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A new interpretation of Madagascar's megafaunal decline: The "Subsistence Shift Hypothesis"

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ABSTRACT

Fundamental disagreements remain regarding the relative importance of climate change and human activities as triggers for Madagascar's Holocene megafaunal extinction. We use stable isotope data from stalagmites from northwest Madagascar coupled with radiocarbon and butchery records from subfossil bones across the island to investigate relationships between megafaunal decline, climate change, and habitat modification. Archaeological and genetic evidence support human presence by 2000 years Before Common Era (BCE). Megafaunal decline was at first slow; it hastened at ~700 Common Era (CE) and peaked between 750 and 850 CE, just before a dramatic vegetation transformation in the northwest that resulted in the replacement of C_3 woodland habitat with C_4 grasslands, during a period of heightened monsoonal activity. Cut and chop marks on subfossil lemur bones reveal a shift in primary hunting targets from larger, now-extinct species prior to ~900 CE, to smaller, still-extant species afterwards. By 1050 CE, megafaunal populations had essentially collapsed. Neither the rapid megafaunal decline beginning ~700 CE, nor the dramatic vegetation transformation in the northwest beginning ~890 CE, was influenced by aridification. However, both roughly coincide with a major transition in human subsistence on the island from hunting/foraging to herding/farming.

We offer a new hypothesis, which we call the "Subsistence Shift Hypothesis," to explain megafaunal decline and extinction in Madagascar. This hypothesis acknowledges the importance of wild-animal hunting by early hunter/foragers, but more critically highlights negative impacts of the shift from hunting/foraging to herding/farming, settlement by new immigrant groups, and the concomitant expansion of the island's human population. The interval between 700 and 900 CE, when the pace of megafaunal decline quickened and peaked, coincided with this economic transition. While early megafaunal decline through hunting may have helped to trigger the transition, there is strong evidence that the economic shift itself hastened the crash of megafaunal populations.

1. Introduction

Whereas it is well known that Madagascar's megafauna declined and vanished after humans arrived, the relative importance of climate and human impacts (whether through hunting or habitat modification) as triggers for megafaunal extinction continues to be debated (see Battistini, 1965; Dewar, 1984; Burney et al., 2003, 2004; Crowley, 2010; Douglass and Zinke, 2015; Burns et al., 2016; Ekblom et al., 2016; Crowley et al., 2017; Salmona et al., 2017; Anderson et al., 2018; Douglass et al., 2018; Hixon et al., 2018). Explanations generally focus on climatic or anthropogenic pressures, or both. Disentangling the effects of "natural" and "human-induced" change can be difficult, especially

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since natural aridification and human disturbance (e.g., fire, deforestation, or agriculture) can have similar effects on the distributions and abundance of endemic plants and animals. Most explanations for the extinction of Madagascar's megafauna posit complex sequences of events. The data, however, do not support the proposed sequences and over the past two decades no consensus has emerged.

The “synergy” hypothesis (Burney et al., 2003, 2004) maintains that humans were the primary triggers for extinction, although periods of aridification prior to human arrival may have increased the vulnerability of the megafauna. According to this hypothesis, human arrival around 2400 years ago was followed in rapid succession by: (1) megafaunal population crash (due to megafaunal hunting primarily in more open habitats), (2) the expansion of open habitats (due to a surge in the intensity of natural fires in grassy biomes now uncontrolled by grazers), (3) shrinking forests (due to the impact of fire), and (4) concomitant extinction of forest-dependent large-bodied lemurs and other creatures. The main inferences of this hypothesis are that the megafaunal crash occurred largely in the first part of the first millennium CE (within several centuries of human arrival), and that it preceded and in effect triggered habitat change through fire. Furthermore, it preceded the introduction of many domesticated plants and animals, which in turn occurred with the expansion of the trade network and early spread of settlement sites almost 1000 years later.

In contrast, Virah-Sawmy et al. (2009, 2010) argued that habitat change occurred in synchrony across Madagascar, but not because of fire set by humans; rather, it was island-wide drought that triggered both habitat change and the megafaunal crash. According to this hypothesis, the megafauna declined long after humans arrived, in association with the peak of a devastating drought. Early episodes of aridification in the northwest (Wang and Brook, 2013), central highlands (Gasse and Van Campo, 1998), southwest (Mahé and Sourdat, 1972; Burney, 1993; Goodman and Rakotozafy, 1997) and southeast (Virah-Sawmy et al., 2009, 2010) were not always synchronous. However, gradual drying between 50 and 1000 CE (1900 and 950 calendar years before present, or cal BP) culminated in an island-wide drought between 950 and 1050 CE that was sufficiently strong to trigger megafaunal extinction (Virah-Sawmy et al., 2009, 2010). This hypothesis posits that habitat change triggered megafaunal extinction, and not the opposite, as is maintained by the synergy hypothesis. It also places the megafaunal crash approximately 1000 years later than does the synergy hypothesis. Clearly, to evaluate these hypotheses, we must better understand the timing of the megafaunal crash, the climate of Madagascar before and during the crash, and what humans were doing at the time. Did the crash occur prior to, just after, or well after human arrival?

Here, we revisit the question of megafaunal extinction by updating and comparing three sources of data that bear on the question. First, the radiocarbon record for subfossil vertebrates has improved significantly since the publication of Burney et al.'s (2004) chronology for late prehistoric Madagascar (97 dates), and indeed since the publication of Crowley's (2010) updated chronology (320 dates). Four hundred and thirty-eight dates are now available (see Crowley and Godfrey, 2013; Crowley and Samonds, 2013; Crowley et al., 2017), 195 of which fall within the period critical for testing extinction hypotheses – i.e., the period during which time large-bodied vertebrates declined and ultimately vanished (between 50 BCE and 1350 CE).

Second, we offer new data on human butchery of extinct lemurs during the past 2000 years. To improve on prior records, we evaluated 183 humeri and femora of *Pachylemur insignis* from Tsirave in the collection of the Université d'Antananarivo. We identified perimortem cut and/or chop marks on several dozen individuals, eight of which we radiocarbon dated (Crowley et al., 2017). We also checked previously-dated humeri and femora of extinct lemurs in the collection at the Université d'Antananarivo for evidence of human butchery.

Our third important new source of data is calcium carbonate cave deposits, or speleothems (such as stalagmites). In recent years, there has been an increased interest in investigating Madagascar's past climate and habitat transformations using speleothems (Brook et al., 1999; Burns et al., 2016; Scroxton et al., 2017; Voarintsoa et al., 2017). Speleothems provide an underutilized (in Madagascar) high resolution and precisely dated record of past climate and environmental changes (Fairchild and Baker, 2012). Depending on the sampling resolution and degree of hydrological averaging in the karst host rock above the cave, speleothem records can range from decadal to subannual in resolution. Recent improvements in mass spectrometry techniques allow for radiometric U–Th disequilibrium dating of speleothems with errors frequently less than 1%, enabling the construction of very precise chronologies (Hellstrom, 2003; Cheng et al., 2013). For example, half of the U–Th dates from a stalagmite from Anjohibe Cave in northwestern Madagascar have 2σ errors that are less than a decade (Scroxton et al., 2017).

In addition to providing precise, accurate chronologies, speleothems provide continual records of changes in past vegetation and rainfall through the use of stable carbon and oxygen isotope ratios respectively (McDermott, 2004; Lachniet, 2009). Carbon isotope values recorded in stalagmites can be used to identify major shifts in vegetation on land overlying caves because, in karst systems, isotope signals are transferred from plants to soil waters to speleothem carbonate (reviewed in McDermott, 2004). The $\delta^{13}C$ values in stalagmites may be affected by a variety of factors, including the amount of isotope discrimination by plants, soil respiration rates, the degree of air-solution CO_2 exchange in the soil and epikarst (Genty et al., 2001; Wong and Breecker, 2015), and the extent of CO_2 degassing at the stalagmite surface. Major changes in the $\delta^{13}C$ values of speleothems, however, may also reflect shifts in vegetation type (i.e., shifts from forest to grassland), which may or may not be climate-driven (Dorale et al., 1998; Burns et al., 2016). When vegetation is dominated by C_3 plants, speleothem carbonates can be expected to yield $\delta^{13}C$ values between $-14‰$ and $-6‰$. In contrast, carbonates deposited in equilibrium with CO_2 respired from C_4 plants will generally exhibit $\delta^{13}C$ values between $-6‰$ and $+2‰$ (McDermott, 2004). Oxygen isotope values in speleothems are also used as records of rainfall variability. In the tropics, and under monsoonal rainfall regimes such as those that typify Madagascar, speleothem $\delta^{18}O$ values typically act as a proxy for the strength of monsoon circulation: oxygen isotopes are fractionated during repeated convection and re-evaporation in the sub-cloud layer (Risi et al., 2008). As a result, under highly convective monsoonal systems, the $\delta^{18}O$ values of precipitation are correlated with regional rainfall amount (Risi et al., 2008; Kurita et al., 2009; LeGrande and Schmidt, 2009). Minor modification of the $\delta^{18}O$ signal can occur during transit through the karst and during speleothem formation, particularly in caves with low humidity and high airflow, which promote evaporation rather than degassing on the speleothem surface. The most reliable speleothem records are taken from caves with low airflow and high humidity.

Burns et al. (2016) produced a sub-decadal stable isotope record from two stalagmites (AB2 and AB3) from Anjohibe cave in northwestern Madagascar. From these stalagmites, a reproducible record of $\delta^{13}C$ values served as a proxy for vegetation changes above the cave, while associated $\delta^{18}O$ records served as a proxy for variation in rainfall. Voarintsoa et al. (2017) analyzed three additional stalagmites from the same cave (MA2, MA3 and ANJ94-5), effectively corroborating many of the conclusions drawn by Burns et al. (2016). Using higher resolution stable oxygen isotope data and detailed mineralogical assessment of an intensively sampled stalagmite, AB2, Scroxton et al. (2017) have since documented changes in rainfall on a quasi-annual scale and identified climate fluctuations at centennial scales. This was a substantial improvement over the sub-decadal record produced by previous studies.

