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A new late Pleistocene subfossil site (Tsaramody, Sambaina basin, central Madagascar) with implications for the chronology of habitat and megafaunal community change on Madagascar's Central Highlands

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ABSTRACT: Madagascar is a complex 'biodiversity hotspot' with a rapidly dwindling biota. The Late Quaternary subfossil record includes many extinct species whose loss is attributed to natural climate change and human impacts. Investigation of the chronology of these events is challenging because few localities document pre-Holocene communities not impacted by humans. Caves with extinct lemurs of large body size comprise some of Madagascar's richest subfossil sites, but provide only a limited window into the island's past. Open highland sites may have fewer primates, but may better document other megafauna, and allow the analysis of the role of the Central Highlands as refugia and as corridors for the dispersal of vertebrates before and after human arrival. Here we present a new subfossil site, Tsaramody (Sambaina basin, Central Madagascar), a high-altitude wetland area that preserves a diverse late glacial and postglacial vertebrate community. Tsaramody bears testimony to fluctuations in the highland flora during the transition from glacial to postglacial conditions, and the composition of a highland vertebrate community before humans arrived. We compare its biota to those of other sites to begin to document the decline and disappearance of megafauna from some of Madagascar's open ecosystems – wetlands dominated by hippopotamuses and crocodylians. Copyright © 2019 John Wiley & Sons, Ltd.

KEYWORDS: Aepyornithidae; Crocodylidae; Hippopotamidae; Quaternary; wetlands.

Introduction

Madagascar is recognized as biodiversity 'hotspot' (Myers *et al.*, 2000). High species endemism (Goodman & Benstead, 2005) can be explained in part by the island's long isolation (Storey *et al.*, 1995), but also by its large size, altitude range, habitat diversity and microclimates (Dewar & Richard, 2007). Current vegetative biomes form distinctive ecoregions, including the humid forest (HF) on the eastern escarpment, dry deciduous forest (DDF) in the west and north, spiny thicket (ST) in the south, succulent woodlands (SW) in the south-west and subhumid forest (SF) on the Central Highlands (Burgess *et al.*, 2004). Many extant vertebrate species have populations in the east and west, but lack representation in the Central Highlands today (Goodman & Raherilalao, 2014; Muldoon & Goodman, 2010), which is largely depauperate of native vegetational communities. Much forest has been lost by burning and clearing for agriculture (McConnell & Kull, 2014); 44% of the island's natural forest cover has disappeared since 1953 (Vieilledent *et al.*, 2018). Despite the Central Highlands being a fairly large region, its natural forests comprise only 2.6% of the nation's total (Dufils, 2003).

Madagascar's living vertebrates exhibit markedly reduced diversity relative to what existed even a few hundred years ago. The island's subfossil (Late Pleistocene and Holocene) record has contributed greatly to our understanding of Madagascar's recent ecological evolution, and aided interpretations of recent environmental change; this record includes large-bodied lemurs, elephant birds, pygmy hippos, crocodyliforms, turtles, bats, carnivorans, rodents and the aardvark-like *Plesiorycteropus* (Burney *et al.*, 1997; Godfrey *et al.*, 1990, 1997; Gommery *et al.*, 2003; Goodman & Muldoon, 2016; Goodman *et al.*, 2006; Samonds, 2007). The arrival of humans, the timing of which is still under debate (Anderson *et al.*, 2018; Dewar *et al.*, 2013; Godfrey *et al.*, 2019; Hansford *et al.*, 2018; Pierron *et al.*, 2017), nevertheless pre-dated the decline and extinction of many of them, including the island's large (> 10 kg) native animals; the megafaunal crash did not occur until sometime during the past two millennia (Burney *et al.*, 2004; Crowley, 2010; Godfrey *et al.*, 2019). Megafaunal extinction is widely believed to have been induced by humans, either directly (via hunting) or indirectly (via landscape transformation), aided by Late Pleistocene and Holocene climatic change (e.g. Burney, 1996, 1997, 1999; Burney & Flannery, 2005; Burney *et al.*, 1997, 2004; Godfrey & Irwin, 2007; Goodman & Jungers, 2014; MacPhee *et al.*, 1985). However, the importance of climate change has been challenged (Burns *et al.*,

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2016; Crowley *et al.*, 2017; Godfrey *et al.*, 2019; Hixon *et al.*, 2018). To resolve this question, it is critical to track changes in faunal composition through recent geological time, paying particular attention to how distributions were affected by climate before human arrival.

Madagascar's known subfossil localities are primarily located in the west and south, with a few in the north and Central Highlands (Goodman & Jungers, 2014). The majority are caves or sinkholes (e.g. Burney *et al.*, 2008; Decary & Kiener, 1970; Duflos, 1968; Rosenberger *et al.*, 2015; Samonds, 2007; Simons *et al.*, 1995a; Standing, 1905). Bones frequently occur in accumulations at the bottom of large sinkholes; however, assessing faunal chronological overlap can be difficult as these types of localities often span a large temporal and/or geographical range. Fossils found here can derive from different environments. More stable depositional environments (such as wetlands) can provide better temporal resolution and representation of past communities.

There has been much speculation about the role of the Central Highlands before, and after, the arrival of humans on Madagascar, both as a barrier to and as a corridor for east–west dispersal of animals (Muldoon *et al.*, 2012). Rainfall, temperature and elevation all probably affect the ecological suitability of highland habitats for different vertebrate communities. Both plants and animals are expected to migrate to lower elevations during cold periods and higher elevations during warm episodes (Burney, 1997; Dewar, 2014). Aridification may impact the suitability of sites at different elevations; high-elevation sites may act as refugia for wet-loving species benefiting from orographic rainfall during periods of high aridity (Rakotoarisoa *et al.*, 2013; Wilmé *et al.*, 2006).

Anthropogenic activities can have major, rapid impacts on natural habitats. Today's extensive Central Highlands grasslands may have resulted from human modification (Gade, 1996; Lowry *et al.*, 1997). They may act as barriers to dispersal for animals that once freely crossed the habitats they replaced. Alternatively, some grass communities may have existed in Madagascar long before human arrival (Bond *et al.*, 2008; Vorontsova *et al.*, 2016); thus, barriers to dispersal of forest-dwelling taxa across the Central Highlands may have existed before human arrival.

Subfossil records on the Central Highlands of extant species currently restricted to eastern rainforest (e.g. *Indri indri*, *Prolemur simus*), as well as extinct, highly arboreal species (e.g. 'sloth lemurs' family Palaeopropithecidae; the 'koala lemur' *Megaladapis*), demonstrate that central Madagascar was at least periodically more forested in the past (Godfrey *et al.*, 1999; Goodman & Rakotondravony, 1996; Goodman & Rakotozafy, 1997; Goodman *et al.*, 2006, 2007; Muldoon *et al.*, 2009, 2012). Additionally, mixed eastern and western faunas exist today in high-altitude pockets of humid and subhumid rainforest topographically part of the Central Highlands, such as Tsinjoarivo (Irwin *et al.*, 2013) and Ambohitantely (Burgess *et al.*, 2004). However, the detailed history of habitat variation across the Central Highlands before human arrival remains poorly known. If we are to understand the decline and extinction of Madagascar's megafauna, we must disentangle the effects of climate, elevation and human activities.

We report here preliminary findings of the newly discovered subfossil site Tsaramody, located within the Sambaina basin (Fig. 1). This is the highest-altitude known subfossil site on the island (1655 m); other high-altitude sites include Morarano-Betafo (1550 m), Masinandraina (1533 m), Vakinankaratra (1500 m), Antsirabe (1490 m) and Ampasambazimba (1036 m). Subfossil vertebrate bones represent hippopotamuses, crocodylians, tortoises and birds (both large-bodied elephant birds and smaller aquatic species). Most highland fossils were excavated during the first half of the 19th century and have poor locality and contextual information. Additionally, Tsaramody represents a preserved wetland system that, perhaps due to its high elevation, may have been more open than other Central Highland sites. Wetland paleoenvironments, which are relatively poorly documented in the subfossil record of Madagascar, provide an opportunity to study past ecosystems that are different from forested habitats more typically preserved at cave sites, and that yield finer-scale evidence of changes in diversity and distribution of communities through time.

