early and Middle Holocene, (2) grasslands expanded during the onset of drier conditions ∼1,000 years ago, and (3) human activities promoted the establishment of fire-adapted trees and ruderal herbs ∼500 years ago (Burney, 1987a,b; Matsumoto and Burney, 1994; Burney et al., 1997; Crowley and Samonds, 2013; Burns et al., 2016; Wang et al., 2019).

We assessed the long-term consequences of climate variability and anthropogenic impacts on the composition of terrestrial vegetation and aquatic ecosystems in southwest Madagascar. Specifically, we used a 1,145-year sediment record from a lake in the Namonte Basin to evaluate responses in aquatic and terrestrial ecosystems to Late Holocene drought, the spread of pastoralism, the extinction of endemic fauna, and recent intensification of forest clearance. We examined physical (X-ray fluorescence and stratigraphy) and biotic indicators (pollen, diatoms and micro- and macro-charcoal particles) in the sediment record to explore past terrestrial and aquatic ecosystem change. Integration of paleoecological, archaeological, and historical data is crucial for developing holistic perspectives on the timing and socio-ecological consequences of human land use in insular ecosystems (Braje et al., 2017; Douglass et al., 2019b). The following research questions were tested in this study: (a) Did increasing fire frequency during dry/wet periods induce changes in vegetation composition? (b) How did excess detrital and organic matter, produced by anthropogenic deforestation and forest burning, affect the aquatic ecosystem? and c) What were the impacts of extinction of large seed dispersers on vegetation?

MATERIALS AND METHODS

Study Area

The Namonte Basin (S 22.12513°, E 43.40634°; ∼30 m asl; **Figure 1A**) is comprised of a system of seasonal and permanent lakes and floodplains in the lowlands of the Mangoky-Ihotry complex in southwest Madagascar. The main chain of lake basins has an area of ∼13 km^2 and a catchment area that is ∼2,000 km^2. However, these lake basins are shallow (maximum water depth up to ∼1.4 m deep in September, 2017), and their areas fluctuate considerably with interannual variation in rainfall. For example, during a 1997–98 drought (100 mm total annual precipitation), the lakes approached desiccation, but during a wet interval in 1999–2000 (1,500 mm annual precipitation), the lakes expanded into the surrounding forest (Tucker, 2020). In 2017, the lake was fresh (conductivity of 261 μS/cm) and mesotrophic. The modern climate is semi-arid, with a mean temperature of 23°C and annual precipitation < 400 mm, which falls mostly during the austral summer (November – March) (Dewar and Richard, 2007). The sandy substrate of Quaternary alluvium in this area includes both active and vegetated dunes.

The landscape is generally characterized by a mosaic of wooded grasslands, dry deciduous and riverine forests, and mangroves that grow near estuaries. The dry deciduous forest is dominated by several plant species, including the endemic family Didiereaceae, the fony baobab tree (*Adansonia fony*), several species of *Euphorbia*, and *Pachypodium geayi* (Grubb, 2003; Aronson et al., 2018). The region is also habitat for several endemic primates, including the ring-tailed lemur *(Lemur catta),* Verreaux's sifaka (*Propithecus verreauxi*), and the reddish-gray mouse lemur (*Microcebus griseorufus*). Other endemic species with restricted distributions include Grandidier's mongoose (*Galidictis grandidieri*) and the Madagascar radiated tortoise (*Geochelone radiata*) (Scott et al., 2006). The Mikea Forest is part of a vegetation mosaic in southwest Madagascar that refers specifically to the dry forest between the urban centers of Toliara and Morombe (Seddon et al., 2000). The northern portion of this forest surrounds the Namonte Basin and has been part of the Mikea National Park since 2012.

Mikea people descend from herding clans settled in the area during the 17th century to escape banditry and oppression by the Maroseragna and Andrevola kings (Tucker et al., 2015). In the late 19th century, the area came under French colonial control, and much of the coastal plains to the east have since been used to produce a variety of cash crops such as maize, cotton, and butterbeans (Blanc-Pamard et al., 2005). Currently, most Mikea living in the Namonte Basin reside in villages that are usually located near lake margins, where they fish, cultivate crops, and herd zebu and goats. Mikea complement their diet with a range of forest products, including wild tubers (*Dioscorea, Colocasia, Ipomoea,* and *Tacca*), honey, and wild meat (*e.g.*, birds, tortoises, tenrecs and feral cats; Tucker, 2007; Douglass and Rasolondrainy, 2021). Deforestation has intensified greatly since the 1970s, with ∼55% of the primary forest lost between 1949 and 2004 (Blanc-Pamard et al., 2005).

Sediment Sampling and Processing

In 2017, a 138-cm-long composite sediment core was retrieved in the deepest part of the Namonte basin (**Figure 1B**). A large-diameter (7 cm ID) mud-water interface piston-corer (Fisher et al., 1992) was used for the collection of upper deposits and a Colinvaux-Vohnout-type corer, modified to use clear polycarbonate core barrels (5.4 cm ID), was used for deeper deposits. Unconsolidated upper deposits were maintained in a vertical orientation and extruded in the field at 2-cm intervals. The sediment core was shipped to the University of Florida (UF), where the deeper portion was split lengthwise and photographed. Samples were then shipped to Pennsylvania State University (PSU) for X-ray fluorescence (XRF), pollen, and charcoal analysis, and to the University of Regina (UR) for diatom analysis. The stratigraphy of the sediment core was characterized based on field observations and lab-acquired digital photographs. Elemental data were produced from XRF scans at 3-cm core intervals, using an Olympus DeltaX model X-ray fluorescence core scanner and Geotek MSCL 7.9 Multi-sensor Core Scanner Innoux 1776 at PSU.

A core chronology was constructed using ^{14}C accelerator mass spectrometry (AMS) dates on five samples of terrestrial plant material (*i.e.,* seeds, charcoal fragments and fragments of plant remains). Samples were pretreated following the protocol of Kennett et al. (2014) and dated at the Radiocarbon Laboratory at PSU. Radiocarbon dates were calibrated using the Southern Hemisphere calibration curve SHCAL20 (Hogg et al., 2020). For the topmost (recent) section of the core, ^{14}C ages were calibrated using the post-bomb (SH 1-2 zone) dataset (Hua et al., 2013). Two dates, PSUAMS-6324 and PSUAMS-6325, were excluded from the age-depth model, as they contain modern (post-bomb) carbon and likely indicate translocation of recent plant material to greater depth during the coring process. Radiocarbon dates were used to generate a Bayesian age-depth model with the rbacon package (v. 2 3.3) for R (Blaauw and Christen, 2011), using default parameters [accumulation rate (acc.mean) = 10 year cm^{-1}, shape distribution of accumulation rate (acc.shape) = 1.5, memory mean (mem.mean) = 0.7, memory strength (mem.strength) = 4] to the full depth of the core. The model was built under the assumption that the top of the sequence corresponds to the year of core retrieval (2017 CE).

The sediment core was subsampled for pollen and spores, microcharcoal, and diatom analysis at 4-cm intervals. Pollen, spores, and microscopic charcoal sample preparation followed standard protocols, including treatment with hydrofluoric acid and acetolysis (Faegri and Iversen, 1989). A tablet of exotic *Lycopodium* spores was added to each sample to