The effects of climate and human activities can be decoupled when carbon and oxygen isotope proxies from stalagmites are considered together. Simultaneous and coherent increases or decreases in the two proxies indicate a likely rainfall control on changes in vegetation, soil and epikarst processes. In contrast, abrupt changes in carbon isotope values, particularly positive excursions (signaling a change from C_3- to C_4-dominated habitats) with no corresponding shifts in oxygen, indicate a non-climatic forcing on vegetation.

In this paper, we generate a new chronology for Late Holocene Madagascar by combining data from our updated radiocarbon, butchery, and stalagmite chronological and isotope records. Ultimately, we seek to use our chronology to test hypotheses and gain new insights on the events that triggered the decline and disappearance of the island's megafauna. Specifically, we address the following questions: (1) What does the radiocarbon record tell us about the trajectory and timing of Madagascar's megafaunal decline? (2) What does the subfossil record tell us about the temporal context of human consumption of large versus small-bodied endemic species? (3) What do $\delta^{18}O$ values from stalagmites at Anjohibe tell us about wet and dry periods in northwestern Madagascar over the period during which the megafauna crashed, and relative to local changes in vegetation? (4) Can we make climate generalizations for other regions of Madagascar on the basis of conditions recorded in the northwest?

2. Materials and methods

2.1. Trajectory of megafaunal decline

We searched for evidence of a temporal shift in the relative prevalence of extinct versus extant animals in subfossil deposits. We restricted our search to the period between 50 BCE and 1350 CE (i.e., 2000 to 600 cal BP) as prior research demonstrates unequivocally that megafaunal decline occurred during this period (Burney et al., 2004; Crowley, 2010). Furthermore, for taphonomic reasons, there are very few radiocarbon-dated extant animal bones that are older than this (Fig. 1). Subfossil sampling is uneven across centuries within this search interval, so tracking simple changes in megafaunal frequency per unit time is not the best metric for understanding megafaunal decline.

Instead, we measured the difference between the ratios of bones of extinct to extant species before and after selected times (or cut-points) within our full search interval (50 BCE to 1350 CE). We constructed a series of two-by-two tables of frequencies of extinct versus extant animals every 100 years across the entire 1400-year period (thus, for example, before and after 50 CE, before and after 150 CE, before and after 250 CE, etc.), and considered the prevalence of extinct and extant animals before and after each. We then measured the “odds ratio” for each table by calculating the ratios of bones of extinct to extant species occurring before and after each selected cut-point, and comparing the two ratios. Changes in the odds ratios across the 2 by 2 tables reflect changes in the pace of megafaunal decline. They can be quantified using any of a series of well-known and intimately-related statistics, such as the odds ratio, the odds themselves, the cross product ratio, or either of the common χ^2 statistics (Pearson or maximum likelihood). Here, we used maximum likelihood χ^2 statistics as our descriptive tool to characterize the trajectory of megafaunal decline.

2.2. Records of human butchery

We investigated human exploitation of extinct versus extant terrestrial vertebrates, looking for evidence of a temporal shift. Published records of dated butchered bones from Madagascar are meagre, but recent surveys and a newly-expanded radiocarbon database have accorded us the opportunity to add significantly to them. Cut and chop marks on fresh bone have features that distinguish them from scratches resulting from natural abrasion, the teeth or claws of predators, or excavation trowels and shovels (Perez et al., 2005; Meador et al., 2017) (Fig. 2). We followed the methods of Perez et al. (2005) in identifying cut and chop marks.

Our present analysis of butchery includes only dated bones that exhibit the pattern of purpose associated with human processing of meat for consumption, and that fall within our search interval. Our tally therefore excludes undated butchered bones of extinct species (e.g., a chopped femur of *Hadropithecus* illustrated by Godfrey et al., 2006a, and modified *Aepyornis hildebrandti* from Antsirabe documented by Hansford et al., 2018), and bones exhibiting postmortem human modification, such as an elephant bird tibiotarsus from Itampolo (Burney et al., 2004). We excluded elephant bird eggshell that is currently being tested for perimortem versus postmortem exploitation, and modified marine shell dated at nearly 3000 years old, all from the Velondriake Marine Protected Area in southwest Madagascar (Douglass, 2016). We also excluded butchered bones of extinct and extant species from Beanka (near Bemaraha in northwestern Madagascar) that are currently being analyzed and dated (LRG and VRP, pers. obs.). Finally, butchered specimens falling well outside our search interval such as limb bones of *Aepyornis maximus* at Christmas River in south central Madagascar and *Mullerornis* sp. from Lamboharana on the southwest coast (Hansford et al., 2018) were excluded from our analysis. Claims of butchery for *Hippopotamus* bones from Anjohibe and *Palaeopropithecus* bones from Taolambiby's Methuen collection have been challenged (cf. Perez et al., 2005; Gommery et al., 2011; Goodman and Jungers, 2014; Anderson et al., 2018). These bones are also outside our search interval and are not further considered here.

We did include butchered hippopotamus and elephant bird bones from Lamboharana and Ambolisatra (MacPhee and Burney, 1991; Hansford et al., 2018) and an extinct lemur from Manombo Toliara that fall within our search interval. Two paleontological sites, Taolambiby and Tsirave, both in south central Madagascar, have sufficient numbers of radiocarbon-dated butchered bones within our search interval to yield information regarding “clusters” of dates. These sites were initially excavated in the early 1900s; Paul Methuen collected at Taolambiby in 1911, and Charles Lamberton at Tsirave in 1930. In 1966, Alan Walker revisited Taolambiby with Paul Martin. Both recognized it as a butchery site; Paul Martin found pottery sherds and a carapace of a tortoise that he believed was artificially perforated (Raison and Vérin, 1967). Walker collected bones of lemurs and other animals, some of which were butchered. Most of the subfossil bones in this collection belonged to extant animals; however, Walker's collection also included some extinct lemurs (*P. insignis*, *Archaeolemur majori*, and *Palaeopropithecus ingens*). This collection was later donated to the University of Massachusetts, Amherst, after which some butchered specimens were radiocarbon dated. A chopped distal ulna of *Palaeopropithecus* reported by Perez et al. (2005) failed to yield a date, but 12 butchered specimens of the extant lemur, *Propithecus*, did; one was modern.

In contrast to Taolambiby, Tsirave was not identified as a butchery site until 2005, when Perez et al. (2005) figured a butchered femur of *P. insignis* from this site. No artifacts have been reported from this site.

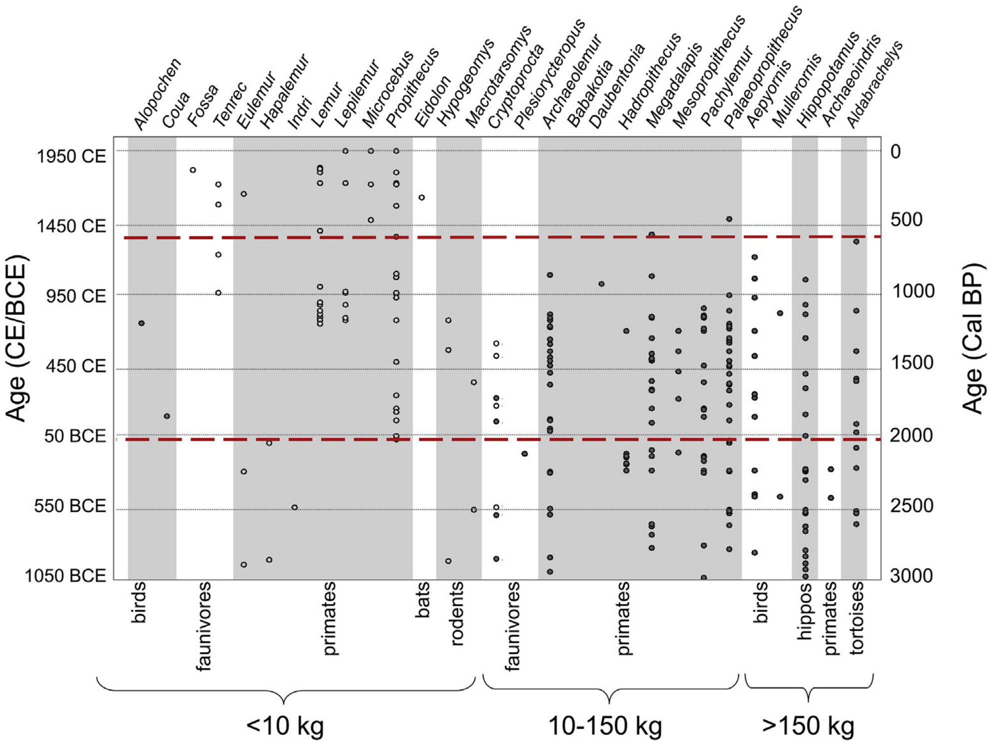

Figure 1. Published radiocarbon records for extinct and extant taxa in subfossil deposits over the past three thousand years (modified from Crowley, 2010). White circles represent extant species. Gray circles represent extinct species. Horizontal dashed lines show the boundaries of our search interval. When both extinct and extant species belonging to a single genus have both been dated (e.g., *Cryptoprocta spelea* and *C. ferox*), single columns can include both white and gray circles. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

To characterize the distribution of radiocarbon dates for specimens within our search interval from these sites, we identified individual clusters as groups of individuals whose ^{14}C dates fall within ±1 standard deviation of one another. For these calculations, we used the standard deviations associated with raw ^{14}C dates, which are appropriate measures of the associated dispersion, and often considerably smaller than standard deviations associated with calibrated ages.