Geologic context

The Sambaina basin (Fig. 1) is surrounded on the north, east and west by the large volcanic Ankaratra Massif (Besairie & Collignon, 1972). The Ankaratra forms a long series of shield volcanos consisting of broad and very thick mounds of mafic to ultramafic lavas extruded from craters and fissures; hydrothermal activity continues in the region today and is associated with the deposition of travertine. Formation of the Ankaratra, starting during the Late Oligocene (Bardintzeff *et al.*, 2010), appears to have blocked the original southward Sambaina drainage to Antsirabe, creating an ancient lake (probably incorporating the Antsirabe, Sambaina and Antanifotsy basins, Fig. 1). This created the Sambaina plains and also filled all the old side-valleys until one of them overflowed, creating a new outlet (the Onive River) to the east. Eventually, filling of the original lake by sediments as well as tectonic movements caused the draining of the entire wetland, resulting in an open plain.

Past work in the Sambaina region

The presence of fossils in the Sambaina basin was first reported in 1922, when L. Monnier announced that local people had discovered fossils while collecting travertine (Anonymous, 1923). Subsequent visits by scientists, including paleontologist Charles Lamberton, were described in the literature (Anonymous, 1923, 1925, 1928a, 1928b; Bertrand & Joleaud, 1924). Early explorers reported finding remains of hippopotamuses, crocodylians and elephant birds (especially *Mullerornis*), as well as two femoral heads of the extinct lemur *Archaeolemur edwardsi* (Anonymous, 1928a). A giant 'rodent' (*Hypogeomys* '*boulei*', Anonymous, 1928a, 1928b), a species that had earlier been named by Grandidier (1912), was also reported to exist here. However, several decades later, Lamberton (1946) recognized that the latter actually belonged to *Plesiorycteropus madagascariensis* rather than *Hypogeomys*. Further expeditions to the surrounding area focused on commercial mining but reported vertebrate fossils within the quarried lignites, including a hippopotamus mandibular fragment, crocodylian vertebrae, teeth and coprolites, a heron ulna, fish spines, and gastropods (Lenoble, 1949). The presence of hippopotamuses, crocodiles and fish is consistent with lake or marsh habitats, but the presence of terrestrial species, including, at least rarely, the extinct primate *Archaeolemur*, demonstrates the existence of nearby open woodland or forest.

Materials and methods

Fossil collection and identification

The site is near the village of Tsaramody (19°36′S, 47°10′E, 1655 m asl), ~50 km south of Ambatolampy and 40 km north of Antsirabe (Fig. 1). This basin contains rich volcanic soils and

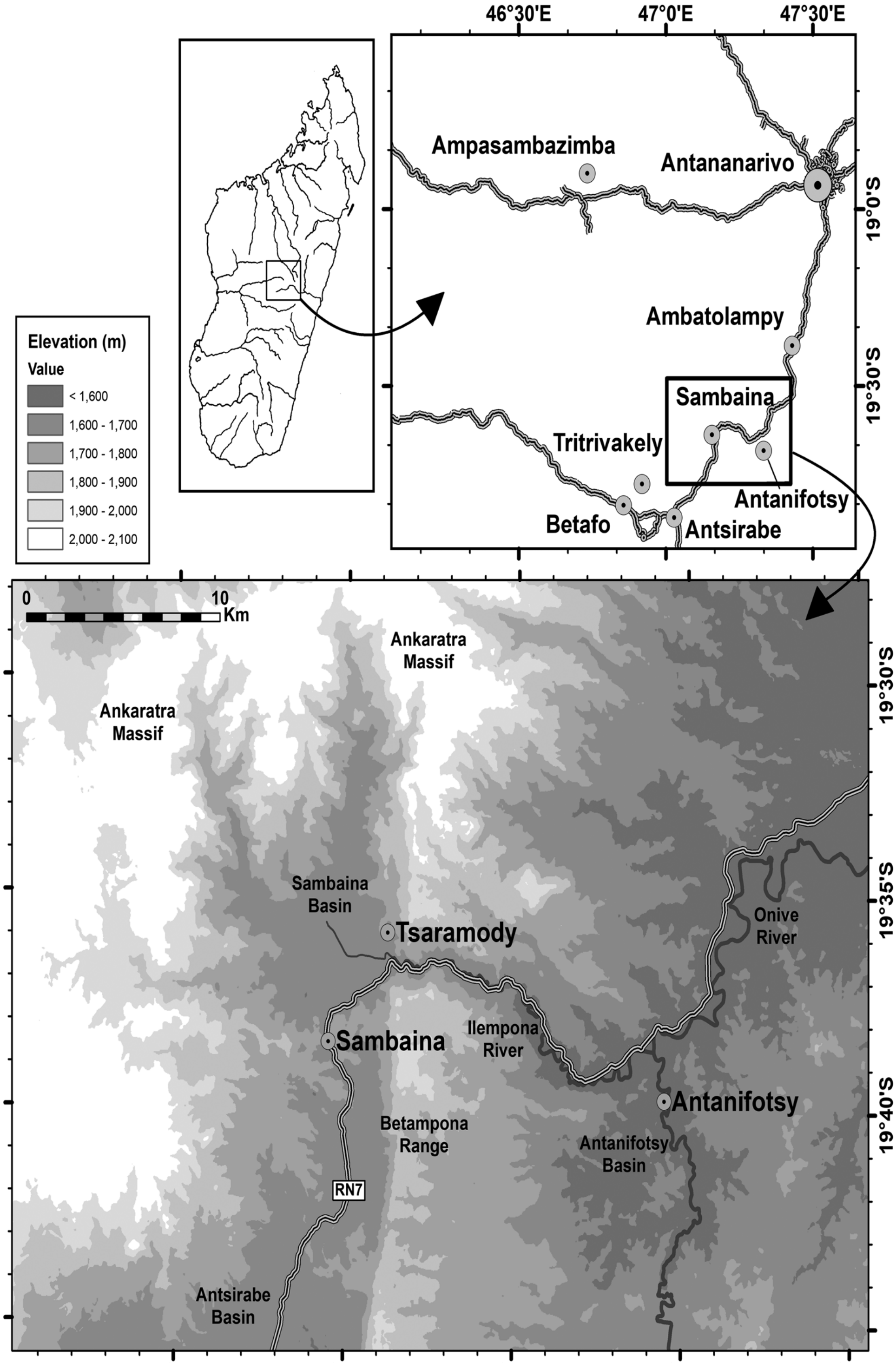

Figure 1. Map showing the location of Tsaramody, Sambaina basin, central Madagascar, and other nearby paleontological and palynological sites. National highways GIS layer is from openstreetmap.org (RN7: National Highway 7). Elevation data are from Aster Global Digital Elevation Model (https://asterweb.jpl.nasa.gov/gdem.asp).

lacustrine sediments that are intensively worked by hand by local farmers. Vegetable plots (e.g. carrots, cabbages) separated by irrigation and drainage canals fill most of the basin (Fig. 2). While the deep underlying sediments are not often disturbed by farming, 1 × 1-m pits are occasionally dug to bring up organic-rich soils for fertilizer, and subfossil bones are found during this process.

Fossils were collected from a portion of the Sambaina basin that local people claimed had never been planted. Twenty-five cubic meters were excavated between 2013 and 2017. Pits were dug by hand in a 1 × 1-m grid system approximately 1.5–2.5 m deep. Hand pumps and buckets were used to remove ground water that filled pits. When possible, fossils discovered *in situ* were photographed and mapped. Mud from each pit was collected and wet screened for smaller fossils. Material was washed, dried, numbered, further prepared using facilities at the University of Antananarivo, and deposited within the collection. Sediment samples were grouped into 10 distinct stratigraphic levels (L1–L10, see Table 1) and defined by sedimentary characteristics and pollen extracted from one pit. Pollen was extracted and counted using methods described in detail by Andriambelomanana (2017).