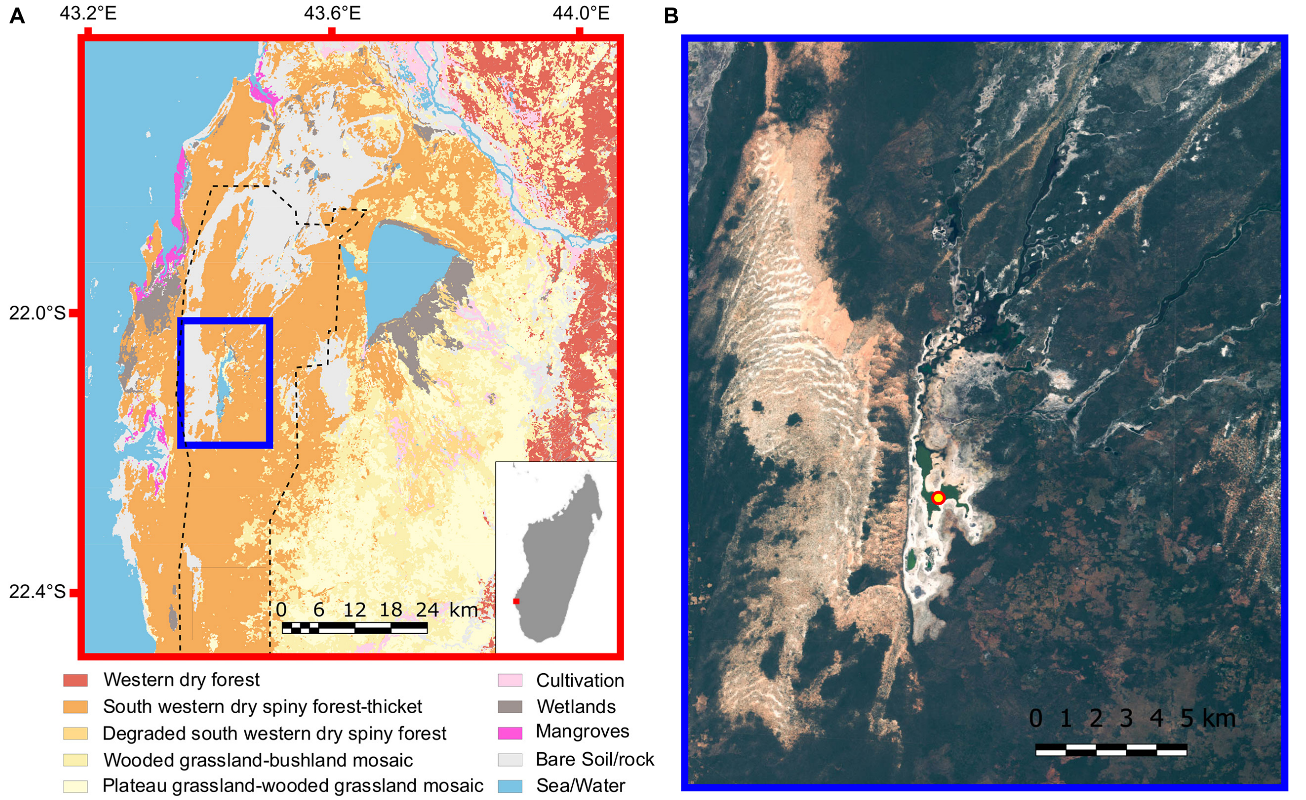

FIGURE 1 | (A) Vegetation map showing the Namonte Basin, circumscribed by the blue rectangle. Inset shows the island of Madagascar, with the red dot in the southwest indicating the study area location. The vegetation map was modified from the Madagascar Vegetation Mapping Project (www.vegmad.org). Extent of the Mikea National Park is marked with a dashed line and includes primarily dry forest (orange). **(B)** Sentinel 2 satellite image of the outlined blue area in **(A)**, showing the region of Namonte, SW Madagascar. The coring site is marked with a red and yellow circle in a portion of the Namonte Basin known as Andramby.

calculate pollen concentration and pollen influx. A total of 36 samples were analyzed for pollen and fungal spores. In each sample, we identified at least 300 pollen grains if possible, excluding aquatic taxa. Pollen grains and fungal spores were identified using the reference collection at PSU and palynological atlases and keys (Gosling et al., 2013; Schüler and Hemp, 2016). To assess temporal changes in pollen taxa that may be correlated with megafaunal extinctions, we assigned a seed dispersal mechanism to each terrestrial pollen taxon as defined by Albert-Daviaud et al. (2020). We grouped plant taxa based on their mode of seed dispersal (*e.g.,* autochorous = self-dispersed by dehiscent fruits, anemochorous = wind-dispersed, or zoochorous = animal-dispersed) (Knowles et al., 1995).

Microcharcoal (15–150 μm) concentrations were determined in the same samples used for pollen analysis. Microcharcoal particles and *Lycopodium* spores were quantified by randomly selecting 200 fields of view in each sample under 40× magnification. Each particle was characterized as woody or herbaceous based on morphology, including presence of stomata, epidermal cells, and an elongated shape (Walsh et al., 2014). Microcharcoal particles are presented as microcharcoal influx, calculated using charcoal concentrations and bulk sedimentation rates derived from the age-depth model.

For macroscopic charcoal analysis from 30 cm to the bottom of the core, continuous sediment subsamples (0.5 cm^3) were retrieved. Samples were processed following the protocol of Mooney and Radford (2001). The remaining fraction was photographed using a digital camera attached to an Olympus microscope. ImageJ software[1] was used to process sample images, quantify the total number of charcoal particles, and estimate total area of each charcoal particle (Halsall et al., 2018). Macrocharcoal was expressed as macrocharcoal influx (particles cm^{-2} yr^{-1}) and macrocharcoal area (mm^2 cm^{-2} yr^{-1}) based on concentration, total area of charcoal particles, and bulk sediment accumulation rate at specific depths.

For diatom analysis, 0.2–0.5 g of dry sediment was processed following the protocol of Battarbee (1986). Permanent slides were mounted in Zrax (RI ~1.7 +). At least 400 valves in each sample were counted. Diatom species were grouped according to ecological guilds and motility into High Profile (HP), High Profile Planktonic (HPP), Low Profile (LP) and Motile Profile (MP), following Passy (2007) and Berthon et al. (2011) (**Supplementary Material 4**). Although most of the studies on diatom functional groups and disturbance have been conducted in rivers and streams, the multi-proxy analyses

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[1] https://imagej.nih.gov/ij/index.html

presented in Velez et al. (2021) showed that they can be used to identify anthropogenic disturbances, including drainage and deforestation, with the consequent changes in water level, water transparency and macrophyte cover. These guilds reflect the forms and life habits of diatoms that are adaptations to particular physical (currents, turbidity) and chemical (nutrients) conditions (Leira et al., 2015; Algarte et al., 2016). Large and colonial forms are included in the HP, short or low-stature species are included in LP, and MP include species that can move. Motile species are very useful to infer physical disturbance such as an increase in water turbidity, shading and burial from excess sediment input (Jones et al., 2014).

Data Analysis

Total pollen sum, excluding aquatics, and total diatom sum were used to calculate the relative abundances of each taxon in each group, respectively, which are presented as percentages. Pollen and diatom diagrams were created using Tilia software (Grimm, 1991). Zones representing thresholds of change in pollen and diatom composition were identified using stratigraphically constrained incremental sum of square clustering (CONISS) (Grimm, 1987). To assess changes in the abundance of plant taxa assigned to a specific seed dispersal mechanism, pollen percentages were normalized by applying a min-max and box-cox transformation and rescaled to z-scores to reduce skewness caused by high variability among samples. Elemental profiles from XRF data were normalized to Zr, because measures of other lithogenic elements Al and Ti were discontinuous due to low abundance. A Principal Component Analysis (PCA) was used to assess changes in XRF data throughout the stratigraphic section. All statistical analyses were performed in R version 3.5.1 (R Core Team, 2013).

RESULTS

Chronology, Lithology and Geochemistry

The sediment core from Namonte is characterized by dark silt (130–0 cm) that overlies primarily medium quartz sand at the base (138–131 cm). The chronology was established based on three AMS radiocarbon ages determined on plant remains. These dates indicate that the sediment record spans ∼1,145 years (**Table 1** and **Figure 2**). Two radiocarbon ages (PSUAMS-6326 and PSUAMS-3520) have relatively wide calibrated 2σ ranges (∼280 and 180 years, respectively), which contributes to high uncertainty in the modeled ages of the lower core section. The distribution of AMS ^{14}C dates with depth suggests two stages of deposition. Continuous deposition occurred from the base of the core at 130 cm to 85 cm depth (0.22 cm yr^{-1} on average between ∼1,145 and 270 cal yr BP). Following this, there was a period of more rapid sedimentation (0.55 cm yr^{-1} on average from ∼270 cal yr BP to present). However, given that the estimated sedimentation rate in the upper section of the core was based on only two AMS dates, we interpreted changes during the recent phase of the chronology with caution.