2.3. *Using stalagmites to assess climate shifts in time and space*

We used five published stalagmite paleoclimate records from Anjohibe (AB2, AB3, MA3, MA2, and ANJ94-5) to assess climatic and vegetative changes in northwestern Madagascar over the past two millennia. Three of these stalagmites (AB2, AB3, and MA3), which were previously analyzed for changes in vegetation, document a shift from predominantly C_3 to predominantly C_4 vegetation

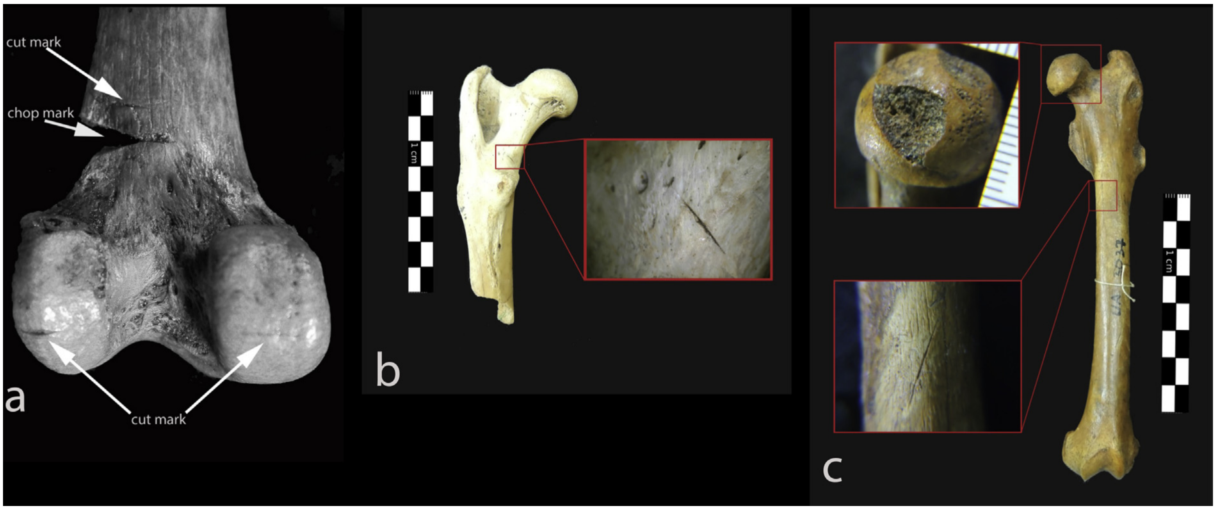

Figure 2. a) UA 3059 left femur of *P. insignis* from Tsirave, originally published by Perez et al. (2005), showing one chop mark and three cut marks (one just proximal to the chop mark and two oriented horizontally across both femoral condyles); b) UA 1451 left femur of *A. majori* from Manombo Toliara, with cut marks indicative of dismemberment, including one on the posteromedial portion of the neck, just distal to the femoral head, and two, also on the posteromedial aspect of the bone, proximal to the lesser trochanter; c) UA 3037 left femur of *P. insignis* from Tsirave, showing anterior aspect, with two chop marks on the femoral head and several cut marks on the anterior shaft, including one just distal to the lesser trochanter. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

beginning in the late 800s CE. This shift was first identified in the $\delta^{13}C$ records of stalagmites AB2 and AB3 (Burns et al., 2016), and replicated in stalagmite MA3 (Voarintsoa et al., 2017). All five stalagmites have been analyzed for $\delta^{18}O$ values, but only one (AB2) at exceptionally high resolution (Scroxton et al., 2017). Its $\delta^{18}O$ record was interpreted as evidence of variation in monsoonal rainfall in northwestern Madagascar over the past 1700 years (the age range covered by AB2; Scroxton et al., 2017). These authors used Bayesian Change Point Analysis (BCPA), a statistical treatment that determines points in time at which changes in the mean state of isotopic variability occur (Ruggieri, 2013), to identify a series of relatively wet and dry periods.

To determine to what extent the stalagmite records of Anjohibe can be considered to reflect regional (as opposed to local) climate variability, Scroxton et al. (2017) compared the new high-resolution Anjohibe stalagmite data with paleoprecipitation records from two sites in East Africa: Lake Challa on the border of Kenya and Tanzania (Buckles et al., 2016), and Lake Naivasha in Kenya (Verschuren et al., 2000). They found regional synchronicity in rainfall variability over the past two millennia on a multi-centennial scale.

To assess intra-Madagascar coherency in modern rainfall (i.e., whether the climate of the northwest is representative of the island as a whole), we correlated rainfall anomalies in the region of Anjohibe with rainfall anomalies across Madagascar using the CRU TS3.23 dataset (Harris et al., 2014), which interpolates climate anomalies from over 4000 high quality weather stations and an existing (1961–1990) climate baseline to produce 0.5° gridded monthly climate data from 1901 to the present. We averaged monthly precipitation anomalies to the hydrological year (July–June) and correlated them with anomalies at the Anjohibe grid cell using the Koninklijk Nederlands Meteorologisch Instituut's (KNMI) climate explorer (Trouet and Van Oldenborgh, 2013). Given the paucity of historical weather station data in Madagascar, variability in the dataset is likely to be of low spatial resolution. However, we observed no significant change in the spatial extent of the correlation when using different time periods varying in length, age, or both. We therefore believe that the spatial correlation is not dependent on the number of weather stations.

3. Results

3.1. Trajectory of megafaunal decline

Our database of 195 radiocarbon-dated subfossil vertebrates falling between 50 BCE and 1350 CE reveals the existence of a constrained period of exceptionally rapid change in the relative frequencies of extinct to extant animals. This can be seen in the maximum likelihood χ^2 values for a sequence of two-by-two subtables, each comparing the frequencies of extinct and extant subfossils before and after a single cut-point (Table 1). Each sub-table necessarily totals 195 individuals, as each considers all individuals within the entire 1400-year interval; they differ only in the cut-point selected for quantifying “before” and “after” odds.

The maximum likelihood χ^2 statistic increases gently (from 14.0 to 16.2 to 19.0) at cut-points 450, 550, and 650 CE, after which it rises sharply (to 30.8) in one century, and then peaks at 32.7 at cut-point 850 CE (Table 1). This peak marks the transition from extinct-dominated odds (>2.5:1, extinct to extant, prior to 850 CE) to extant-dominated odds (<1:1, extinct to extant, after 850 CE). The maximum likelihood χ^2 statistic then falls sharply over the next two centuries (Table 1). The steep decline in χ^2 values between 850 and 950 CE (from 32.7 to 20.9) mirrors the steep rise (from 19.0 to 30.8) between 650 and 750 CE; the subsequent fall (from 20.9 to 6.9 between 950 and 1050 CE) exceeds that of the rise (from 16.2 to 19.0) between 550 and 650 CE. After 1050 CE, megafaunal populations were likely very small, and their further decline did little to alter the extinct to extant odds in subfossil deposits.

In summary, the period of greatest change in odds ratios began between 650 and 750 CE (prior to which the odds decisively favored extinct animals) and ended between 850 and 950 CE (by which time the opposite was true). By 1050 CE, megafauna were rare across the island.

3.2. Records of human butchery or modification of fresh bone

Figure 3 shows the geographic distribution of subfossil specimens with cut- or chop marks that fall within our search interval (i.e., 50 BCE to 1350 CE). Dated, butchered individuals belonging to five extinct species (*Hippopotamus lemerlei*, *A. maximus*, *Mullerornis* sp., *A. majori*, and *P. insignis*) come from four sites (i.e., Ambolisatra, Lamboharana, Manombo-Toliara, and Tsirave) (Table 2). Butchered bones of the extant species, *Propithecus verreauxi*, are all from Taolambiby. Of the 24 specimens listed on Table 2, 22 fall within a narrow period from 770 to 1140 CE.

New records of butchery include an *A. majori* from Manombo-Toliara (southwestern Madagascar) and eight specimens of *P. insignis* from Tsirave, all of which fall within our search interval (Table 2). Tsirave proves to have been a site with heavy butchery activity, and our new radiocarbon dates enable us to combine butchery records from Tsirave with those previously collected at Taolambiby (Perez et al., 2005) in analyzing temporal changes in human butchery practices. Using our single standard deviation cluster-search rule, seven of the eight radiocarbon-dated butchered bones of *Pachylemur* from Tsirave form a cluster with a mean age of 834.3 CE and range of 825–870 CE. One individual, at 940 CE, falls outside this cluster. The full date range for 41 *P. insignis* from Tsirave covers 2990 years; the clustering we observe in the modified bones is not random. It appears that Charles Lamberton dug through a human occupation layer at this paleontological site without recognizing it as such. Eleven radiocarbon-dated butchered bones of *Propithecus* from Taolambiby form three clusters: the first at 942.5 CE ($n = 6$, range 930–955 CE), the second at 1023.3 CE ($n = 3$, range 1000–1065 CE) and the third at 1135 CE ($n = 2$, range 1130–1140 CE) (Table 2).

The observed date clusters for butchered extinct and extant lemurs from Taolambiby and Tsirave, each spanning less than 100 years, exist within sites that individually span ~4000 years (1805 BCE to modern for Taolambiby, $N = 71$; and 1850 BCE to 1810 CE for Tsirave, $N = 61$). Thus, the existence of time-constrained clusters at these sites is not an artifact of limited time sampling at single sites. Rather, the temporal clustering of butchered specimens at Taolambiby and Tsirave provides possible evidence for the existence of human occupation layers that were destroyed by excavation. The single cluster of butchered *Pachylemur* from Tsirave (825–870 CE) is older than all three clusters of extant *Propithecus* from Taolambiby (i.e., 930–955, 1000–1065, and 1130–1140 CE). Moreover, clusters for extinct and extant lemurs fall on opposite sides of our estimated inversion point for extinct-extant subfossil odds (850 CE).