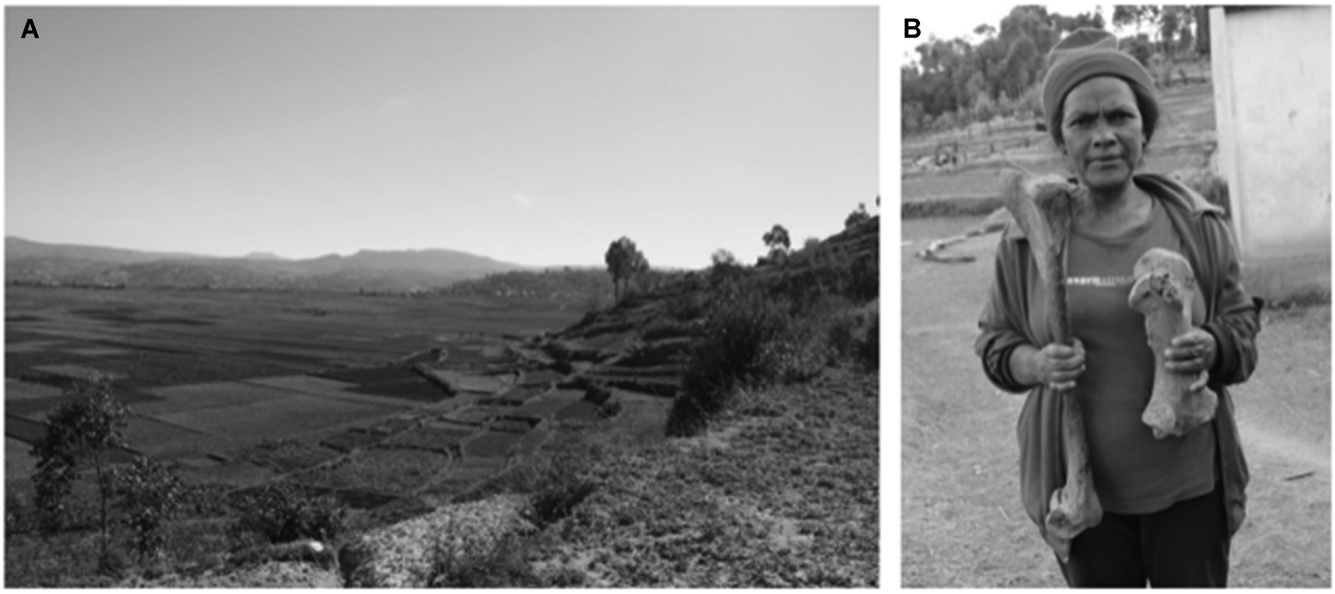

Figure 2. (A) Sambaina basin, central Madagascar; (B) Mme. Medelina Razamandrasoa displays subfossil bones found while farming.

Radiocarbon dating and isotopic analysis

Approximately 150 mg of bone was sampled from a hippopotamus phalanx collected from the deepest level (Level 2) and prepared at the Quaternary Paleoecology Laboratory (University of Cincinnati). After coarse crushing, the bone underwent decalcification and gelatinization following Sparks and Crowley (2018). The sample was decalcified in 0.5 M HCl at 4 °C and rinsed in ultrapure water. Humic acids were removed in 0.001 M NaOH at room temperature and again rinsed in ultrapure water. The sample was then gelatinized in 0.01 M HCl at 80 °C, filtered through 1.5-µm glass fiber filters and lyophilized. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes were analyzed in the Stable Isotope Biogeochemistry Laboratory (University of Cincinnati) and corrected for size, scale and drift (following Skrzypek, 2013). We further corrected the $\delta^{13}C$ value by −1.22‰ to account for isotopic changes in atmospheric CO_2 values following the industrial revolution (the Suess Effect; see Godfrey & Crowley, 2016).

Collagen preservation was confirmed using sample yield, stable isotope data and atomic C:N ratio. The bone was then radiocarbon-dated at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. The conventional radiocarbon age estimate (based on a 5568-year half-life) was ^{13}C-corrected and includes a background subtraction based on simultaneously prepared modern and ^{14}C-free bone standards. The date was calibrated to 2σ calendar years before present (cal a BP) using Calib 7.10 (Stuiver & Reimer, 1993) and the Southern Hemisphere calibration curve SHCal13 (Hogg *et al.*, 2013). The 2σ calibrated dates were rounded to the nearest 5-year interval and the mean calibrated date ± 1σ was calculated.

Results

To date, 845 vertebrate specimens have been collected at Tsaramody, representing four of the five major Malagasy 'megafaunal' groups (hippopotamuses, crocodylians, elephant birds and testudines, but notably no large primates), as well as other smaller vertebrates, such as aquatic birds (Fig. 3). Subfossils demonstrate a wide range of preservation, and include largely complete jaws, cranial bones, isolated teeth, and complete and partial postcranial elements.

Major changes in the site lithology, fossils and pollen are summarized in Table 1 and described below (see also Andriambelomanana, 2017). Level 1 (at a depth of 86 to >100 cm) lies directly below blocks of travertine of variable thickness (~5–10 cm). Whereas sediments from this level yielded no animal fossils, seeds and fossil wood were recovered. Preliminary analyses of pollen (Andriambelomanana, 2017) indicate a high incidence of heath (Ericaceae [*Philippia*]: 72.3%) and low incidence of grasses (7.9%) and aquatic plants (e.g. *Cicatricosisporites*: 0.14%; Cyperaceae: 0.19%).

Most fossils were recovered from Level 2, at a depth of 74–86 cm, and containing blocks of travertine. Vertebrate bones were often found just superior to the travertine, and many were encrusted with large nodules, signaling prolonged hot spring activity (Fig. 4). Pollen from this level shows a marked decrease in Ericaceae (from 72.3% in Level 1 to 6.8%), and an increase in grass (from 7.9% to 30.3%), woodland species and marsh plants, such as bladderworts (Lentibulariaceae; Andriambelomanana, 2017). The hippopotamus phalanx (from Level 2) yielded a Suess-corrected $\delta^{13}C$ value of −15.9‰ and a $\delta^{15}N$ value of 2.4‰. Its age is 14 580 ^{14}C a BP (17 565 ± 1150 cal BP); this is the oldest directly dated hippopotamus specimen from Madagascar.

Level 3 (59–74 cm depth) also contains abundant vertebrate fossils and is characterized by a further decrease in heath plants (to 0.3%) but also a decrease in the relative incidence of grasses (to 21.6%), and an increase in woody C3 plants, including figs (Moraceae; 25%). The first signs of human presence (pollen of cultivated and introduced plants) also occur in the muds of this level.

Vertebrate fossils continue to occur in Level 4 (56–59 cm) and shallower levels (5–7), but their concentrations are lower than in Levels 2 and 3. The incidence of grass also rises again in Level 4, but the incidence of heath plants remains trivial here and in upper levels. Grasses fall again (to 22.9%) in Level 5 (41–56 cm), while aquatic plants increase to 15% from incidences of 10% or lower in all deeper levels. A dramatic spike in aquatic plants (to 54.2%) occurs in Level 6 (38–41 cm), which is a thin 'wet' lens consisting of compact

Table 1. Stratigraphy, lithology, fossils and pollen of the Tsaramody subfossil site (adapted in part from Andriambelomanana, 2017).

Level number	Depth (cm)	Fossils	Lithology	Pollen and plant analysis
L10	0–10	No fossils	Brown-yellow dark soil	Many penetrating roots. Fluctuating incidence of aquatic plants (Cyperaceae and Podostemonaceae)
L9	10–22	No fossils	Gray clay; very dark soil	
L8	22–23		Brown dark soil, fine-grained, containing roots	Increase in incidence of grass pollen (to >45%) (Gramineae/Poaceae)
L7	23–38	High concentration of waterbird bones (~25 cm)	Dark brown clayey soil with sediments ranging from fine-grained to coarse	Grass (26.2%), heath incidence very low
L6	38–41	Fossil concentration low	Very dark brown clay and soil, containing peat	Very high incidence of aquatic plants (Podostemonaceae); spike in dung fungus *Sporormiella*
L5	41–56	Fossil concentration low	Brown grayish peat, very dark	Grass (22.9%), heath incidence very low
L4	56–59	Fossil concentration low	Black peat, fine grained and friable	Grass increases (to 33.6%), heath incidence very low
L3	59–74	High concentration of hippopotamuses, crocodylians, other vertebrate fauna	Black peat, very fine grained	Decrease in grass pollen (to 21.6%), increase in figs; further decrease in heath plants (to <1%); montane plants; some cultivated and introduced plant pollen
L2	74–86	High concentration of hippopotamuses, crocodylians, other vertebrate fauna	Travertine, very dark gray; containing some associated clay, sand and peats with grains of different sizes and class	Dramatic decrease in heath plants (to 6.8%), and increase in grass pollen (to 30.3%); many marsh plants
L1	86–100	Petrified wood, seeds, no vertebrate bones	Brown clay, very dark, with grains not very consolidated	High incidence of heath pollen (72.3%); low incidence of pollen from grasses (7.9%) and aquatic plants

mud. This level also has a high count of spores of the mega-dung fungus *Sporormiella* (= *Preussia*; see Arenal *et al*., 2007).