The evidence suggests no obvious major depositional hiatuses or sediment mixing in the sediment core. The inference is based on observations that (1) the sediment lithology of the core is relatively homogenous throughout the sediment core; (2) pollen preservation is good, as less than 5% broken or shriveled pollen grains were observed in each sample; (3) seeds of *Carex* and other Cyperaceae were common in the core and diatoms were found in all samples, suggesting that the coring site has been continuously covered with water.

Elemental analysis of the Namonte sediment core documents differences between sediments from 129 to 60 cm depth and those from the overlying section (**Supplementary Material 1**). The lower core section possesses relatively abundant Ni and Cd, whereas the overlying section (60–33 cm depth) includes more Ca, K, Cl, Fe, and Zr. The first two principal components of a PCA conducted on the correlation matrix of all elemental profiles explain nearly 65% of the variance and highlight the distinct geochemical compositions of the lower section (129–60 cm) and upper sections (60–33 cm) of the core (**Supplementary Materials 1, 2**). PC1 (46.4% variance explained) values generally increase up-core, despite peaks in S that occur at 91–81 cm and 59–39 cm. The change in sign of PC1 values up-core at ∼60 cm depth coincides with decreases in Ca/Zr and Si/Zr values and increases in Fe/Zr and K/Zr (**Figure 3**). These measures are sensitive to authigenic carbonate precipitation, deposition of biogenic silica, and weathering regime. Specifically, relatively more Ca deposition may have been associated with carbonate precipitation during dry conditions and low lake levels (Haberzettl et al., 2007; Kylander et al., 2011), or associated with higher primary production. Increased runoff could deposit detrital calcite and increase Ca/Zr values, but the alluvium around Namonte is almost entirely quartz sand. Deposition of biogenic silica, with only traces of lithogenic elements such as Zr, can drive increases in Si/Zr values (Agnihotri et al., 2008; Dickson et al., 2010). Here, we consider that changes in Si/Zr are driven mainly by changes in diatom productivity, given that the diatom analysis revealed good diatom preservation and a concomitant shift in the diatom assemblage over time. Mobile elements such as K, and sometimes Fe, are more likely to accumulate and drive high K/Zr and Fe/Zr values during times of relatively greater physical, as opposed to chemical weathering (Piva et al., 2008; Kylander et al., 2011; Aufgebauer et al., 2012). Given that the lake is shallow, we suspect that it has been consistently well-oxygenated and that changes in redox conditions have likely contributed very little to variation in Fe/Zr values.

Microfossil Analysis

Pollen and Microcharcoal

We identified 78 pollen taxa in the sediment core from Namonte. Pollen preservation was good as each sample contained less than 5% damaged or shriveled pollen grains. Pollen concentration was variable throughout the core (mean = 41,800 grains cm^{-3}), likely attributable to depth-associated variability in overall pollen preservation and/or bulk sedimentation rate (Zhao et al., 2009). Cluster analysis identified five major pollen zones (P1, P-2a and 2b, P-3, P-4) within the sequence (**Figure 4**). Poaceae was the most abundant pollen type through the entire record, followed by *Euphorbia* and *Ephedra*, suggesting that grasslands and the

TABLE 1 | AMS Radiocarbon dates used to construct the age-depth model for Namonte core 22-IX-17-1B, southwest Madagascar.

Lab code	Sample ID	Depth (cm)	Material	^{14}C age (BP)	Error	Calibrated age (BP)
*PSUAMS-6324	NA-30	55	Seeds and unidentified plant remains	-20	20	-6
*PSUAMS-6325	NA-33	70	Charcoal and unidentified plant remains	-295	20	-7
PSUAMS-6326	NA-34	85	Seeds and unidentified plant remains	170	20	133
PSUAMS-6327	NA-35	101	Wood	495	25	506
PSUAMS-3520	NA-1	128	Twig	1300	20	1,197

**Dates excluded from the age-depth model.*

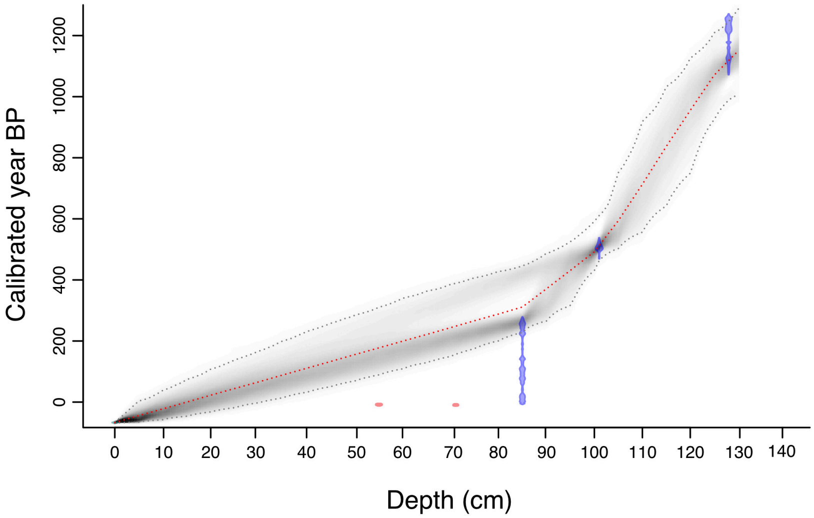

FIGURE 2 | Age-depth model from Namonte sediment core 22-IX-17-1B, southwest Madagascar. All ^{14}C dates pictured in blue were calibrated with SHCAL20 (Hogg et al., 2020), the gray line represents the 95% confidence interval, and the red dotted line is the best-fit model based on a weighted mean. ^{14}C dates indicated in red were excluded from the age-depth model. The sediment surface (-67 cal yr BP) was included in the Bayesian modeling.

dry deciduous forest dominated the landscape for at least the last ∼1,145 years (**Figure 4** and **Table 2**). Taxa characteristic of drylands (*Ephedra*, *Uapaca*, Anacardiaceae) were relatively common between ∼1,145 and 200 cal yr BP, followed by a transition period, between ∼190 and 20 cal yr BP. This transition was characterized by a decline in *Ephedra* and *Euphorbia* and sporadic appearance of Arecaceae, *Ficus,* Ericaceae, *Pandanus,* and *Syzygium*. Most recent zone P-4 is differentiated by a dramatic decrease in abundance of *Ephedra* and an increase in *Prosopis*, an indicator of soil disturbance.

Charcoal particles were found in all the samples analyzed throughout the core, and numerous charcoal peaks were observed, indicating past fire activity (**Figure 5**). A macrocharcoal peak was recorded ∼1,040 cal yr BP and a second peak of macrocharcoal area occurred between ∼470 and 400 cal yr BP. Between ∼240 and 125 cal yr BP, both macrocharcoal influx and macrocharcoal area increased abruptly, followed by sharp decreases between 120 and 70 cal yr BP.

Our analyses also revealed differential trends regarding relative abundances of taxa with distinct seed-dispersal pathways throughout the core. Pollen of plants with wind-dispersed seeds (anemochory) dominate the pollen assemblage and tend to increase over time (**Figure 6**). In contrast, pollen of taxa with seeds dispersed by animals (zoochory) fluctuate over time. Pollen from plant taxa dispersed only by lemurs show a relative decrease in more recent pollen zones P-3 and P-4, in comparison to earlier zones P-1, P-2a, and P-2b. Pollen of plants with seeds dispersed by lemurs and other animals show a relative increase in abundance during pollen P-2a, decreases in P-2a and P-3, and a slight increase in P-4.

Diatom Analysis

We identified 62 diatom species and grouped them according to functional groups. We identified three main diatom zones (D1-3), with zone D1 divided into sub-zones D1-a and D1-b (**Figure 7**) based on the cluster analysis, as described in **Table 3**.