3.3. Stalagmite records of shifts in climate in space and time

Figure 4a-i document the concurrent climate and vegetation histories reflected in stalagmites AB3 (Fig. 4a-c), AB2 (Fig. 4d-f), and MA3 (Fig. 4g-i) at Anjohibe. A very large monotonic shift observed in the $\delta^{13}C$ values of stalagmites AB3 and AB2 by Burns et al. (2016) and replicated in MA3 by Voarintsoa et al. (2017) beginning in the late 800s CE was interpreted as evidence for a vegetation shift from a landscape dominated by C_3 vegetation to one dominated by C_4 vegetation (Fig. 4b, e, and h, yellow box). Conversely, the $\delta^{18}O$ records from Anjohibe stalagmites (Fig. 4c, f, and i) demonstrate that

Table 1

The pace of change in extinct-to-extant subfossil odds, quantified using the maximum likelihood χ^2 statistic for eight 2 × 2 tables, each with a different temporal cut-point, within our search interval (50 BCE to 1350 CE).

Cutpoint (yrs CE)	Time bin	Frequency extinct	Frequency extant	Maximum likelihood χ^2
1150	1150 CE—1350 CE	2	4	4.334
	50 BCE—1150 CE	141	48	
1050	1050 CE—1350 CE	7	9	6.858
	50 BCE—1050 CE	136	43	
950	950 CE—1350 CE	10	18	20.884
	50 BCE—950 CE	133	34	
850	850 CE—1350 CE	20	29	32.718 (peak)
	50 BCE—850 CE	123	23	
750	750 CE—1350 CE	47	40	30.775
	50 BCE—750 CE	96	12	
650	650 CE—1350 CE	67	42	19.022
	50 BCE— 650 CE	76	10	
550	550 CE—1350 CE	78	44	16.175
	50 BCE—550 CE	65	8	
450	450 CE—1350 CE	93	47	13.974
	50 BCE—450 CE	50	5	

there was no dramatic, sustained change in rainfall at any time over the past two millennia, but that some modest variability did occur at the centennial scale (Scroxton et al., 2017).

Before the carbon excursion at 890 CE, AB3 exhibits a δ^{13}C value around −9‰ and the new AB2 record registers similar values at −7‰. These values are within the expected range for a landscape with primarily C_3 plant cover, such as the dry deciduous forests that occur today in pockets in the modern northwest (Burgess et al., 2004). One hundred years after the beginning of the carbon excursion, AB3 registers a δ^{13}C value of 0‰, which is well within expectations for a C_4 dominated landscape such as open grassland. The δ^{13}C record for AB2 matches the excursion exhibited over 100 years in AB3 but shows a continual rise to +3‰ or higher (indeed, to +6‰) over a somewhat longer period. The magnitude of the carbon excursion, inferred from two stalagmites, was at least 8.5‰ in a 100-year period, and it increased to 11.5‰ or higher with time. Terminal values of +2 to +6‰ are highly enriched and leave no doubt that the dominant terminal landscape was open grassland. Natural variability in δ^{13}C values was ~4.5‰ prior to the excursion and 4‰ after, both of which are typical of natural variability associated with moderate fluctuations in soil respiration rates and air—water interactions in the epikarst. The steep, replicable, δ^{13}C increase, with no associated δ^{18}O increase, indicates that the change in dominant vegetation occurred independently of climatic change.

The δ^{18}O records from Anjohibe stalagmites are interpreted as proxies for past strength of the northwest Madagascar monsoon, likely correlated to precipitation amount in the region. No long-term trend or monotonic shift is observed in the δ^{18}O records, indicating that no substantial drying occurred over the last 1700 years (the length of the records). On a centennial scale, however, some centuries were modestly wetter or drier than others. Using Bayesian Change Point Analysis of the high resolution δ^{18}O record from stalagmite AB2 (Fig. 4f), Scroxton et al. (2017) documented fluctuations in wet and dry conditions every ~500 years over the last 1700 years. Notably, there was a decrease in stalagmite δ^{18}O values indicating a period of relatively wet conditions between 480 and 960 CE, with the wettest conditions of the last 1700 years between 780 and 960 CE. This wetter period was followed by increased stalagmite δ^{18}O values between 960 and 1485 CE, which we interpret as reduced precipitation. This transition from wet to dry is identified at 960 CE by Bayesian Change Point analysis but is unlikely to have been instantaneous. A period of climatic transition between 930 and 1000 CE is supported by the speleothem δ^{18}O record.

Other stalagmites from Anjohibe do not show comparable δ^{18}O increases. However, they do present other evidence for decreased precipitation such as hiatuses or decreases in growth rates. The lack of isotopic replication suggests that any precipitation decrease during the 10th and 11th centuries was modest, certainly not enough to have had major impacts on regional flora and fauna. In any case, the decrease in precipitation observed does not reflect a dry period of any severity. Speleothem δ^{18}O values in stalagmite AB2 during the 11th and 12th centuries are not unusually high (dry) in comparison to other dry periods such as the 5th or the 20th centuries (Scroxton et al., 2017). We conclude that northwestern Madagascar likely underwent a period of decreased precipitation in the late 10th/early 11th centuries, linking the wettest period of the last 1700 years with a period that was drier but not dramatically so.

There is a difference in timing between different stalagmite records regarding both the δ^{13}C and δ^{18}O changes: stalagmite AB2 appears to lead by 50—70 years, a margin larger than the subdecadal 2σ errors for most of the nearest U—Th ages, suggesting that the difference is not due to age model errors. One explanation could be recrystallization of stalagmite AB2, which would lead to uranium loss and anomalously older ages. Evidence for this includes anomalously low uranium concentrations in two of the three nearest ages in AB2 (1—2 ppm vs. 5—13 ppm in the remainder of the stalagmite). In addition, Scroxton et al. (2018) documented that portions of AB2 have been recrystallized from aragonite to calcite. Higher uranium concentrations in the stalagmite elsewhere suggest that the AB2 age model remains robust at other depths.

Therefore, we conclude that the land-use transition above Anjohibe started no earlier than 830 CE, but more likely began around 900 CE. Similarly, the modest drying began no earlier than 930 CE but more likely around 1000 CE. Crucially, as both the vegetation and climate proxies come from different depths in the same stalagmites, the evidence for (modest) drying occurs after the δ^{13}C change and associated land-use change.

The climate and vegetation signals generated by stalagmites from a single cave such as Anjohibe cannot necessarily be extrapolated to represent conditions everywhere on Madagascar. However, there are several reasons to infer that the results from the stalagmites are indicative for much of the island. For one, sediments from lakes across Madagascar, including Kavitaha, Tritrivakely, Mitsinjo and Amparihibe, show increases in charcoal and/or Gramineae pollen percentages sometime between 700 and 1100 CE (Burney, 1987a,b; Matsumoto and Burney, 1994; Gasse and Van Campo, 1998; Burney et al., 2004). The lake records do not have the

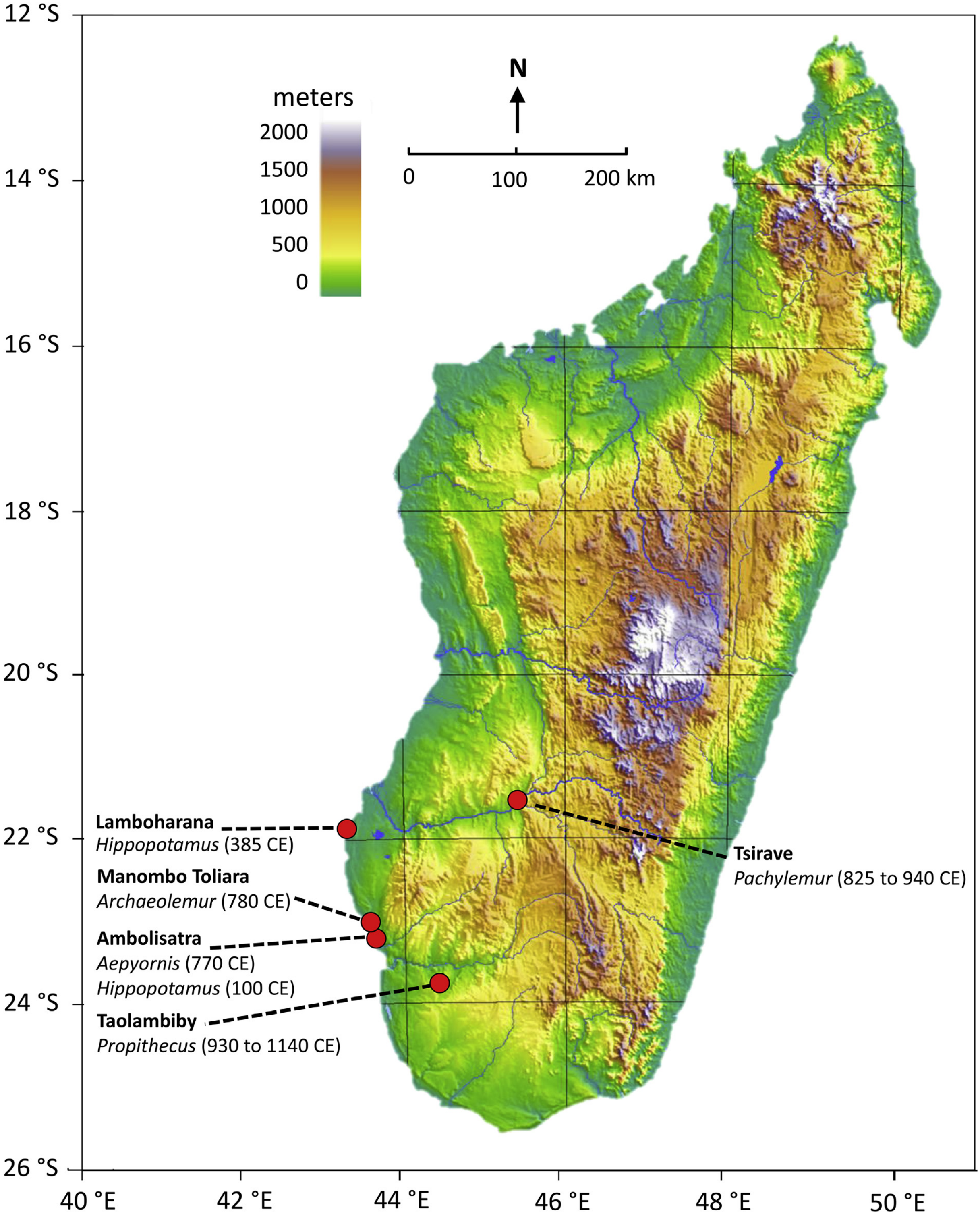

Figure 3. Map showing locations of sites with butchered subfossil vertebrate bones that fall within our search interval (50 BCE to 1350 CE). Butchered taxa and dates are indicated. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

precise chronological control of the speleothem records, but provide evidence of a similar landscape change over a broad area.