Level 7 (23–38 cm) includes a distinct lens (at ~25 cm) with a concentration of pristine and delicate bones of extinct and extant water birds. There is a very sharp rise in grass pollen (to 45.0%) in Level 8 (22–23 cm). The three top levels (8–10) have not yielded fossils.

Best represented vertebrate families are the Hippopotamidae and Crocodylidae; each comprises approximately 40% of the total number of identifiable specimens (NISP). The hippopotamuses appear to be *H. guldbergi*, which is apparently the most terrestrial species (Stuenes, 1989; Fovet et al., 2011; Rakotovao *et al*., 2014).

Two crocodylian species, *Voay robustus* and *Crocodylus niloticus*, are reported to occur at subfossil sites in Madagascar. Subfossil material of *C. niloticus* is rare and cannot be distinguished morphologically from its extant counterpart on mainland Africa (Brochu, 2007); most Tsaramody specimens appear to belong to *V. robustus*.

Giant flightless elephant birds, *Aepyornis hildebrandti* and *Mullerornis* sp., comprise 8% and 3%, respectively, of the Tsaramody subfossils, followed by Testudines (*Aldabrachelys* 4%), and flighted birds (3%). The bird taxa include two anatids, the extinct Malagasy shelduck (*Alopochen sirabensis*) initially described from Antsirabe (Andrews, 1897), the still-extant red-billed teal (*Anas erythrorhyncha*), great egret (*Ardea alba*: Ardeidae) and Madagascar long-eared owl (*Asio madagascariensis*: Strigidae).

Discussion

Several lines of evidence (radiocarbon, pollen, faunal composition and stable isotopes) converge to support the conclusion that an open wetland blanketed much of the Sambaina basin at the end of the glacial period (~17 000 cal a BP) and during the transition to postglacial conditions. It is clear from the radiocarbon date obtained from the hippopotamus phalanx near the base of Level 2 that the subfossil record at this site begins in the late glacial or early postglacial period. Sediment coring at another highland locality, Lake Tritrivakely, has shown that the last glacial period ended and deglaciation (the interval during which global ice melted and sea level rose) began locally around 17 000 BP (Gasse & Van Campo, 1998).

The dominance of heath plants and low grass pollen in Level 1 suggests an open habitat and low temperature, matching glacial sediments from Lake Tritrivakely. Furthermore, the pollen transition manifested in Level 2 (with decreasing incidence of heath plants and rising grass) also matches that for early postglacial deposits at Lake Tritrivakely. The absence of fossil vertebrates below Level 2 suggests that temperatures were prohibitively low at high altitudes during the last glaciation, and therefore only hospitable for a smaller subset of animals (e.g. some birds and small mammals).

The travertine blocks at the base of Level 2 may be associated with heightened activity of the Vakinankaratra volcanic field around 19 000 years ago (19 000 ± 2000 ca al BP; Rufer *et al*., 2014). Mietton *et al*. (2018) correlated these volcanics with the time of deposition of late glacial deposits at Lake Tritrivakely, when the incidence of heath pollen at this site was very high and grasses scarce. At Lake Tritrivakely, the transition from glacial (cold) to postglacial (warm) conditions occurred in two steps, first at ~16 900 cal a BP and next at ~15 100 cal a BP, with a significant drop in heath plants and rise in grasses at each (Gasse & Van Campo, 1998). The brief intervening cold episode (with high incidence of heath plants) appears to correspond globally with the cold Heinrich 1 event.

Figure 3. Representative subfossil bones from Tsaramody, Sambaina basin, Madagascar: (A) *Hippopotamus guldbergi* tibia (TSM15282) in anterior view; (B) *Voay robustus* right femur (TSM17044) in ventral view; (C) *Aepyornis* distal tarsometatarsus (TSM15259); (D) *Alopochen sirabensis* right humerus in cranial view (TSM17106). Scale bars = 5 cm.

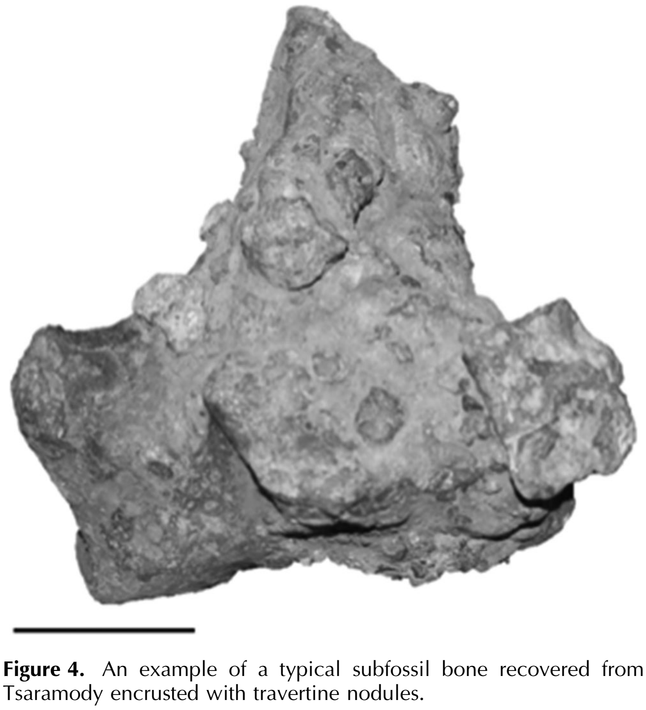

Figure 4. An example of a typical subfossil bone recovered from Tsaramody encrusted with travertine nodules.

Following this (beginning at 15 100 cal a BP), deglaciation resumed without a break until the beginning of the Holocene (11 650 cal a BP).

Levels 2 and 3 at Tsaramody may span the glacial transition and part (or all) of the deglaciation period. The simultaneous decrease in heath and grass coupled with an increase in woody C_3 plants suggests further contraction of open habitat. The sharp rise in grasses in Level 8 suggests a return to more open savanna; indeed, the incidence of grass at this level exceeds that of any deeper level. Given that introduced and cultivated plants also occur in the upper strata, the possibility that humans caused this spike in grasses must be considered.

Assuming that the presence of introduced and cultivated plants is not intrusive (i.e. mixed from younger layers) in Level 3, the latter may extend into the human period in Madagascar (now known to have begun in the early Holocene; see Hansford *et al.*, 2018). Level 2, which is the most fossiliferous, shows no evidence, palynological or otherwise, of human presence. High counts of spores of the mega-dung fungus in Level 6 may signal the continued presence of endemic megafauna, the appearance of introduced domesticated animals, or both.

Preliminary stable isotope data allow us to compare the habitat at Tsaramody with those at other sites. The $\delta^{13}C$ value for the Tsaramody hippopotamus differs from those reported for continental African hippopotamuses (today or in the past), as well as *Hippopotamus* material from other early to late Holocene subfossil sites in Madagascar. Isotope data for African *Hippopotamus amphibius* reflect its tendency to graze primarily, if not exclusively, on C_4 grasses in open habitats (Cerling *et al.*, 2008). Conversely, published $\delta^{13}C$ values suggest that Madagascar's pygmy hippos fed exclusively or mostly on C_3 plants (Table 2; Godfrey & Crowley, 2016). The Tsaramody hippopotamus falls squarely in the middle. Its $\delta^{13}C$ value (− 15.9‰) indicates a mixed C_3 and C_4 diet (Table 2), which may in turn suggest a mixed habitat. Tsaramody hippos may be ecologically comparable to the African pygmy hippo, *Choeropsis liberiensis*, which consumes a mixed diet of C_3 and C_4 plants, including ferns, dicotyledons and grasses (Collen *et al.*, 2011; Grubb & Eltringham, 1993).