DISCUSSION

This multi-proxy environmental reconstruction enabled us to assess the role of Late Holocene climate change, human occupation, and megafaunal extinctions on terrestrial and aquatic ecosystems of southwest Madagascar (**Figure 8**). The pollen record shows that grasslands and dry deciduous forests dominated the vegetation for at least the last ∼1,145 years and that a major turnover in the plant community took place between ∼195 and 20 cal yr BP, when grasslands expanded

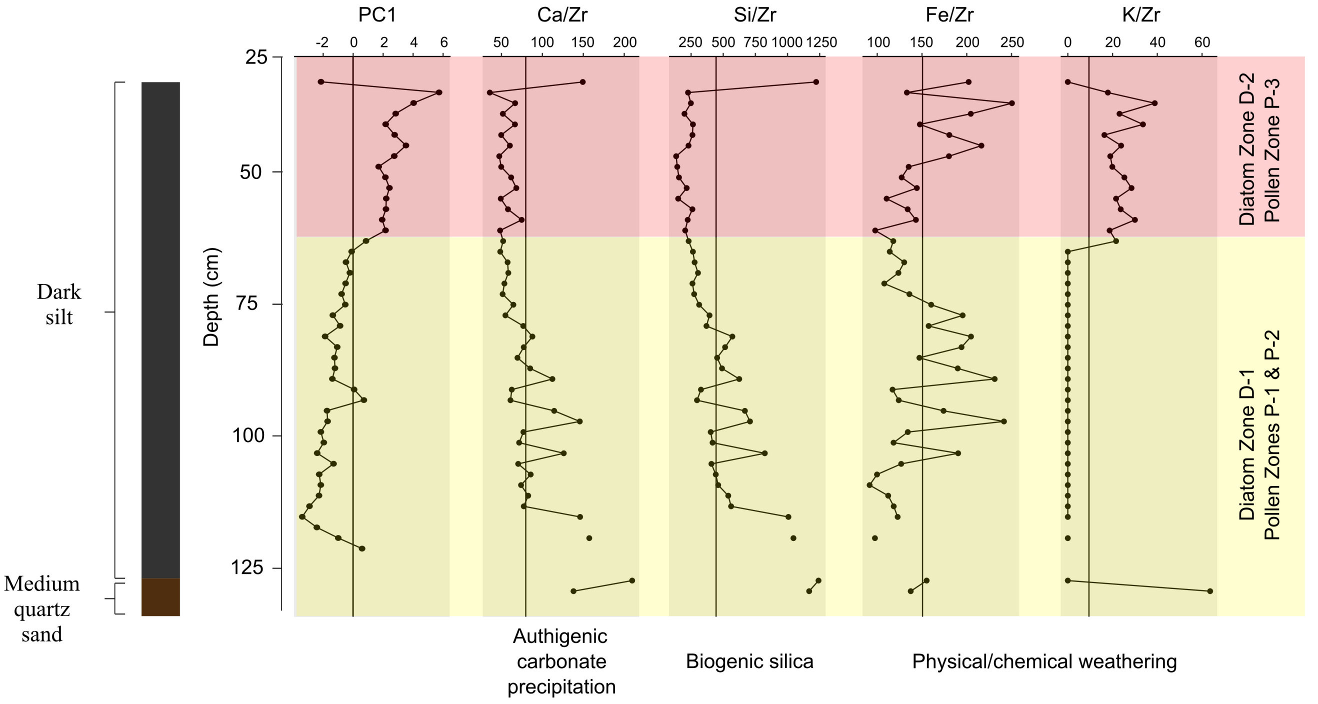

FIGURE 3 | Depth versus XRF-PC1 and XRF-derived element abundances normalized to Zr, from the Namonte sediment core, southwest Madagascar. Mean values are indicated by vertical lines and pollen and diatom zones are marked by different colors.

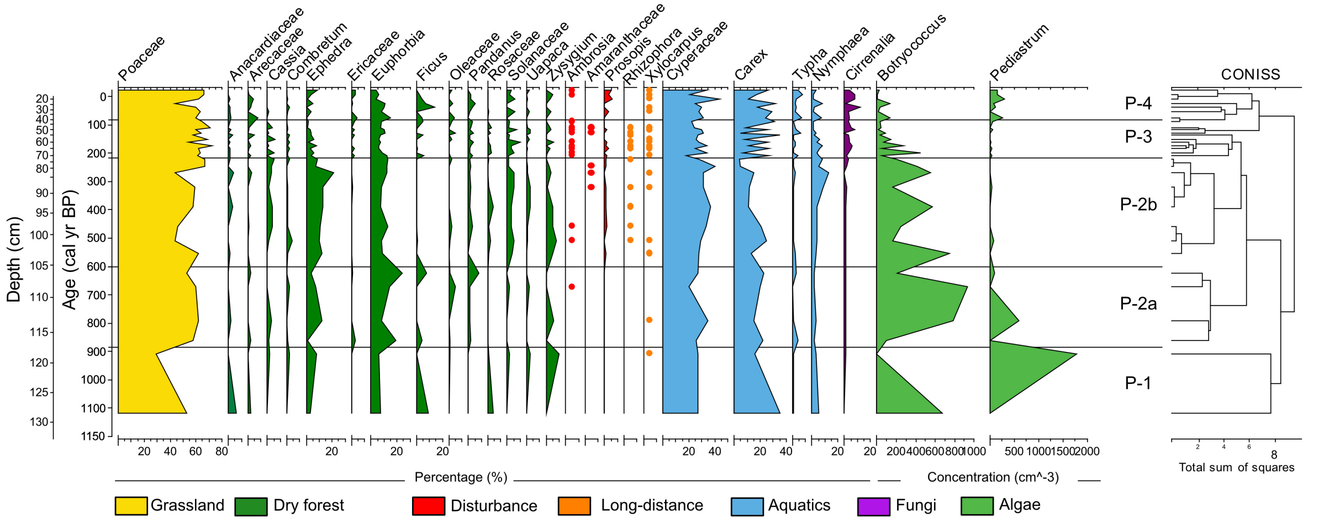

FIGURE 4 | Pollen relative abundance and algae concentration versus depth and calibrated radiocarbon age in the sediment core from Namonte, southwest Madagascar. CONISS analysis on the right side of the diagram shows the four major pollen zones, with zone P-2 divided into two subzones.

and elements of the dry deciduous forest declined. The decline of forest taxa (*Euphorbia* and *Ephedra*) was accompanied by a relative increase in fire-resistant vegetation (*Prosopis* and Ericaceae), along with plants that thrive in disturbed soils (Amaranthaceae and *Ambrosia*) (**Supplementary Material 3**). The last ~60 years were characterized by continued degradation of regional dry forests.

Alterations to the aquatic environment are reflected by changes in the diatom assemblage. Between ~270 and 70 cal yr BP, HP species were replaced by MP taxa, and *C. meneghiniana* became more abundant. This turnover in the composition of the diatom community suggests an increase in disturbance, likely associated with increasing water turbidity resulting from greater influx of soil particles from the watershed, increased

TABLE 2 | Zones of Namonte pollen record. Zonation was based on the CONISS analysis.