Also, under monsoon systems, stalagmite $\delta^{18}O$ values are typically better indicators of regional rainfall than local precipitation because the precipitation $\delta^{18}O$ values typically record convective processes rather than the point location rainfall amount (Risi et al., 2008; Kurita et al., 2009; LeGrande and Schmidt, 2009). As Anjohibe is located near the northwest coast of Madagascar and its yearly rainfall is dominated by the summer monsoon season, $\delta^{18}O$ values in AB2 should reflect the history of rainfall variability in the southwestern Indian Ocean during the austral summer (or northwestern Madagascan) monsoon. Analysis of instrumental records using data from Harris et al. (2014) supports the hypothesis that the wet and dry climate phases observed at Anjohibe were regional in

Table 2
Dated human-modified subfossil bones within our search interval (50 BCE to 1350 CE), ordered by date (^{14}C dates are listed here are uncalibrated; CE dates are based on calibrated ^{14}C dates).

^{14}C yr BP ± SD	Yr CE ± SD	Lab #	Element	Spec #	Taxon	Site[a]	Source[b]
915 ± 35	1140 ± 120	CAMS 147113	Femur	TAO-66-25	*Propithecus verreauxi*	1	1
940 ± 40	1130 ± 90	CAMS 147114	Femur	TAO-66-24	*Propithecus verreauxi*	1	1
1045 ± 30	1065 ± 75	CAMS 143128	Tibia	TAO-66-50	*Propithecus verreauxi*	1	2
1035 ± 25	1005 ± 135	CAMS 147111	Humerus	TAO-66-2	*Propithecus verreauxi*	1	1
1055 ± 30	1000 ± 140	CAMS 147628	Femur	TAO-66-23	*Propithecus verreauxi*	1	1
1130 ± 30	955 ± 65	CAMS 147036	Femur	TAO-66-21	*Propithecus verreauxi*	1	1
1130 ± 30	955 ± 65	CAMS 147035	Femur	TAO-66-FemA	*Propithecus verreauxi*	1	1
1155 ± 25	940 ± 50	CAMS 147117	Femur	TAO-66-FemC	*Propithecus verreauxi*	1	1
1160 ± 25	940 ± 50	CAMS 147116	Femur	TAO-66-5	*Propithecus verreauxi*	1	1
1150 ± 15	940 ± 50	UCIAMS 159131	Humerus	UA 3629 HPL 13	*Pachylemur insignis*	2	2
1165 ± 25	935 ± 55	CAMS 147115	Femur	TAO-66-FemB	*Propithecus verreauxi*	1	1
1165 ± 30	930 ± 40	CAMS 147332	Femur	TAO-66-30	*Propithecus verreauxi*	1	1
1215 ± 20	870 ± 95	UCIAMS 158554	Femur	UA 3093 FPL 163	*Pachylemur insignis*	2	2
1230 ± 25	835 ± 65	UCIAMS 158553	Femur	UA 3088 FPL 192	*Pachylemur insignis*	2	2
1245 ± 20	830 ± 55	UCIAMS 158552	Femur	UA 3047 FPL 80	*Pachylemur insignis*	2	2
1240 ± 15	830 ± 55	UCIAMS 159129	Humerus	UA 3610 HPL 100	*Pachylemur insignis*	2	2
1255 ± 15	825 ± 55	UCIAMS 159132	Humerus	UA 3695 HPL87	*Pachylemur insignis*	2	2
1265 ± 20	825 ± 60	UCIAMS 158555	Femur	UA 3133 FPL 74	*Pachylemur insignis*	2	2
1250 ± 15	825 ± 55	UCIAMS 159130	Humerus	UA 3619 HPL 24	*Pachylemur insignis*	2	2
1295 ± 25	780 ± 90	CAMS 142604	Femur	UA 1451 FAL 117	*Archaeolemur majori*	3	3
1297 ± 24	774.5 ± 98	OxA-33535	Tarsometatarsus	MNHN MAD 6662	*Mullerornis* sp.	?	4
1296 ± 32	772.5 ± 93	UBA-19725	Tibiotarsus	MNHN MAD 1906-16	*Aepyornis maximus*	4	4
1740 ± 50	385 ± 145	TO-1437	Femur	MNHN MAD 1709	*Hippopotamus lemerlei*	5	5
1970 ± 50	100 ± 130	AA 2895	Femur	MNHN MAD 1711	*Hippopotamus lemerlei*	4	5

[a] Site: 1 = Taolambiby, 2 = Tsirave, 3 = Manombo, 4 = Ambolisatra, 5 = Lamboharana.
[b] Source: 1 = Crowley and Godfrey (2013); 2 = Crowley et al. (2017); 3 = Crowley (2010); 4 = Hansford et al. (2018); 5 = MacPhee and Burney (1991).

scope. Rainfall variability at Anjohibe from 1901 to 2014 is significantly correlated with rainfall across much of Madagascar including the northwest, north-central, north, part of the west, and even part of the east (14 to 18°S, 43 to 48°E) (Fig. 5). The region of high correlation encompasses four World Meteorological Organization stations and so is not a point source of correlation but a real field. Outside of this field, the δ^{18}O values of stalagmite AB2 may record a proportion of rainfall variability. As AB2 δ^{18}O likely records past variability in the northwestern monsoon, the regional correlations outlined above allow us to assume this record likely reflects rainfall in other areas where the great majority of annual rainfall derives from the northwestern monsoon. Consequently, the δ^{18}O record from Anjohibe may help explain a substantial amount of rainfall variability in other parts of Madagascar where monsoonal rainfall is significant, although it cannot be expected to capture variability in alternate moisture sources. In effect, as the proportion of monsoonal rainfall to total rainfall decreases, the ability for the stalagmite δ^{18}O values from Anjohibe to account for past rainfall variability also decreases proportionately.

Of particular interest is southwest Madagascar, as virtually all of our butchery data and a substantial portion of the subfossil chronology records derive from this part of the island. Due to the rainshadow effect of the Madagascan highlands blocking easterly trade wind moisture, rainfall along the entire west coast is dominated by austral summer moisture from the northwestern monsoon. Therefore, while southwest Madagascar is substantially drier than the northwest, the vast majority of its rain nevertheless falls during the northwestern monsoon. Local conditions such as sea-surface temperatures may locally modulate rainfall (Zinke et al., 2005). The Anjohibe speleothem δ^{18}O record agrees well with the Itafy Reef/Tulear Coral SST reconstruction from 1660 to 1975 CE (compare Scroxton et al., 2017 and Zinke et al., 2014). This suggests that local and regional oceanic and atmospheric conditions have acted upon rainfall in the same direction during at least the last 350 years, and therefore that the speleothem δ^{18}O record of monsoonal variability from Anjohibe is applicable to the fossil sites of the southwest, at least during the late Holocene when baseline climatic conditions would have been similar to today. Testing this theory, and whether or not it applies during times of substantially different climate regimes such as the last glacial period, is an area of ongoing research.

Further afield, records of centennial rainfall variation in East Africa over the last 2000 years also match those for northwestern Madagascar (Scroxton et al., 2017). At Lake Challa (on the borders of Kenya and Tanzania), a wet period beginning 650 CE and ending at 950 CE was followed by an extended dry period between 1170 and 1300 CE, with drying conditions between the two (Buckles et al., 2016). The major wet and dry phases of the climate records of northwestern Madagascar also broadly correlate with climate records at Lake Naivasha, Kenya, which experienced a dry period beginning around 1000 CE and lasting until 1270 CE (Verschuren et al., 2000). This dry period followed a wet period of unspecified duration; records for Lake Naivasha begin only around 1100 years ago. The broad similarities between these three sites may relate to the fact that East Africa and northwestern Madagascar share a dominant source of moisture, i.e., the equatorial West Indian Ocean.

4. Discussion

4.1. Chronological overview

We can now summarize chronological data for megafaunal decline, butchery of wild animals, climate change, and vegetational shifts in Madagascar. Specifically we can compare the trajectory of megafaunal decline (as summarized using maximum likelihood χ^2 statistics) and the trajectory of human population growth on Madagascar (derived from human genetic studies, Pierron et al., 2017) to: (1) the shift in wild lemur prey targeted by human hunters from mostly extinct to mostly extant species; (2) the record of vegetation change from C_3 to C_4; and (3) the record of change in rainfall amount in the northwest, measured at close to annual resolution and showing centennial scale variability. With these comparisons, we can address our main questions regarding climate