Recent research on the grasses of Madagascar's Central Highlands may shed further light on the paleohabitat of Tsaramody. Solofondranohatra *et al.* (2018) show that the grasses of highland forests differ in morphology, composition and isotopes from those that characterize highland grasslands or woodlands. This implies that the isotopes of highland species that selectively consumed a lot of grasses can be used to ascertain whether the dominant habitat was likely to be forest or grassland/woodland. The δ^{13}C value for the Tsaramody hippopotamus thus suggests not merely that this animal consumed a mixed diet of C_3 and C_4 plants, but that it did so in an open grassy or woodland habitat.

As the relationship between δ^{15}N and moisture is well established (Cormie & Schwarcz, 1994; Craine *et al.*, 2009; Crowley *et al.*, 2011; Handley *et al.*, 1999; Swap *et al.*, 2004) the value for the Tsaramody hippopotamus (2.4‰) indicates that this individual lived in a wet environment (Table 2). The only other site with a comparable mean value is Antsirabe (2.6 ± 0.6‰), which is also the only other very high-altitude site (Table 2). Nitrogen isotopes for hippos at all other sites suggest drier habitats. Overall, nitrogen isotope values do not correlate with age or with carbon isotope values. This suggests that some wet sites were much more forested than others in the past.

Comparative faunal incidence data provide another useful proxy for tracking habitat change over time and space. For example, Goodman (1999) used bones of birds to compare paleohabitats at Antsirabe and Ampasambazimba; he documented a dominance of aquatic bird species at Antsirabe (69%), and of terrestrial birds at Ampasambazimba. Tsaramody is much like Antsirabe in this regard, although higher representation of Aepyornithecidae at Antsirabe suggests that the latter was more forested than Tsaramody. Three of the four (75%) non-aepyornithid bird species at Tsaramody are water-dependent (two anatids and a heron).

The dominant megafaunal vertebrate fauna provides further corroboration of a moderately open wetland habitat at Tsaramody (Table 3). At Antsirabe, both terrestrial (e.g. elephant birds) and water-dwelling (e.g. hippopotamuses, crocodylians) megafauna are well represented. The Aepyornithidae were singled out as the best represented vertebrate family at Antsirabe when this site was first explored (Forsyth Major, 1897); the site yielded 1000 elephant bird bones in only 1 month of excavation, rivalling or exceeding its representation of *Hippopotamus*. This contrasts strongly with our record for Tsaramody, with its very high count of water-dwelling hippopotamuses and crocodylians, and relatively low count of elephant birds.

Also of interest is the identity of the species of *Aepyornis* at Tsaramody. On the basis of variation in their brain morphology and implied sensory ecology, Torres and Clarke (2018) inferred variation in habitat preferences for different species of elephant birds. In particular, they argue that *A. hildebrandti*, the species we found at Tsaramody, probably occupied more open habitats than other species of *Aepyornis*, such as *A. maximus*, which in turn probably preferred more forested habitats. The dietary preferences of different elephant bird species are under study (Hansford, 2018); the intersection of studies of brain morphology and stable isotopes of elephant birds ought to be quite revealing.

For now, we note merely that the difference in the relative dominance of various megafauna at Antsirabe and Tsaramody implies that the former was more forested than the latter. Like us, Lamberton found in 1927 a dominance of water-dwelling megafauna within the Sambaina basin; he noted with a certain degree of surprise that almost all the subfossils he found here were *Hippopotamus* (Anonymous, 1928a).

In general, large-bodied extinct primates are not present at high-elevation subfossil sites. An exception is *Archaeolemur*, which was probably the least arboreal of extinct lemurs; *A. edwardsi* has been recorded at Masinandraina (1533 m asl), Morarano-Betafo (1550 m asl), Vakinanakaratra (1500 m asl) and the Sambaina basin (although not yet at Tsaramody). *Megaladapis grandidieri* has also been recorded at Masinandraina (Godfrey & Jungers, 2002); unfortunately, none of these specimens has been dated. Several extinct lemur species, including ones that were far more arboreal than *Archaeolemur*, occur at Antsirabe (just under 1500 m asl), and at mid-altitude sites such as Ampasambazimba (1036 m asl; Table 3). One *Archaeolemur edwardsi* from Ampasambazimba yielded a date of 33 168 ± 3563 cal a BP (Crowley, 2010).

Table 2. Subfossil sites with radiocarbon-dated *Hippopotamus*, arranged chronologically, from oldest to youngest, with collagen isotope data when available. Sample sizes (*N*) are given in parentheses. Average ^{14}C dates were calibrated with Calib 7.10 and the SHCal13. Carbon isotope values have been corrected for the Suess effect (− 1.22‰).

Site	Age range (cal a BP)	Bioclimatic zone*	Elevation (m above sea level)	δ^{13}C (‰)†	δ^{15}N (‰)‡	Source(s)§
Belobaka	>20 572.5 (1)	DDF	64	–	–	1
Tsaramody	17 565 (1)	SF	1655	−15.9 (1)	2.4 (1)	2
Christmas River	10 962.5 (1)	SW	793	–	–	3
Anjohibe	7150–2635 (7)	DDF	109	−23.8 ± 1.4 (7)	7.0 ± 0.8 (7)	4
Taolambiby	2970–1313 (9)	ST	247	−20.2 ± 1.8 (9)	8.9 ± 2.1 (8)	5
Ampoza	2875–2505 (4)	SW	628	−23.2 ± 0.6 (2)	10.4 ± 2.0 (2)	6
Mananjary	2323 (1)	HF	6	−18.4 (1)	–	7
Ankilibehandry	2255 (1)	DDF	8	−21.1 (1)	9.3 (1)	8
Lamboharana	2053–1645 (2)	ST	12	–	–	9
Andolonomby	1933 (1)	ST	190	–	–	10
Antsirabe	1720–1080 (3)	SF	1490	−26.3 ± 0.3 (3)	2.6 ± 0.6 (3)	11
Itampolo	910 (1)	ST	15	–	–	12

[*] Bioclimatic Zone: DDF = dry deciduous forest, SF = dubhumid forest, ST = dpiny thicket, SW = ducculent woodland, HF = humid forest (Burgess *et al.*, 2004).

[†] Hippopotamuses with δ^{13}C values < −21.5‰ had C_3 diets, those with δ^{13}C values between − 21.5 and − 18‰ consumed mostly C_3 foods, those with δ^{13}C values between − 18 and − 14‰ consumed a mixture of C_3 and C_4 foods, and those with δ^{13}C values > −14‰ consumed mostly C_4 foods (Godfrey & Crowley, 2016).

[‡] δ^{15}N values are inversely correlated with habitat moisture.

[§] Sources: 1. Faure *et al.* (2010); 2. This paper; 3. Muldoon *et al.* (2012); 4. Burney *et al.* (1997); Samonds (2007); Crowley and Samonds (2013); Crowley *et al.* (2017); 5. Crowley (2010); Crowley and Godfrey (2013); Godfrey and Crowley (2016); Godfrey *et al.* (2016); 6. Burney *et al.* (2004); Crowley (2010); Crowley and Godfrey (2013); 7. Burney *et al.* (2004); 8. Crowley (2010); Crowley and Godfrey (2013); 9. MacPhee and Burney (1991); 10. MacPhee and Burney (1991); 11. Crowley (2010); Godfrey *et al.* (2016); 12. Mahé and Sourdat (1972).

To reconstruct the chronology of habitat change before human arrival, we compiled a list of all subfossil vertebrates with calibrated radiocarbon dates exceeding 10 000 years. This limited record allows some preliminary observations regarding how elevation affected faunal distributions before human arrival (Table 4). There are nine subfossils that date to the glacial period (> 17 000 cal a BP); they come from lowland sites (Faux Cap, Belobaka, Antsiroandoha), one mid-altitude site (Ampasambazimba) and two high-altitude sites (Antsirabe and Tsaramody). The deglaciation period (between 17 000 cal a BP and the beginning of the Holocene) is represented by seven individuals from Ampasambazimba and two lowland sites (Andrafiabe and Ankilitelo). The early Holocene (before 10 000 years ago) is represented by nine subfossils from two mid-altitude sites, Ampasambazimba and Christmas River, as well as the lowland site, Ankilitelo. The radiocarbon record for the rest of the Holocene is much richer.