Zone	Stratigraphic position	Age range (cal yr BP)	Dominant taxa	Microcharcoal influx	Macrocharcoal influx	Description
P-4	20 – 12 cm	∼18 cal yr BP – present	Poaceae (64%). *Carex* (17%) and other Cyperaceae (73%). *Botryococcus* (1,317 cm^{-3}).	Woody = 429,310 particles cm^{-2} yr^{-1}, herbaceous = 14,848 particles cm^{-2} yr^{-1}	Not recovered	Grass pollen remains dominant. *Euphorbia* pollen declines in abundance. Sedges pollen remain relatively stable. *Nymphaea* pollen appears sporadically. *Pediastrum* (200 cm^{-3}) concentration increases. *Botryococcus* concentration remains low. Microcharcoal influx decreases.
P-3	63.5 – 24 cm	195 – 35 cal yr BP	Poaceae (60%). *Carex* (22%) and other Cyperaceae (27%).	Woody = 2,586,854 particles cm^{-2} yr^{-1}, herbaceous = 249,975 particles cm^{-2} yr^{-1}	Influx = 106 particles cm^{-2} yr^{-1}, area = 204 mm^{2} cm^{-2} yr^{-1}	Poaceae pollen remains dominant, while *Euphorbia* pollen declines. Pollen from Arecaceae, *Ficus*, *Combretum*, *Pandanus*, and Solanaceae increase. *Ambrosia*, Amaranthaceae, and *Prosopis* pollen are common. Sedges pollen increase, while *Nymphaea* pollen decreases. *Botryococcus* concentration decrease relatively and fungal spores of *Cirrenalia* increase slightly. Large increase in microcharcoal influx. Macrocharcoal influx and area decline sharply.
P-2b	103.5 – 63.5 cm	∼545 – 195 cal yr BP	Poaceae (58%) and *Euphorbia* (9%). *Carex* (14%) and other Cyperaceae (30%). *Botryococcus* (28,623 cm^{-3})	Woody = 1,142,554 particles cm^{-2} yr^{-1}, herbaceous = 106,019 particles cm^{-2} yr^{-1}	Influx = 776 particles cm^{-2} yr^{-1}, area = 736 mm^{2} cm^{-2} yr^{-1}	*Ephedra* pollen declines toward the end of the pollen zone. Several pollen taxa (Anacardiaceae, *Cassia*, and *Pandanus*) exhibit peaks in abundance, while Solanaceae pollen remains relatively constant (2.3%). Pollen of plant indicators of disturbance (*Ambrosia*, Amaranthaceae and *Prosopis*) are commonly found at low abundances ($<$ 1%). *Botryococcus* concentration decreases and *Pediastrum* concentration becomes rare. Microcharcoal influx increases sharply. Macrocharcoal influx and area decrease significantly.
P-2a	118.5 – 103.5 cm	∼915 – 545 cal yr BP	Poaceae (58%), *Euphorbia* (14%), and *Ephedra* (7%). *Carex* (19%) and other Cyperaceae (27%). *Botryococcus* (55,638 cm-3)	Woody = 162,311 particles cm^{-2} yr^{-1}, herbaceous = 26,410 particles cm^{-2} yr^{-1}	Influx = 1891 particles cm^{-2} yr^{-1}, area = 702 mm^{2} cm^{-2} yr^{-1}	Pollen of other dry forest taxa (Arecaceae, *Combretum*, *Cassia*, *Pandanus,* and *Uapaca*) remains low. *Botryococcus* concentration increases, but *Pediastrum* concentration decreases. Microcharcoal influx increases. Macrocharcoal influx and area decrease slightly.
P-1	128 – 118.5 cm	∼1,116 – 915 cal yr BP	Poaceae (41%), *Uapaca* (5%), *Euphorbia* (6%) and *Ephedra* (5%). Sedge pollen (*Carex*, *Uncinia*, and other Cyperaceae) (95%). *Botryococcus* and *Pediastrum* (33,574 and 891 cm^{-3}, respectively)	Woody = 309,774 particles cm^{-2} yr^{-1}, herbaceous = 18,966 particles cm^{-2} yr^{-1}	Influx = 1937 particles cm^{-2} yr^{-1}, area = 1261 mm^{2} cm^{-2} yr^{-1}	Relative high percentages of pollen of Poaceae, *Uapaca*, *Euphorbia* and *Ephedra*. Microcharcoal influx is relatively high. Macrocharcoal influx and area are abundant.

organic input from cattle excreta, and/or from people, cattle, and other domestic animals resuspending sediments along the littoral zone of the lake.

Dynamics of Vegetation and Aquatic Ecosystems

The fossil pollen record shows that grasslands and dry forest were the dominant vegetation components between ∼1,145 and 545 cal yr BP (Zones P-1 and P-2a), when arid climate conditions prevailed in southwest Madagascar. The pollen assemblage was characterized by the presence of Poaceae, *Euphorbia*, *Ephedra* and other native taxa such as *Cassia*, *Pandanus*, *Uapaca,* and *Syzygium*. Regional speleothem records indicate that much of this period, from ∼900 to 400 cal yr BP, was characterized by successive megadrought episodes, attributed to northward shifts in the position of the Intertropical Convergence Zone (ITCZ) and changing phases of the Indian Ocean Dipole (IOD) (**Figure 8**,

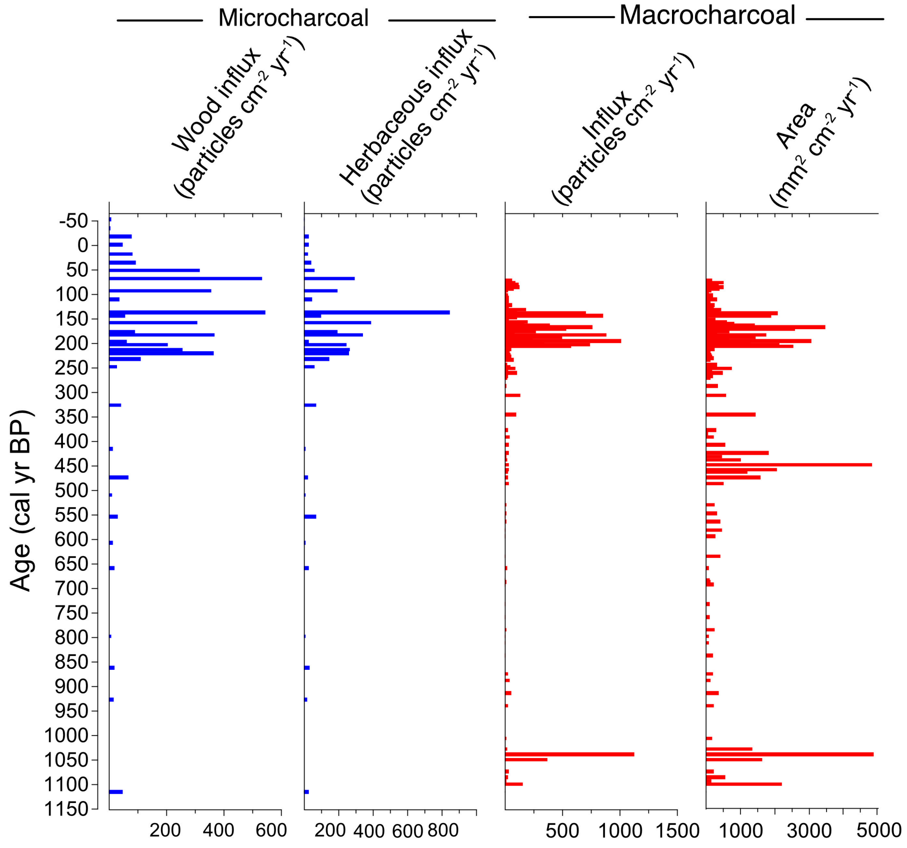

FIGURE 5 | Microcharcoal influx (particles cm^{-2} yr^{-1}), macrocharcoal influx (particles cm^{-2} yr^{-1}), and macrocharcoal area (mm^2 cm^{-2} yr^{-1}) from the Namonte sediment core, southwest Madagascar.

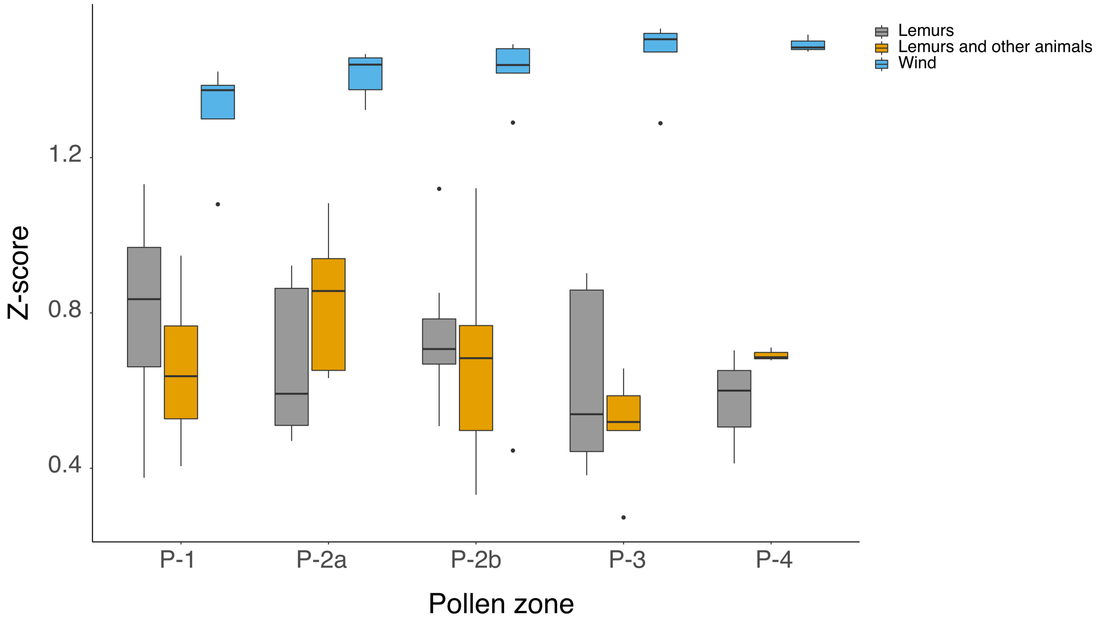

FIGURE 6 | Box-and-whisker plots of the normalized abundances (z-score) for pollen types, distinguished by seed dispersal mechanism, in the sediment core from Namonte, southwest Madagascar.