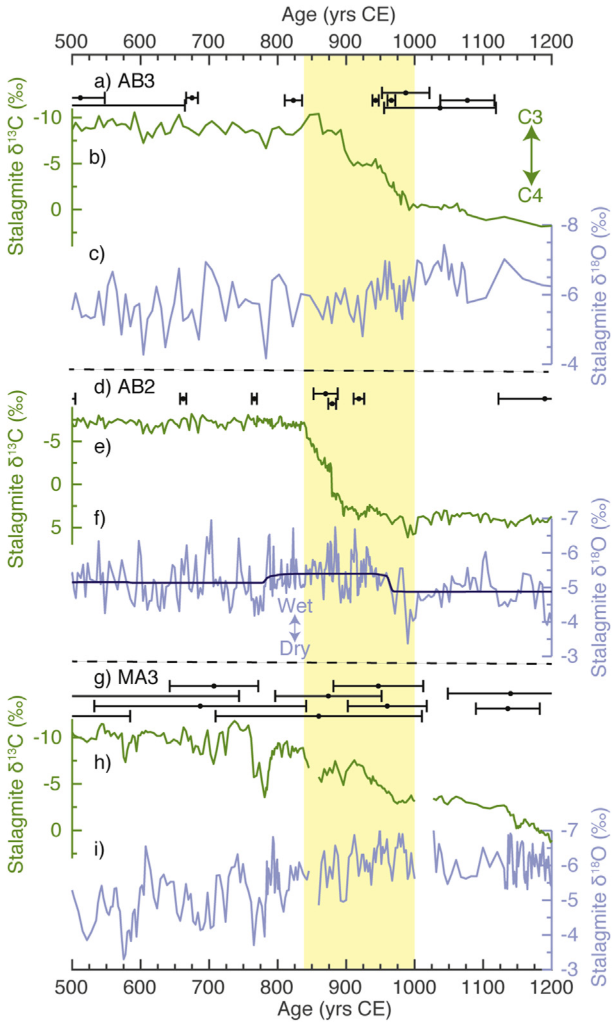

Figure 4. Speleothem evidence of vegetation changes and paleoclimate transitions between 500 and 1200 CE. a) Stalagmite AB3 ages with ±2 standard deviation error; b) Stalagmite AB3 $\delta^{13}C$ values; c) Stalagmite AB3 $\delta^{18}O$ values; d) Stalagmite AB2 ages with ±2 standard deviation error; e) Stalagmite AB2 $\delta^{13}C$ values; f) Stalagmite AB2 $\delta^{18}O$ values, with Bayesian Change Point Analysis modeled mean (dark blue line); g) Stalagmite MA3 ages with ±2 standard deviation error; h) Stalagmite MA3 $\delta^{13}C$ values; i) Stalagmite MA3 $\delta^{18}O$ values. Yellow box highlights transition from C_3 to C_4 vegetation.

variability and human activities as they do or do not relate to megafaunal decline.

It is clear from the data described above and pictorially represented in Figure 6 that the greatest change in extinct-to-extant vertebrate odds at subfossil sites (Fig. 6a) occurred between 700 and 900 CE, just as the human population of Madagascar began to expand markedly (Fig. 6b) (Pierron et al., 2017). Towards the end of that 200-year period of rapid megafaunal decline, human hunters in southwest Madagascar shifted from targeting now-extinct to still-extant species (Fig. 6c). Simultaneously, there was a significant shift in the northwest from a landscape dominated by C_3 to C_4 plants, likely signaling a local economic change from hunting/gathering to more dedicated agropastoralism (Fig. 6d). All of this preceded a moderate change in rainfall amount from wet to dry in the same region (Fig. 6e).

This chronology challenges both the aridification and the synergy hypotheses. With regard to the aridification hypothesis, while our data support dry conditions during the late 10th and early 11th centuries CE in the northwest, they also show that extreme drought did not occur during that time. There was no major, island-wide drought at around 950 years ago. Furthermore, the megafaunal crash pre-dated this period, as did the transition in the northwest from a C_3- to a C_4-dominated landscape. Indeed, that transition occurred almost entirely during an unusually wet period. Finally, no trend toward increasing aridification is recorded in the stalagmite climate records of northwestern Madagascar over the past 1700 years.

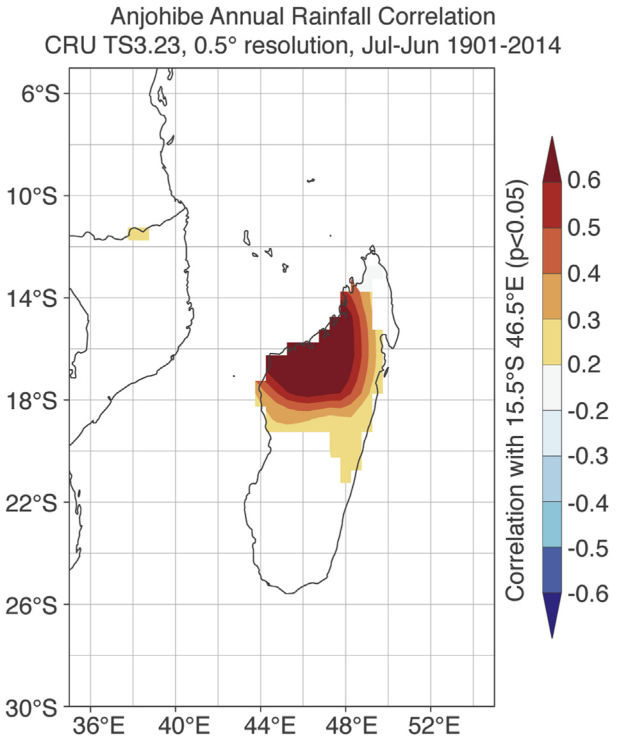

Figure 5. Spatial correlation of rainfall anomalies between Anjohibe and a regional 0.5° grid. Data were collected from the CRU TS3.23 dataset (Harris et al., 2014) using the hydrological year (July–June) from 1901 to 2014, and assessed using the KMNI climate explorer (Trouet and Van Oldenborgh, 2013). Colored regions have correlations significant at $p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

The synergy hypothesis fares a bit better. According to this hypothesis, at any given location, megafaunal decline preceded episodes of habitat transformation; in effect, one can infer that the decline of the megafauna sparked habitat loss rather than the other way around. Our data lend some support for this inference, as evidence of a hunting economy pre-dates the expansion of grasslands in the northwest and elsewhere. However, the synergy hypothesis holds that the megafaunal crash occurred within a few centuries of human arrival and well prior to the introduction of cattle and expansion of agropastoralism. This argument in turn depends on evidence of humans arriving only a few centuries prior to the start of the 1st millennium, megafauna declining early in the 1st millennium, and cattle arriving late in the 1st millennium. Support for this chronology was derived from research on megafaunal butchery at Taolambiby in south central Madagascar, and the abundance of spores of a mega-dung fungus called *Sporormiella* (= *Preussia* spp., see Kruys and Wedin, 2009) in sediments at four sites: Ambolisatra and Belo-sur-Mer on the west coast, Amparihibe in the northwest, and Kavitaha in central Madagascar (Burney et al., 2003, 2004; Perez et al., 2003, 2005). Because of the life history requirements of *Sporormiella*, counts of its spores in stratigraphic columns at various sites have been used as proxies for large-animal abundance.

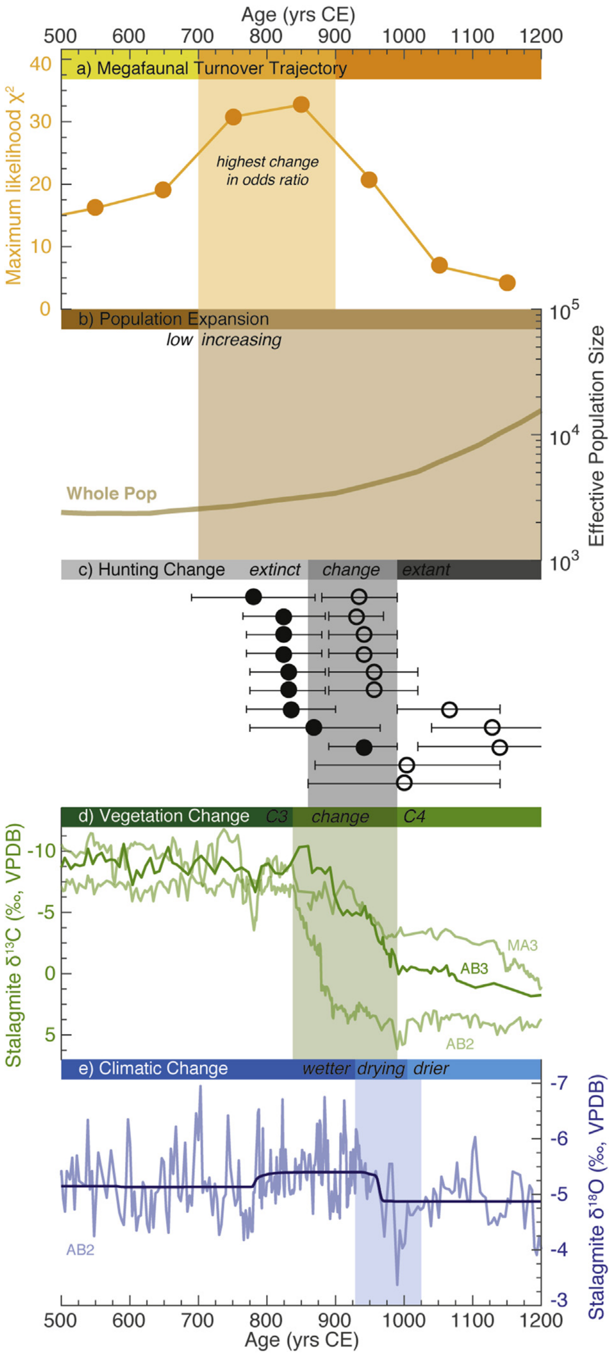

Figure 6. Evidence of changes in extinct:extant animal odds, vegetation, climate, and human population between 500 and 1200 CE. a) Plot of maximum likelihood χ^2 statistics for comparisons with different cut-points, showing inversion in extinct:extant subfossil odds at ~850 CE; b) Estimation of changes in the effective population size across time, using genome-wide identity-by-descent (IBD) sharing (Pierron et al., 2017); c) Radiocarbon ages of subfossil bones with butchery marks, showing extinct species (filled circles) and extant species (open circles), with error bars of ±1 standard deviation; d) Speleothem $\delta^{13}C$ values from stalagmites AB3, AB2 and MA3 from Anjohibe Cave (green lines) (Burns et al., 2016; Scroxton et al., 2017; Voarintsoa et al., 2017); e) Speleothem $\delta^{18}O$ from stalagmite AB2 from Anjohibe Cave (blue), with mean $\delta^{18}O$ values as modeled using Bayesian Change Point Analysis (dark blue line). In all panels, shading indicates most likely period of change.