Faunal composition and stable isotope values suggest that both high- and mid-altitude sites on the Central Highlands were not densely forested during the last glaciation. There is no direct evidence that large-bodied primates or other forest-dependent vertebrates occupied sites above ~1500 m asl at this time; however, as mentioned above, *Archaeolemur edwardsi* did occupy the mid-altitude site, Ampasambazimba, at 33 168 ± 3563 cal a BP (Table 4). This specimen has a $\delta^{13}C$ value of − 16.7‰ (Crowley, 2010; Godfrey *et al.*, 2016), similar to that for the late glacial Tsaramody hippo (− 15.9‰), suggesting that, during the last glaciation, this *Archaeolemur* at Ampasambazimba, like the Tsaramody *Hippopotamus*, consumed a mixture of C_3 and C_4 resources. Such a carbon signal is unusual for *Archaeolemur*, which normally consumed exclusively or mostly C_3 foods (Crowley & Godfrey, 2013; Crowley *et al.*, 2011). This datum provides evidence that, during the last glaciation, mid-altitude sites, like those at higher elevation, were fairly open. By the end of the last glaciation, a vibrant vertebrate community existed at Tsaramody, but it probably did not include forest-dependent animals. Water birds that are now extinct (*Alopochen sirabensis* and *Centrornis majori*) populated the high-altitude wetlands of Madagascar (Antsirabe) at this time.

Mid-altitude sites became much more densely forested during the deglaciation period. Many more primates occupied Ampasambazimba at that time (Table 4), including *Pachylemur jullyi*, *Megaladapis grandidieri*, *Propithecus* sp. and *Eulemur* sp. Their carbon isotope values indicate primary or exclusive consumption of C_3 resources, which are common in more shaded woodland or forested habitats. Palynological evidence at higher altitude Tsaramody suggests some contraction of open habitat during this time.

Beginning in the early Holocene, forest-dependent animals, such as lemurs, were common at high as well as middle and low elevations (Table 5). With the exceptions of highly specialized genera such as *Hadropithecus* and *Daubentonia* (see Godfrey *et al.*, 2016), and insectivorous cheirogaleids, lemurs primarily consumed C_3 resources, regardless of altitude (Crowley, 2010; Crowley *et al.*, 2011; Faure *et al.*, 2010; Muldoon *et al.*, 2012; Simons *et al.*, 1995b). This includes an early Holocene *Archaeolemur edwardsi* from Ampasambazimba (11 610 cal a BP; Crowley, 2010), whose $\delta^{13}C$ value (− 24.0‰) contrasts strongly with the *Archaeolemur* at the same site during the last glaciation ($\delta^{13}C = -16.7$‰).

During the Holocene, common wetland taxa (e.g. hippopotamuses) continued to thrive at all elevations in the Central Highlands (from 1036 m at Ampasambazimba to ~1500 m at sites such as Antsirabe and Masinandraina). However, their carbon values also suggest that they all depended on C_3 resources (although not necessarily exclusively), which in turn suggests that the Holocene habitat of the mid- and high-altitude Central Highlands included forest. For example, late Holocene hippopotamuses from Antsirabe have $\delta^{13}C$ values indicative of exclusive C_3 resource consumption. Dry periods during the mid-Holocene may have resulted in forest loss at sites over 1500 m (an *Aepyornis* from Masinandraina with a calibrated age of 5075 cal a BP has a $\delta^{13}C$ value of − 15.2‰; Burney *et al.*, 2004). More data will clarify possible effects of aridification on high-altitude sites during the Holocene, but mid-altitude sites do not appear to have been dry during that time.

Tsaramody may have existed above an elevational threshold for most forest-dependent megafauna, as there is only very sparse evidence of subfossil primates (and i.e., limited to *Archaeolemur edwardsi*) in the broader Sambaina area. Of course, the dearth of primates in the region may simply reflect the fact that our results are based on preliminary excavations. When Forsyth Major first explored Antsirabe in 1895, he found only a handful of bones of primates (his '*Nesopropithecus*' = *Archaeolemur*). Since that time, many primate species have been recorded at Antsirabe, but always in low relative abundance. Although it is possible that primates will be recovered at Tsaramody during further excavation, it is also possible that they were absent here, at least during the terminal glacial. If this is indeed the case, then the highest elevations of

Table 3. Wetland sites from the Central Highlands (subhumid forest, SF) that preserve pre- Holocene fossils, with site coordinates and representative vertebrate families.

Site	Vertebrate families represented in subfossil deposits	Source
Elevation (m) Latitude, longitude		
Tsaramody 1655 m −19°36′, 47°10′	Aepyornithidae, Anatidae, Ardeidae, Crocodylidae, Hippopotamidae, Strigidae, Testudinidae. In the greater Sambaina basin: Archaeolemuridae, Plesiorycteropodidae	This paper
Antsirabe 1490 m −19°52′, 47°02′	Aepyornithidae, Crocodylidae, Eupleridae, Hippopotamidae, Nesomyidae (including the extinct *Hypogeomys australis*), Plesiorycteropodidae, Primates (Archaeolemuridae, Lemuridae, Megaladapidae and Palaeopropithecidae), Testudinidae, many flighted birds (including extinct species *Alopochen sirabensis*, *Centrornis majori*, and *Hovacrex roberti*)	Goodman and Jungers (2014)
Ampasambazimba 1036 m −18°54′, 46°44′	Aepyornithidae, Crocodylidae, Cuculidae (the extinct *Coua berthae*), Eupleridae, Hippopotamidae, Nesomyidae, Tenrecidae, Testudinidae, Plesiorycteropodidae; Primates (Archaeolemuridae, Cheirgaleidae, Indriidae, Lemuridae, Lepilemuridae, Megaladapidae and Palaeopropithecidae), many flighted birds (including extinct anatids *Alopochen sirabensis* and *Centrornis majori* and accipitrids *Stephanoaetus mahery* and *Aquila* spp.)	Goodman and Jungers (2014)

Table 4. Dated vertebrate subfossils older than 10 000 cal a BP from Madagascar, ordered by mean calibrated age. ^{14}C dates were calibrated with Calib 7.10 and the SHCal13. Dates presented are based on 2σ ranges rounded to the nearest 5 years.