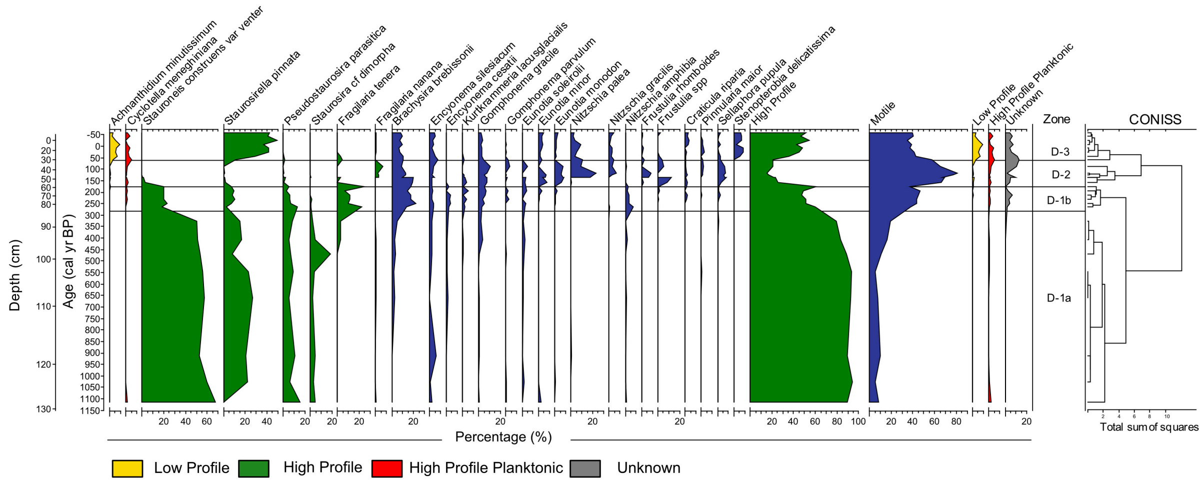

FIGURE 7 | Diatom relative abundance and functional group sums versus depth and calibrated radiocarbon age in the sediment core from Namonte, southwest Madagascar. CONISS analysis on the right side of the diagram shows the three major diatom zones, with zone D-1 divided into two subzones.

TABLE 3 | Zones of Namonte diatom record. Zonation was based on the CONISS analysis.

Zone	Stratigraphic position	Age range (cal yr BP)	Dominant taxa	Description
D-3	32–0	70 – present	*S. pinnata* increases again (30%), species from D-2 are still present but in low percentages. *Achnanthidium minutissimum* and *Cyclotella meneghiniana* increase although with small abundances.	High Profile and Motile Profile diatoms are dominant. There is an increase in Low Profile and Planktonic diatoms.
D-2	60–32	180–70	*Brachysira brebissonii* (5%); other species increase (2.5%) such as *Nitzschia palea, Sellaphora pupula, Eunotia monodon, Fragilaria nanana*	Motile species dominate over High Profile diatoms.
D-1b	85–60	∼270–180	*S. construens* var *venter* (10%), *Brachysira brebissonii* (10%), *S. pinnata* (5%), *Fragilaria tenera* (<5%),	High Profile diatoms are still abundant, and Motile Profile diatoms increase.
D-1a	128–85	∼1,116–270	*Staurosira construens* var *venter* (> 50%) *Staurosirella pinnata (20%), Pseudostaurosira parasitica (10%)*	Dominance of High Profile diatoms.

Virah-Sawmy et al., 2016; Li et al., 2020). Vegetation turnover was also documented during this period at other sites on the island, and it has typically been attributed to the displacement of the ITCZ. For example, near Lakes Mitsinjo and Anjohibe, grasslands expanded ∼1,000 cal yr BP (Matsumoto and Burney, 1994; Crowley and Samonds, 2013), and, near Andolonomby, xerophytic bush intermixed with palm trees expanded between ∼1,000 and 500 cal yr BP (Virah-Sawmy et al., 2016).

The XRF analysis of the core identified relatively high Ca/Zr values during the period between ∼1,145 and 400 cal yr BP, which likely was a consequence of drier conditions that resulted in $CaCO_3$ precipitation (Haberzettl et al., 2007; Kylander et al., 2011). Aridity during the start of this interval is consistent with records from East Africa that document relatively dry conditions during the Medieval Warm Period (1000-700 cal yr BP), followed by a wetter interval coincident with the latter part of the Little Ice Age (∼300 cal yr BP) (Newton et al., 2006; Tierney et al., 2013).

The diatom assemblage also indicates relatively stable shallow lacustrine conditions between ∼1,145 and 270 cal yr BP (**Figure 8**, Sub-zones D-1a and D1b). Dominance of HP diatoms, especially *S. construens,* during that time suggests relatively little disturbance (Passy, 2007). Similar patterns have been observed in other records, including the one from Lake Tritrivakely, Madagascar (Gasse and Van Campo, 2001). Presence of *S. construens* var. *venter, S. pinnata, P. parasitica,* high abundance of pollen of sedges (*Carex* and other Cyperaceae) and high concentrations of the green alga *Botryococcus*, also suggest shallow and mesotrophic to eutrophic waters (**Supplementary Material 4**) (Wünnemann et al., 2010). An increase in *Nymphaea* (water lily) implies a slight increase in water levels between ∼400 and 200 cal yr BP. The persistence of taxa in the paleoecological record throughout this period suggests that both terrestrial and aquatic ecosystems were resistant in the face of a relative decrease in precipitation that impacted southern Madagascar.

A major change in terrestrial plant composition took place between ∼405 and 50 cal yr BP (P-2b and P-3). During that period, grasslands expanded and fire-resistant taxa (Ericaceae and *Prosopis*) and disturbance taxa (Amaranthaceae and *Ambrosia*) became more abundant. Vegetation turnover was associated with an increase in fire activity at both local and regional scales, as expressed by increases in both macro- and microcharcoal influx. This shift in vegetation and fire activity coincided with two dry periods recorded in speleothem $\delta^{18}O$ and in *Adansonia* tree-ring $\delta^{13}C$ values from ∼320 to 260 cal yr BP and ∼100 to 0 cal yr BP in northwest and southwest Madagascar, respectively (Scroxton et al., 2017; Razanatsoa, 2019). A similar