Burney et al. (2003) interpreted drops in *Sporormiella* spores at Ambolisatra and Belo-sur-Mer during the early part of the 1st millennium as signals of decimation of megafaunal populations, and they interpreted spikes in *Sporormiella* spores at Amparihibe and Kavitaha almost 1000 years later as evidence of the introduction of cattle. However, radiocarbon records on Madagascar's subfossils across the island support rapid megafaunal loss coeval with spikes in *Sporormiella* spores toward the end of the 1st millennium.

There is excellent evidence that humans arrived much earlier, indeed, in the early Holocene. Hansford et al. (2018) report megafaunal butchery during the early and middle Holocene at several sites in the interior of Madagascar. These dates were derived from elephant bird specimens showing clear and purposeful perimortem damage; the oldest such records (at Christmas River, south central Madagascar) exceed 10,000 years. These dates match dates for unmodified bones from the same stratigraphic layer (Muldoon et al., 2012). Butchered *Mullerornis* at Lamboharana on the west coast dates to over 6000 years (Hansford et al., 2018).

Interestingly, two bird species, long believed to have been introduced to Madagascar by early human settlers (Hawkins and Goodman, 2003; Blench, 2008), are now confirmed to have been present on Madagascar in the late Pleistocene or early Holocene (Goodman et al., 2013). Early radiocarbon dates at Ankilitelo for the helmeted guineafowl (*Numida meleagris* at >13,000 years agp) and the pied crow (*Corvus albus*, at 9000 years agp) were taken by Goodman et al. (2013) as evidence of natural dispersal from Africa, a possibility that cannot be ruled out. However, guineafowl are virtually flightless, and easily transported as food on boats; wild corvids are known to travel as stow-aways on ships, and the Malagasy pied crow is morphologically identical to members of the same species in Africa. Hansford et al.'s (2018) dates for early megafaunal butchery lend strong support for a very early human colonization of the island of Madagascar, and make plausible the notion that >13,000 year-old helmeted guineafowl (*N. meleagris*) and >9000 year-old pied crow (*C. albus*) at Ankilitelo were introduced by humans.

Pierron et al. (2017) found no genetic evidence of such an early human colonization. However, they could not exclude the existence of small early populations effectively leaving no genetic signature. They did identify two splits of proto-Malagasy populations from Austronesian and southern African Bantu relatives, the first from south Borneo between 3000 and 2000 years ago, and the second from Africa around 1500 years ago. Recognizing the need to account for the potential incompleteness of their comparative Austronesian and African samples, they also stated that divergence could have been earlier. In other words, there is a possibility that DNA from descendent populations from the common ancestor population at the time of the earliest split was not included in the analysis, or that such a population no longer exists in the place of origin. This implies a minimum age of population divergence between 2000 and 3000 years ago. As stated by Pierron et al. (2017: p. E6502), "…these dates reflect the age of the oldest possible common ancestors between Malagasy and the African/Indonesian sampled populations, meaning that the departure to Madagascar is not later but could be earlier than these dates".

There are additional records of human presence on Madagascar more than 2000 years ago. For example, Douglass (2016) reports the existence of marine shell middens from the coastal site of Velondriake in southwest Madagascar; a worked marine shell from this locality has yielded a calibrated age between 825 and 504 BCE. In addition, optically simulated luminescence (OSL) dates on quartz grains associated with stone artifacts (microliths) at Lakaton'i Anja Cave in northwest Madagascar place foragers on this part of the island more than 4000 years ago (Dewar et al., 2013). These dates were rejected by Anderson et al. (2018) on the basis of discrepancies between the OSL dates and much younger ^{14}C dates for charcoal in the same stratigraphic layers. However, Dewar et al. (2013) explained the contradictory dates as resulting from termites causing downward migration of younger charcoal via bioturbation. Dewar et al. (2013) noted that the OSL dates are in stratigraphic order and the ^{14}C dates are not; the latter are clearly disturbed. Termites can be expected to deliberately move fresh and charred wood into lower strata for food; charcoal is also transported downward by termites for underground moisture control. Termites would not deliberately move rocks. Thus, Dewar et al. (2013) inferred that the stone artifacts in the lower layers are indeed in situ and over 4000 years old. The counterargument that these artifacts are also intrusive must depend on accidental mixing. There is no evidence, furthermore, that the tools in the lower layers are coeval with introduced crops (Pomerantz, 2017), which do not appear at this site until after 1000 CE (Crowther et al., 2016). Finally, bones with cut marks have been found at Lakaton'i Anja Cave, but have not been described (Ekblom et al., 2016).

It is curious that Anderson et al. (2018) rejected early human butchery for the nearly-2000-year-old hippopotamus bones from Ambolisatra and Lamboharana that MacPhee and Burney (1991) reported as anthropogenically modified. While accepting anthropogenic modification for these bones, Anderson et al. (2018) argued that they may have been damaged by excavators or museum preparators. These bones were collected in southwest Madagascar by Guillaume Grandidier at the turn of the twentieth century (e.g., Grandidier, 1900; see summary by Chanudet, 1975). Ambolisatra was a marsh at that time; sometimes collectors had to wade into water that was neck deep and dive under water to retrieve subfossils. When Grandidier sent these bones to Paris, he reported that some showed perimortem human modification. To confirm this, MacPhee and Burney (1991) ran chopping experiments on subfossil hippo bone from Ampoza as well as fresh cow bone, and found that the subfossil bone splintered, while fresh bone did not. It was precisely for this reason that MacPhee and Burney (1991) rejected excavation damage as a viable explanation for the chops they documented on Grandidier's hippo bones from Lamboharana and Ambolisatra.

Pierron et al. (2017) provide evidence of human population admixture and a rapid expansion of the effective breeding population of humans well after initial human arrival on Madagascar. That expansion was coincident with archaeological evidence for a changing economy, from one that depended primarily on hunting/foraging to one that depended much more on herding/farming (Table 3). It began in the north around 700 CE (= 1250 BP), and then spread to other parts of Madagascar (Pierron et al., 2017). Archaeological evidence of intensified forest resource extraction and clearing of land appeared along the east coast in the 7th century CE and extended through the 11th century (Agarwal et al., 2005).

The expansion of the human breeding population was linked to a growing Indian Ocean trading network that connected Madagascar, China, India, Indonesia, Arabia, and Africa (Blench, 2008; Fuller and Boivin, 2009; Boivin et al., 2013; Dewar, 2014; Douglass and Zinke, 2015; Radimilahy and Crossland, 2015; Crowther et al., 2016; Ekblom et al., 2016; Pomerantz, 2017; Prendergast et al., 2017). From ~700 CE onward, Madagascar experienced an influx of wild and domesticated plants and animals from continental Africa and from Asia (Dewar, 2014). Iron tools became more central to the economy (Dewar, 2014). Villages and hamlets spread throughout the island. Between 700 and 1200 CE, waves of Sama-Bajaw Austronesians brought crops, such as coconuts (*Cocos*), yams (*Dioscoria*), rice (*Oryza*), saffron (*Crocus*) and cotton (*Gossypium*), to moist and highland habitats (Crowther et al., 2016; Beaujard, 2017). Bantu people, mostly from the Swahili/Sabaki group, brought cattle (*Bos*), goats (*Capra*), chickens (*Gallus*), and perhaps wild boars (*Potamochoerus larvatus*) (Blench, 2008), as well as plants adapted to thrive in dry habitats, including sorghum (*Sorghum*), groundnuts (*Vigna*), and taro (*Colocasia*) (Beaujard, 2017). Bananas (*Musa acuminata*) also arrived early, although their geographic origin is uncertain. Arabian traders established large trading posts in Madagascar and India (Chaudhuri, 1985), while Indonesians established a trade network that connected southeast Asia with Madagascar, East Africa and the Swahili city-states (Boivin et al., 2013).

4.2. The subsistence shift hypothesis

We offer the “Subsistence Shift Hypothesis” to explain megafaunal extinction in Madagascar. This hypothesis maintains that the trigger for rapid megafaunal decline in Madagascar was the expansion of the Indian Ocean trade network and the concomitant transition from an economy that depended largely on hunting and foraging to one that relied increasingly on agropastoralism, trade and urbanism. Megafaunal decline intensified as Madagascar received an influx of settlers bringing new crop plants and domesticated animals.

The subsistence shift hypothesis is supported by the fact that the megafaunal crash was not coincident with initial human arrival, nor did it follow human arrival within a few centuries. It was not triggered by aridification. It did, however, begin at around the time cattle were introduced to Madagascar, and it peaked as human populations began to grow rapidly. The availability of alternative foods (such as cattle, goats, sheep) did not relieve pressure on the megafauna, which increased as human populations grew until the large-bodied endemic animal species could no longer maintain viable populations. Megafaunal hunting then declined in economic importance not because alternative introduced foods were now available, but because the megafaunal populations themselves had crashed. As Dewar et al. (2013: 12587) observed, “The activities of foraging [human] populations have environmental consequences that differ in both degree and nature from those of Iron Age farmers and pastoralists, and changes in paleoenvironmental proxies interpreted as signaling ‘human arrival’ may in fact be signals of a change in human economy.”

Our hypothesis does not deny that there were dramatic fluctuations in climate during the late Pleistocene and Holocene, or that these fluctuations resulted in local changes in species distributions. Nor does it deny that, prior to the subsistence shift described here, hunters and foragers may have had negative impacts on Madagascar's megafauna. It does not preclude the notion that natural fires would have increased in frequency and intensity as megafaunal populations declined. We do argue, however, that human arrival, by itself, does not trigger extinction; rather, the degree to which terrestrial vertebrate species are threatened depends on human population size and human subsistence strategy, as well as the reproductive dynamics of the targeted species. The expansion of Madagascar's trade network, influx of new settlers, and economic transition from hunting and foraging to herding and farming triggered rapid growth in the size of the effective human breeding population, greater direct exploitation of wild (in addition to domesticated) animals, and more rapid habitat modification (a change in the fire ecology of the island). Prior to this, small human populations appear to have continually or intermittently occupied Madagascar over an extended period of time without triggering extinction. Coastal populations likely exploited marine food resources while people living in the interior relied more on endemic terrestrial animals and wild plants. Megafaunal extinction occurred only after the expansion of the Indian Ocean trade network. Following that expansion, coastal people may have continued to exploit marine resources, minimally impacting terrestrial vertebrates, but forest clearance through cutting and burning would have served the economic needs of both herders and farmers, who would have also hunted wild animals to varying degrees (as is true today).