Site (bioclimatic zone*)	Taxon and specimen number	^{14}C date ± 1σ (a BP)	Mean calibrated age ± 1σ (period) (cal a BP)	Elev. (m)	Radiocarbon lab number	Source†
Faux Cap (ST)	*Aepyornis* sp. (eggshell) no spec. no.	>50 000	Too old to calibrate (glacial)	23	OZF 857	1
Ampasambazimba (SF)	*Archaeolemur edwardsi* UA-1204	29 240 ± 1730	33 170 ± 3565 (glacial)	1036	CAMS 143055	2
Antsiroandoha (DDF)	*Megaladapis grandidieri* – no spec. no.	26 150 ± 400	30 715 ± 1295 (glacial)	170	β-30982 ETH 53–55	3
Ampasambazimba (SF)	*Alopochen sirabensis* UA-360	22 500 ± 170	26 750 ± 470 (glacial)	1036	β-63116	4
Antsirabe (SF)	*Alopochen sirabensis* UA-142	19 250 ± 110	23 165 ± 330 (glacial)	1490	β-63117	4
Antsirabe (SF)	*Centrornis majori* UA-214	17 370 ± 90	20 915 ± 295 (glacial)	1490	β-63119	4
Belobaka (DDF)	*Hippopotamus laloumena*‡	>17 070 ± 530	>20 570 ± 1310 (glacial)	64	SacA 12198	5
Antsirabe (SF)	*Alopochen sirabensis* UA-119	17 100 ± 100	20 575 ± 300 (glacial)	1490	β-63118	4
Tsaramody (SF)	*Hippopotamus guldbergi*	14 580 ± 460	17 565 ± 1150 (late glacial)	1655	CAMS 173568	6
Ampasambazimba (SF)	*Pachylemur jullyi* UA-1675	13 830 ± 90	16 665 ± 325 (deglaciation period)	1036	CAMS 143102	2
Andrafiabe (DDF)	*Megaladapis grandidieri* – no spec. no.	12 760 ± 70	15 085 ± 290 (deglaciation period)	170	CAMS 6394, β-61703	3
Ampasambazimba (SF)	*Propithecus* sp. UA-8733	11 580 ± 60	13 370 ± 125 (deglaciation period)	1036	CAMS 144107	2
Ankilitelo (ST)	*Numida meleagris* DLC 18 875	11 310 ± 40	13 140 ± 90 (deglaciation period)	272	β-355564	7
Ampasambazimba (SF)	*Megaladapis grandidieri* UA-3984	11 360 ± 70	13 180 ± 125 (deglaciation period)	1036	CAMS 143117	2
Ankilitelo (ST)	cf. *Aepyornis* (eggshell) DLC 18 916	11 220 ± 50	13 015 ± 135 (deglaciation period)	272	β-355561	7
Ampasambazimba (SF)	*Eulemur* sp. UA-8939	10 140 ± 90	11 660 ± 345 (deglaciation period)	1036	CAMS 142618	2
Ampasambazimba (SF)	*Archaeolemur edwardsi* UA-1203	10 090 ± 90	11 555 ± 295 (early Holocene)	1036	CAMS 143044	2
Christmas River (SW)	*Hippopotamus lemerlei* no spec. no.	9655 ± 60	10 965 ± 215 (early Holocene)	793	Hela 1828	8
Christmas River (SW)	*Pachylemur insignis* DLC 24156	9450 ± 30	10 645 ± 90 (early Holocene)	793	CAMS 147038	8
Christmas River (SW)	*Aepyornis maximus* USNM A605209	9430 ± 55	10 620 ± 135 (early Holocene)	793	UBA-31590	9
Christmas River (SW)	*Archaeolemur* sp. DLC 24153a	9265 ± 30	10 380 ± 120 (early Holocene)	793	CAMS 147334	8
Ankilitelo (ST)	*Numida meleagris* DLC 18 875	8970 ± 40	10 055 ± 145 (early Holocene)	272	β-355565	7
Christmas River (SW)	*Aepyornis* sp. no spec. no.	9610 ± 60	10 930 ± 225 (early Holocene)	793	Hela 1829	8
Christmas River (SW)	*Aepyornis* sp. No spec. no.	9535 ± 70	10 835 ± 260 (early Holocene)	793	Hela 1774	8
Ampasambazimba (SF)	*Lepilemur mustelinus* UA-8819	9000 ± 80	10 010 ± 235 (early Holocene)	1036	CAMS 143063	2

[*] For Bioclimatic Zone abbreviations, see Table 2.

[†] Sources: 1. Clarke *et al.* (2008); 2. Crowley (2009); 3. Simons *et al.* (1997); 4. Goodman (1999); 5. Faure et al. (2010); 6. This paper; 7. Goodman *et al.* (2013); 8. Muldoon *et al.* (2018); 9. Hansford *et al.* (2019).

[‡] Date derived from calcite in associated breccia.

the Central Highlands may have functioned as barriers to primate and other forest-dependent animal dispersal before human arrival and perhaps afterwards.

The question of whether the Central Highlands served as megafaunal refugia during the Holocene, particularly during the time of the megafaunal crash, remains to be addressed. This requires that we examine the geographical locations of late occurrences for extinct species. Most 'late dates' for extinct species are for individuals from lowland sites; this is true for elephant birds and most of the extinct lemurs (Table 6). It also includes species, such as *Alopochen sirabensis*, that while known from the south and south-west (Goodman & Rakotozafy, 1997), also occupied the highest Central Highland sites during the last glaciation. The latest dates for subfossils from high-elevation sites are for hippopotamuses, present around 1000 years ago at Antsirabe

(Table 6). Some large-bodied primates (*Megaladapis grandidieri*, *Mesopropithecus pithecoides* and *Pachylemur jullyi*) survived at mid-altitude Ampasambazimba at, or past, this point in time (Table 6). However, the late date for *Hippopotamus* at Antsirabe pertains to an individual at considerably higher elevation.

Ethnohistoric records provide credible parallel evidence for very recent survival of hippopotamuses in the Central Highlands, and for many taxa, including hippopotamuses, in the lowlands (Burney & Ramilisonina, 1998; Godfrey, 1986; Raybaud, 1902). Elephant birds apparently survived into the late 1600 s in lowlands of the extreme south (Hébert, 1998), and hippopotamuses reportedly survived in the highlands (near Ampasambazimba), as well as the lowlands, into the 19th and 20th centuries. If true, this would mean hippopotamuses survived in the Central Highlands after the mid-altitude forests largely disappeared, which is not surprising, given that we now have isotopic evidence that they could exploit C_4 plants.

We perhaps know least about what happened to the horned crocodylian, *Voay robustus*. This species lived all over Madagascar, from the lowlands to sites high on the Central Highlands, including Tsaramody. Documenting its extinction is difficult because its bones are often confounded with the *Crocodylus niloticus* that lives today on Madagascar. It appears, however, that almost all crocodylians reported from subfossil sites (including all highland sites) are *Voay*, which suggests that *Crocodylus niloticus* may have only arrived very recently. A single date for *Voay* from the coastal site of Ankilibehandry in western Madagascar proves that this species, like Madagascar's other megafauna, survived into the late Holocene (1920 ± 30 ^{14}C a BP, or 1813 ± 78 cal a BP, CAMS 167399; previously unpublished). A single radiocarbon date for subfossil *Crocodylus niloticus* from Anjohibe in the north-west is more recent (360 ± 25 ^{14}C a BP, or 385 ± 75 cal a BP, CAMS 150524; Crowley & Samonds, 2013; Mathews & Samonds, 2016). These two dates are consistent with the recent arrival of *C. niloticus* to Madagascar but fail to resolve the question of possible prolonged temporal overlap between *V. robustus* and *C. niloticus*, or specifically whether *Crocodylus* may have outcompeted *Voay*, or if *Voay* disappeared before *Crocodylus* arrived (Brochu, 2007; Burney *et al.*, 1997).

Future data on the habitat history of Tsaramody and other highland sites should shed light on the role humans may have played in the evolution of Madagascar's open grassy biomes and the disappearance of Madagascar's native woodland and forest habitats. We can summarize our current knowledge as follows. First, during the late glacial and early part of the deglaciation period, well before humans arrived, high-elevation sites in the Central Highlands supported hippopotamuses and crocodylians, but apparently not primates and other forest-dependent species. At the height of the last glaciation, mid-altitude sites were hospitable only to the least arboreal of primates, and probably also had limited forest. However, a large community of forest-dependent species did occupy localities as high as ~1000 m asl early in the deglaciation period, and this continued through the Holocene, when localities at even higher elevation also became at least partially forested.

Open grassy biomes are far more extensive today than they were even during the late glacial or early deglaciation periods. Grasses extend today from the lowlands to the highest elevations in the Central Highlands. They thus create a far more formidable barrier to dispersal by forest-dependent taxa than they did in the past. It is not unreasonable to assume that the reason hippopotamuses were among the last (if not the last) of the megafauna to have disappeared from the Central Highlands is that, unlike forest-dependent species, they can survive in more open biomes.

We are beginning to track the precise timing of the very recent spread of grasslands across the highlands and the lowlands of Madagascar. For example, at Anjohibe (a north-west lowland site which today has dry deciduous forest), a dramatic and rapid transformation occurred over a 100-year interval beginning around 1100 years ago (Burns *et al.*, 2016). This transformation was attributed to anthropogenic fire; it occurred during the wettest time within the past 2000 years and therefore cannot have been triggered by aridification (Burns *et al.*, 2016; Scroxton *et al.*, 2017). Other habitat transformations occurred at approximately the same time (Godfrey *et al.*, 2019). Whether the spike in grass

Table 5. A chronological perspective on Malagasy habitat variation during the late Pleistocene and Holocene.