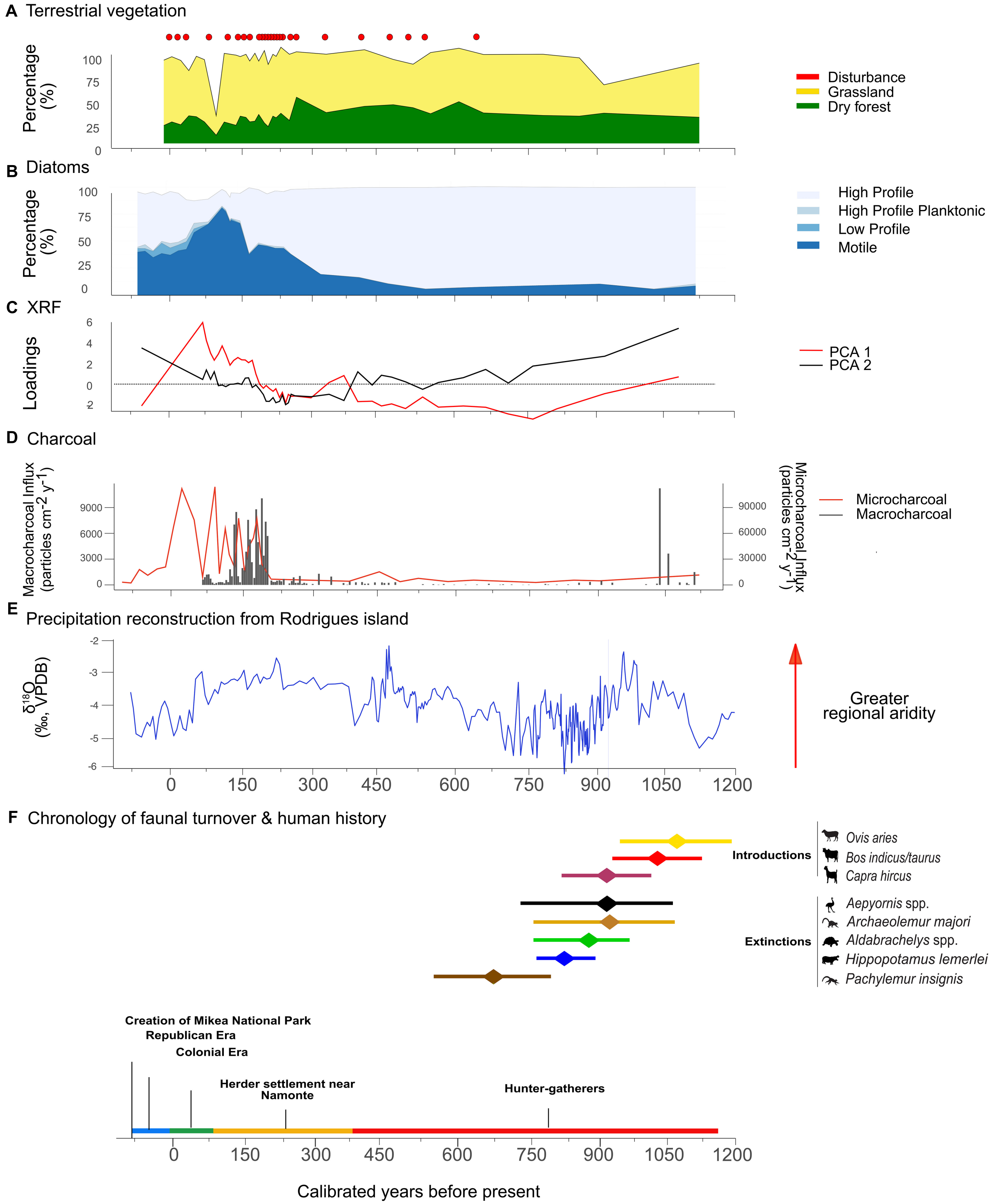

FIGURE 8 | Abbreviated paleoecological diagram for the last ∼1,145 years, inferred from the Namonte core, southwest Madagascar. **(A)** Pollen percentages of disturbance taxa, grasslands, and dry forest, **(B)** percentages of diatom guilds, **(C)** PCA1 and PCA2 of XRF analysis, **(D)** Influx of macrocharcoal and microcharcoal particles, **(E)** Precipitation reconstruction from the Rodrigues Island, Indian Ocean, speleothem $\delta^{18}O$ record (Li et al., 2020), and **(F)** chronology of faunal turnover (based on classical confidence intervals from Hixon et al., 2021a) and approximate human history based on archaeological, written and oral records (Douglass et al., 2019b).

vegetation trend was recorded at Lake Longiza, where grasslands expanded in association with an abrupt increase in charcoal particles and coprophilous fungi between 580 and 30 cal yr BP (Razanatsoa et al., 2021b). These results likely indicate that vegetation turnover was a consequence of changing climate conditions that favored ignition of vegetation and spread of fires, but changes in human activities may have also driven vegetation change and a decline in dry forest extent.

Changes in terrestrial ecosystems between ∼180 and 70 cal yr BP coincided with a dramatic turnover in the freshwater diatom community of the lake (D-2). MP diatoms increased in abundance during that period, which likely indicates increased physical disturbance of the aquatic environment, possibly by higher soil erosion in the watershed and increased detrital input to the lake (Jones et al., 2014). Motile diatoms fare relatively well during physical disturbance, because they possess the ability to move away from disturbed areas (Jones et al., 2014) and compete well for nutrients in eutrophic environments (Passy, 2007). Higher sediment input, most likely from soil erosion, is supported by relatively rapid sedimentation rates (0.54 cm yr^{-1}) and high K/Zr and Fe/Zr values (Piva et al., 2008; Kylander et al., 2011; Aufgebauer et al., 2012).

The diatom assemblage also suggests increased variation in lake levels and water quality. *C. meneghiniana* increases in abundance ∼90 cal yr BP, likely associated with an increase in water turbidity (Hassan, 2013). Species of *Eunotia* and *Pinnularia* also become more common during that time, which could indicate periods of low water level (Gasse and Van Campo, 2001). The turnover in the diatom community suggests significant changes in the physical and chemical characteristics of the lake around ∼180 cal yr BP, which persisted until ∼70 cal yr BP. Relatively low Si/Zr values in sediment since ∼180 cal yr BP reflect relatively low deposition of biogenic silica, which may have resulted from a combination of declines in diatom production and increased detrital input (Agnihotri et al., 2008; Dickson et al., 2010). Further geochemical studies on the lake sediment will provide additional information regarding the factors that influence biogenic silica variation through time.

During the last ∼70 years, the dry deciduous forest declined, while grasslands expanded, and extra-local taxa increased. The presence of Amaranthaceae, *Ambrosia,* and *Prosopis* suggests degradation of dry forests associated with the establishment of species that are resistant to fire, trampling, and browsing pressures. The aquatic community of Namonte also displays evidence of considerable change during this time. Increases in abundance of colonizers *S. pinnata*, and *A. minutissimum* (Berthon et al., 2011) and LP and MP species, indicate intermittent physical disturbance, possibly associated with habitat degradation, highly variable lake levels, and environmental changes in the watershed (Passy, 2007; Berthon et al., 2011; Velez et al., 2021). High variation in the abundance of sedges and a relative increase in the abundance of *Typha* also support an inference for changes in lake level and periodic swampy conditions. These changes were previously linked to overgrazing and social conflict in the region, which forced local people into sedentism (Irwin et al., 2010). Ecosystem degradation today is likely exacerbated by aridification associated with climate change and abandonment of traditional land-management practices (Tucker et al., 2010; Virah-Sawmy et al., 2016; Razanatsoa et al., 2021a).

Fire Activity

Charcoal particles are useful proxies for past fire activity. Macrocharcoal is usually considered evidence of local fires, and microcharcoal as evidence of more distant fires (Clark and Royall, 1996). The spatial scale reflected by charcoal particle size depends on the environmental characteristics of the site, such as topography and predominant wind direction (Whitlock and Larsen, 2002). In the case of Namonte, macrocharcoal particles could originate from burning within the small lake catchment or from fires on the coast, ∼11 km to the west. Fires that burn areas $> 0.02 \text{ km}^2$ can produce convective columns that extend > 1 km into the air and are capable of transporting macrocharcoal as much as ∼10 km (Clark, 1988). Thus, macrocharcoal recovered from Namonte probably came from the lake basin proper and/or the coast. In contrast, microcharcoal can travel several to > 100 km from its source, so microcharcoal in Namonte may have traveled from fires at considerable distances from the waterbody (Clark, 1988).

High values of charcoal particles suggest that fire activity was widespread around Namonte and in nearby areas during the last ∼1,145 years (average microcharcoal influx: 1,435,304 particles cm^{-2} yr^{-1}). Macrocharcoal particles were common between 1,145 and 1,000 cal yr BP, at a time when hunter-gatherers and possibly early pastoralists were present in the region (Douglass et al., 2019a; Hixon et al., 2021a). Large concentrations of macrocharcoal (> 200 particles cm^{-3}) during that early period indicate the occurrence of large fires near Namonte. Although it is possible that people used fire for hunting and possibly land clearing for livestock grazing, arid conditions likely favored the ignition and spread of natural fires in the fire-prone grasslands (Virah-Sawmy et al., 2009). The relatively great abundance of charcoal of all size classes suggests both high fire activity within the lake catchment and long-distance transport, perhaps from the coast, associated with foraging (Douglass et al., 2018).