Table 3
Subsistence transition illustrated by plants or animals recorded at archaeological sites, or possible human occupation zones at paleontological sites, within our search interval (50 BCE to 1350 CE).

Site	Time (CE)	Plants and Animals	Sources
Ambolisatra, SW coastal	100 CE	†_Hippopotamus_ butchery site	MacPhee and Burney (1991)
Lamboharana, SW coastal	385 CE	†_Hippopotamus_ butchery site	MacPhee and Burney (1991)
Lakaton'i Anja (Andavakoera Gorge), N Coastal	5th to 10th centuries CE	Mollusks Wild terrestrial animals	Dewar and Rakotovololona (1992)
Velondriake, SW coastal, Antsaragnagnangy (ANGY I)	Phase I occupation begins ~550 CE and ends ~1050 CE	Fish (including Emperors, Breams, Unicorn fish, Parrotfish, Groupers, and Rabbitfish) Terrapins Turtles Tortoises Frogs Birds (including *_Gallus gallus_ or *_Numida meleagris_) Bats Tenrecs Small and medium-sized lemurs	Douglass et al. (2018)
Sarodrano, SW coastal	Beginning in the mid-1st millennium	*_Bos_ Fish	Battistini and Vérin (1971) Andrianaivoarivony (1987)
Irodo, NE coastal	7th century	*_Bos_ Fish	Andrianaivoarivony (1987)
West Mikoboka Plateau, cave #13, SW	710 CE	*_Rattus rattus_	Crowley et al. (2017)
Ambolisatra, SW coastal	770 CE	†_Aepyornis maximus_ butchery site	Hansford et al. (2018)
Manombo Toliara, SW coastal	780 CE	†_Archaeolemur majori_ butchery site	This paper
Ampasimahavelona NE coastal	8th to 10th centuries CE	Shell midden *_Musa acuminata_ *_Oryza sativa_	Crowther et al. (2016)[a] Pomerantz (2017)
Ampasimaiky Rock Shelter, SW interior	Dating uncertain; possibly associated stone tools	*Rock art depictions of humped cattle	Rasolondrainy (2012)
Tsirave, SC interior	825-940 CE	†_Archaeolemur_ and †_Pachylemur insignis_ butchery site	This paper
Amparihibe, NW coastal	780–1010 CE (single date, 2 SD)	*Proliferation of cattle inferred from increase in _Sporormiella_ spore count	Burney et al. (2003)
Anjohibe, NW	Beginning 890 CE, over a period of 100 years	*Proliferation of cattle inferred from intense burning episode recorded in stalagmites	Burns et al. (2016)
Mahilaka, NW coastal	Beginning in the late 1st millennium	*_Bos_ *_Capra_ *_Ovis_? *_Gallus gallus_ *_Potamochoerus larvatus_ *_Rattus rattus_ *_Mus musculus_ *_Musa acuminata_ *_Oryza sativa_ *_Gossypium arboretum_	Radimilahy (1998) Crowther et al. (2016) Pomerantz (2017) Prendergast et al. (2017)
Tsiandrora, Maliovola, Mokala, Ambinanibe, Ndrenany, SE	Possibly beginning in the late 9th century; mostly early 2nd millennium, from the 11th through the 13th centuries	*_Bos_ (at Tsiandrora) *_Oryza sativa_ (at Maliovola) *_Colocasia esculenta_ (at Maliovola) Fish Shellfish Small wild animals (hunted)	Rakotoarisoa (1998)
Kavitaha, CH interior	900–1260 CE (single date, 2 SD)	*Proliferation of cattle inferred from increase in _Sporormiella_ spore count	Burney et al. (2003)
Taolambiby, SW interior	930–1140 CE	_Propithecus verreauxi_ butchery site	This paper
Andaro, S	10th – 13th centuries CE	*_Bos_ *_Capra_ or _Ovis_ *_Gallus gallus_ *_Potamochoerus larvatus_	Parker-Pearson et al. (2010)
Andranosoa, S	Beginning in the 10th century CE	*_Bos_ *_Ovis aries_ *_Capra_? *_Felis cattus_ *_Canis familiaris_ *_Potamochoerus larvatus_ Fish Shellfish _Tenrec_	Rasamuel (1984) Andrianaivoarivony (1987) Rakotozafy and Goodman (2005) Boivin et al. (2013)

(continued on next page)

Table 3 (_continued_)

Site	Time (CE)	Plants and Animals	Sources
		†Giant tortoise †_Hippopotamus_[b]	
Lakaton'i Anja, Andavakoera Gorge, upper layers, N coastal	11th – 12th centuries CE	Fish and shellfish †Giant tortoise Tenrecs Birds †Giant lemurs *_Bos_ *_Capra_ or _Ovis_ *_Potamochoerus larvatus_ or possibly domesticated pig? *_Gossypium arboretum_	Dewar and Rakotovololona (1992) Crowther et al. (2016)
Talaky, S coastal	11th – 13th centuries CE	Mollusks †_Aepyornis_ (eggshell)	Battistini et al. (1963)
Ankadivory D'Ralambo, CH interior, NE of Antananarivo	12th –14th centuries CE	*_Bos_ *_Musa acuminata_ *_Oryza sativa_	Rakotovololona (1993) Pomerantz (2017)
Lakaton'ny akanga, N coastal (Grotte des Pintades)	13th century CE	†Subfossil (extinct animal) bones and bones of other forest animals Fish and shellfish †_Aepyornis_ (eggshell debris) (No remains of domesticated animals)	Dewar and Rakotovololona (1992)
Rezoky, SC interior	13th – 15th centuries CE	*_Bos_ *_Capra hircus_ *_Ovis aries_ *_Canis familiaris_ *_Potamochoerus larvatus_ _Tenrec ecaudatus_ *_Numida meleagris_ Mollusks	Vérin and Battistini, 1972 Rakotozafy and Goodman (2005) Boivin et al. (2013) Douglass et al. (2018)
Asambalahy, SC interior	14th century onward CE	*Bovids †_Hippopotamus_ (undated, possibly cut-marked, unverified) *_Numida meleagris_ *_Canis familiaris_	Rakotozafy and Goodman (2005) Boivin et al. (2013)

†Extinct, *Introduced to Madagascar.

[a] Crowther et al. (2016) did not find charred food crop remains at Ampasimahavelona, but Pomerantz (2017) identified phytoliths of bananas and rice here.

[b] _Hippopotamus_ teeth from Andranosoa found in a garbage pit were illustrated and described as “giant subfossils,” but not identified as hippos by Rasamuel (1984).

The complete transformation of dry forested habitats to savannas such as that seen at Anjohibe at 890 CE (Burns et al., 2016) cannot be attributed to natural fire. This transformation was abrupt and it was complete in little more than a century, which strongly suggests habitat modification by humans. Megafauna also disappeared from wetter regions such as the subhumid Central Highlands and the rainforests of the eastern escarpment and lowlands. They disappeared from habitats that were previously forested and from old woodland and savanna habitats. We suggest that megafauna were hunted and that fires were set by people in all habitats. However, in wetter areas, forest regrowth was rapid, and habitat transformation was relatively slow. For this reason, megafauna disappeared from the eastern forests without wholesale destruction of the forested habitats. The disappearance of the megafauna from all habitats suggests that these animals were hunted everywhere, even as habitat transformation varied across the island.

Human populations tend to expand with increased agropastoralism because of increased carrying capacity; it is carrying capacity that controls the maximum human population size that can be supported by available resources (Bettinger, 2016; Zahid et al., 2016). In general, carrying capacity is much higher for plants than animals, for domesticated plants than wild plants, and for domesticated animals than wild animals. This is related to the reproductive resilience of the targeted food resource species, which in turn is affected by their density, growth rate and life history characteristics (Winterhalder and Goland, 1993). Many of the large, endemic animals of Madagascar were slow reproducers and therefore vulnerable to extinction (Johnson, 2002; Richard et al., 2002; Schwartz et al., 2002, 2007; Godfrey et al., 2006b; Catlett et al., 2010). Those endemic species that reproduce rapidly, such as tenrecs, persist, despite the fact that they were hunted in the past (their bones appear often in the middens of archaeological sites), and continue to be hunted heavily in some areas today. Domesticated species such as cattle can sustain large human populations because individuals grow rapidly to large body size, sexually mature early (in less than two years), and have short interbirth intervals (Marshall, 1989).

5. Conclusions

In summary, we are arguing that explanations for megafaunal extinction must consider subsistence strategies and human population size. We suggest that, in Madagascar, a fundamental shift in how humans interacted with their natural environment occurred as trade connections expanded and reliance on agropastoralism and urbanism grew. Counterintuitively, and despite the availability of alternative resources, hunting pressure on wild animals increased with agropastoralism, impacting large animals in all habitats. Habitat modification through burning had a compounding, negative effect on large-bodied endemic species.

Our more fundamental argument is that human presence is not automatically catastrophic, but that certain human activities can be catastrophic, and their effects can be entirely independent of climate change. We acknowledge that while our data on the megafaunal crash are island-wide, our data on changes in rainfall derive mainly from the northwest, and our butchery data derive from southwestern and south central Madagascar. It is critical that future research focus more precisely on the temporal and spatial dynamics of human activities, climate variation and extinction in Madagascar (e.g., Douglass et al., 2018). Regional variation in subsistence norms and human population density must be a critical part of the discussion.

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