Elevation (m)	Glaciation >17 000 cal a BP	Deglaciation 17 000–11 650 cal a BP	Holocene <11 650 cal a BP
High (generally ~1500 m asl or higher)	Open habitat, wetlands, ericaceous heathland. This is replaced at Tsaramody by savanna during the transition to deglaciation. The habitat was hospitable to waterbirds, and as grass replaced heaths at the end of the glacial period, a rich megafaunal community (hippopotamuses, crocodylians and elephant birds but not primates) lived here. At Tsaramody during the late glacial, there is evidence that hippos consumed both C_3 and C_4 resources.	Pollen spectra show some contraction of open habitat and increase in wooded habitat.	Primates and other forest-dependent species occur at elevations up to ~1500 m asl (e.g. Antsirabe). C_3 plants are the primary resources for these animals. A mid-Holocene dry event may have reduced wooded habitat at high-altitude sites. At Masinandraina, there is evidence that *Aepyornis* consumed a mixture of C_3 and C_4 resources; this is an animal that elsewhere consumed primarily C_3 resources.
Mid (~1000 m asl)	Habitat at Ampasambazimba was sufficiently wooded to support *Archaeolemur*, which survived on a diet of mixed C_3 and C_4 resources. There is no evidence of occupation by more arboreal primates.	Primates and other forest-dependent species are now abundant at mid-altitude sites such as Ampasambazimba. C_3 plants are their primary resources. Forested habitat inferred.	Primates and other forest-dependent species occur here. C_3 plants are the primary resources for large-bodied lemurs.
Low (coastal to ~500 m asl)	Primates and other forest-dependent species occur here.	Primates and other forest-dependent species occur here. C_3 plants are the primary resources for large-bodied lemurs.	Primates and other forest-dependent species occur here. C_3 plants are the primary resources for large-bodied lemurs.

Table 6. Late occurrences of hippopotamuses, crocodylians, elephant birds, geographically widespread primates and extinct waterbirds at subfossil sites in Madagascar. ^{14}C dates were calibrated using Calib 7.1 and the SHCal13. Dates presented are based on 2σ ranges rounded to the nearest 5 years.

Taxon	Site (bioclimatic zone[*])	^{14}C age ± 1σ (a BP)	Mean calibrated age ± 1σ (cal a BP)	Spec no.	Laboratory no.	Source[†]
Hippopotamus	Taolambiby (ST)	1440 ± 30	1315 ± 40	Uncat.	CAMS 142734	1
	Antsirabe (SF)	1260 ± 25	1125 ± 65	Uncat.	CAMS 142540	1
	Antsirabe (SF)	1215 ± 25	1080 ± 100	Uncat.	CAMS 143065	1
	Itampolo (ST)	980 ± 200	910 ± 355	Not given	Gak 1506	2
Voay robustus	Ankilibehandry (Belo-sur-mer) (DDF)	1920 ± 30	1815 ± 80	BSM Square 4, layer 6 70–90 cm	CAMS 167399	3
Elephant birds	Maroaloke (ST)	1415 ± 40	1270 ± 85	Not given	OxA-5078	4
	Ankilibehandry (Belo-sur-mer) (DDF)	1280 ± 60	1165 ± 115	BSM 95–10	β-103349	5
	Irodo (DDF)	1150 ± 90	1045 ± 145	Not given	Gak	2
	Andrahomana (ST)	1000 ± 150	910 ± 270	Not given	UCLA 1893	6
	Manambovo (ST)	840 ± 80	740 ± 105	Not given	Not given	7
Alopochen sirabensis	Anavoha (ST)	1380 ± 90	1235 ± 180	Not given	β-63675	8
Archaeolemur	Anavoha (ST)	1265 ± 25	1150 ± 90	UA 1337	CAMS 142613	1
Megaladapis	Ampasambazimba (SF)	1035 ± 50	875 ± 95	BMNH M 9927	Pta-739	9
	Ankilitelo (ST)	630 ± 50	585 ± 65	Not given	Not given	10
Mesopropithecus	Ampasambazimba (SF)	1410 ± 40	1260 ± 80	Not given	NZA 18523	11
Pachylemur	Ampasambazimba (SF)	1300 ± 30	1175 ± 95	UA 1708	CAMS 142605	1
	Tsirave (SW)	1050 ± 20	890 ± 70	UA 3041	UCIAMS 167925	12
Palaeopropithecus	Ankazoabo Grotte (ST)	1150 ± 160	1010 ± 290	UA-AM 6184	NZA	13
	Ankilitelo (ST)	510 ± 80	475 ± 155	Not given	Not given	10

[*] For Bioclimatic Zone abbreviations, see Table 2. All highland sites are SF.

[†] Sources: 1. Crowley (2010); 2. Mahé and Sourdat (1972); 3. This paper; 4. Parker Pearson et al., 1997; 5. Burney (1999); 6. Berger et al., 1975; 7. Battistini et al., 1963; 8. Goodman and Rakotozafy (1997); 9. Tattersall (1973); 10. Simons (1997); 11. Burney *et al.* (2004); 12. Penn State, unpublished; 13. Karanth et al., 2005.

pollen (to 45%) that we observed in Level 7 sediments at Tsaramody occurred at this time has yet to be determined.

Conclusions

Sites like Tsaramody provide a unique opportunity to study how the Central Highlands may have functioned as a barrier to dispersal of forest-dependent species and/or as a sanctuary for other vertebrates before, and after, the arrival of the first human settlers to Madagascar. Here we provide preliminary observations (within a comparative framework) of the flora and fauna at Tsaramody, which is 1655 m above sea level. The pollen profile reveals a vegetation history dating back to the last glacial period. The ericaceous heathland that blanketed the Sambaina region at the height of the Last Glacial Maximum changed gradually into an open wetland habitat dominated by grasses and marsh plants, and populated by water-dwelling megafauna (hippopotamuses and crocodylians), as well as aquatic birds and some terrestrial vertebrates. Tsaramody became increasingly (though never densely) forested as temperatures increased and deglaciation proceeded; heath plant abundance remained very low and grasses fluctuated between ~20% and 35% of the total pollen count. In an upper stratigraphic level, grass abundance rises to 45%; whether this late surge was human-induced remains to be determined, but it is underlain by sediments with evidence of human presence (in the form of a spike in the dung fungus *Sporormiella*, and the presence of introduced and cultivated plants).

Our data indicate that, even during glacial times, diverse megafaunal communities occupied the Central Highlands, although high-elevation sites were inhospitable to forest-dependent animals. As the climate warmed and open habitat shrank, forest-dependent species spread to higher elevations. The Central Highlands functioned as a barrier to non-volant forest-dependent species during the last glaciation, but during deglaciation and well into the Holocene, some mid-altitude sites became corridors for their dispersal. High-altitude sites may have remained inhospitable to many such species until the Holocene, when scansorial and arboreal primates occupied forests as high above sea level as Antsirabe (~1500 m). Sites at elevations below the Central Highlands (i.e. below 800 m) may not have served as barriers to dispersal. This includes Christmas River which (at 793 m) lies just below the lower limit for the Central Highlands. The early Holocene fauna of Christmas River included not merely water-dwelling fauna such as hippos and crocodiles, but also more terrestrial and forest-dependent fauna including *Aepyornis maximus*, euplerids, archaeolemurids, megaladapids and lemurids (Hansford *et al.*, 2018; Muldoon *et al.*, 2012).

The question of whether Madagascar's open grassy biomes are ancient or human-induced presents a false dichotomy; they are both. Today's grasslands, occurring in non-specialized habitats (marshes, high elevation and particular geological substrates), largely maintained by anthropogenic activities, are more expansive than were the natural grassy biomes of the last glaciation and deglaciation periods. What is needed is greater attention to the taxonomic differences between ancient and human-induced grasslands, and the extent to which the former have been replaced by the latter. In the past, sparsely forested habitats accommodated many megafauna, with the exception of primates, particularly when they were also wet. Hippopotamuses were dominant members of these communities. Primates were not. Interestingly and not surprisingly, the Central Highlands continued to provide refugia for hippopotamuses after the forests declined in the past millennium.

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Abbreviations. DDF, dry deciduous forest; HF, humid forest; NISP, number of identifiable specimens; SF, subhumid forest; ST, spiny thicket; SW, succulent woodlands.

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