Between ∼1,000 and 70 cal yr BP, macrocharcoal values increased dramatically, with a peak between ∼205 and 130 cal yr BP (macrocharcoal influx = 4,303 particles cm^{-2} yr^{-1}, macrocharcoal area = 1,392 mm^2 cm^{-2} yr^{-1}), suggesting continued large-scale landscape transformation near Namonte. High charcoal influx overlaps with a decline in tree taxa, suggesting that forests were intentionally burned to expand grasslands for zebu and ovicaprids (Douglass et al., 2018; Hixon et al., 2021a,b). A peak in macrocharcoal area (average 1,896 mm^2 cm^{-2} yr^{-1}) between ∼460 and 425 cal yr BP could also indicate intense fire activity associated with vegetation clearing by local pastoralists and management of grasslands. The abundance of macrocharcoal particles (2,600 ± 4,207 particles cm^{-3}) is similar to that found in sediments associated with large-scale landscape clearance (> 200 particles cm^{-3}) in Mauritius (Gosling et al., 2017). Moreover, a similar increase in fire activity was observed ∼589 cal yr BP at Lake Longiza and ∼450 cal yr BP in southeast Madagascar, during a period of cultural transformation, when the size of settlements increased and cattle herding activity intensified (Razanatsoa et al., 2021b).

A large peak in woody and herbaceous microcharcoal influx (average 2,395,921 and 227,006 particles cm^{-2} yr^{-1}, respectively) is observed between ~230 and 35 cal yr BP. Intense fire activity during that period may have been the product of maintenance of grazing areas for herds of zebu. Microcharcoal influx decreased over time but remained relatively high through the period of French colonization (1897–1958 CE) and following the establishment of the Malagasy Republic (1958 to present). Despite colonial and post-Independence state-imposed sanctions designed to discourage burning and reduce deforestation and soil erosion (Kull and Laris, 2009), paleoecological and historic records show that fires remained common in the region. The period of French colonization was characterized by rapid and widespread resource exploitation, such as maize production, that involved changes in the local economy and impacted the livelihoods of native people (Wietzke, 2015). During the last 40 years, fire activity has decreased near Namonte. This could be the consequence of changes in pastoral practices and intensification of cash-cropping (Scales, 2011). Persistence of charcoal in the record, however, reflects continued use of fire to prepare fields for agriculture, produce fuel charcoal, control pests, mitigate the impacts of wildfires, and protest political and economic regimes (Kull, 2002; Kull and Laris, 2009).

Results from this study suggest that the landscape transformation was the product of fire intensification, likely associated with the management of grasslands for introduced cattle (Bloesch, 1999; Kull, 2002; Davis and Douglass, 2021). High concentrations of charcoal particles are associated with the concomitant increase of Poaceae (~65%) over time in the region. A similar pattern was detected in sediment deposited between 1,250 and 850 cal yr BP in several water bodies across Madagascar, including Lakes Amparihibe, Kavitaha, Longiza, Mitsinjo, Ranobe, and Tritrivakely (Burney, 1987a; Matsumoto and Burney, 1994; Gasse and Van Campo, 1998; Burney et al., 2004; Hixon et al., 2021b; Razanatsoa et al., 2021b). This evidence indicates a close relationship between forest burning and grassland expansion and the important role that herders played in the transformation of the landscape during the last millennium.

Legacy of Megafauna Extinction

Several megafauna (> 45 kg) species inhabited southwest Madagascar during the Late Holocene, including giant lemurs (*e.g., Megaladapis edwardsi* and *Hadropithecus stenognathus*), elephant birds (*e.g.*, *Mullerornis modestus* and *Aepyornis* spp.), pygmy hippos (*Hippopotamus* spp.), and giant tortoises (*Aldabrachelys* spp.) (Crowley, 2010; Goodman and Jungers, 2014). These species played key ecological roles, including seed dispersal of native plants, maintenance of grasslands through grazing, and nutrient cycling in aquatic and terrestrial ecosystems (Godfrey et al., 2008; Godfrey and Crowley, 2016). Directly ^{14}C-dated assemblages of megafauna bones from southwest Madagascar suggest that populations of large animals started to decline by ~2,500 cal yr BP and disappeared from the record by ~1000 cal yr BP (Crowley, 2010; Hansford et al., 2021; Hixon et al., 2021a). The long-term ecological consequences of these extinctions provide critical context for current conservation and reintroduction/rewilding efforts, yet they remain poorly understood (Pedrono et al., 2013; Godfrey et al., 2019).

Southwest Madagascar is inhabited by several tree species that rely on large-bodied animals for seed dispersal (*e.g.*, species of *Adansonia*, Didiereaceae, Arecaceae) (Albert-Daviaud et al., 2020). Remnant lemur species, introduced bushpigs, and people may continue to disperse endemic seeds, yet multiple plant taxa are considered to have been "orphaned" by the extinction of their seed dispersers (Federman et al., 2016). In Namonte, the pollen record reveals the legacy of megafauna extinction on terrestrial ecosystem composition. The abundance of plant taxa dispersed exclusively by animals, particularly lemurs, decreased from ~1,145 cal yr BP to present. In contrast, plants with wind-dispersed seeds became more abundant over time. Reduced coverage of dry forests may have been, in part, a consequence of megafauna extinctions, because: (1) several plant species lost their seed dispersers, which negatively impacted their life cycles by creating a bottleneck for seed germination and seedling recruitment; (2) the seed shadow pattern was altered, resulting in limited dispersal in both space and time; and (3) the population genetic structure of plant species was negatively affected because gene flow via seed movement was restricted (Guimarães et al., 2008; Pires et al., 2018). Plants that lost dispersers prior to 1,100 cal yr BP may today be more vulnerable to extinction in the face of climate change and land use intensification because they are unable to increase their geographic distribution.

Burney et al. (2003) suggested that a decline in megafauna probably led to proliferation of fires in the dry forest, but results from our study do not show a clear connection between fire prevalence and loss of large animals. Both the microcharcoal and macrocharcoal records from Namonte show that fires were widespread in the region during the last ~1,145 years. The high incidence of fire over the last millennium was likely a consequence of arid climate conditions, combined with the settlement of agro-pastoralists, decline of megafauna, and expansion of grasslands in the region.

CONCLUSIONS

The paleoecological record in southwest Madagascar suggests that environmental impacts of anthropogenic activities were significant over the last ~1,145 years. People have managed and modified this landscape over the last millennium, particularly following settlement of agro-pastoralists and the introduction of zebu and ovicaprids. Extensive cattle pastoralism evidently involved the use of fire to promote regrowth of palatable grasses at the expense of dry forest taxa. Pastoralism also impacted aquatic diatom communities, which probably responded to the effects of deforestation, soil erosion, and organic input to the lake. Interactions among humans, an increasingly arid climate, and disappearance of endemic megafauna, likely favored the establishment of fire-resistant vegetation and the reconfiguration of vegetation communities in the Malagasy drylands. This study highlights the advantages of integrating multiple paleoecological, archaeological and historical records to make inferences about long-term legacies of climate change and anthropogenic activities on terrestrial and aquatic ecosystems. It also highlights the vulnerability of insular ecosystems to intensifying anthropogenic impacts today.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

SH, MB, JC, and DK designed the research and collected the samples. KD organized and managed fieldwork. AD, SH, MV, and BC analyzed the samples. AD, SH, and MV wrote the draft of the manuscript. SI and KD assisted with the analysis. All authors commented, provided input to the manuscript, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.688512/full#supplementary-material

Supplementary Material 1 | Principal component analysis of XRF data from the Namonte sediment core, southwest Madagascar, with loadings illustrated by vectors. The lower core section (129-60 cm depth), corresponds to diatom zone D-1 and pollen zones P-1 and P-2, has a geochemical composition that is distinct from the upper core section (60-33 cm depth), which corresponds to diatom zone D-2 and pollen zone Z-3.

Supplementary Material 2 | XRF data from the Namonte sediment core, southwest Madagascar.

Supplementary Material 3 | Ecology of the main plant taxa found in the Namonte sediment record, southwest Madagascar (Vincens et al., 2007).

Supplementary Material 4 | Ecology of the main diatoms found in the Namonte sediment record, southwest Madagascar.

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