Research

EDITOR'S CHOICE

Ecography 40: 901–912, 2017
doi: 10.1111/ecog.02376

Subject Editor: Jacquelyn Gill. Editor-in-Chief: Miguel Araújo. Accepted 4 May 2016

Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar

Brooke E. Crowley, Laurie R. Godfrey, Richard J. Bankoff, George H. Perry, Brendan J. Culleton, Douglas J. Kennett, Michael R. Sutherland, Karen E. Samonds and David A. Burney

B. E. Crowley (http://orcid.org/0000-0002-8462-6806) (brooke.crowley@uc.edu), Dept of Geology and Anthropology, Univ. of Cincinnati, 500 Geology Physics Building, Cincinnati, OH, USA. – L. R. Godfrey, Dept of Anthropology, Univ. of Massachusetts Amherst, Amherst, MA, USA. – R. J. Bankoff, G. H. Perry, B. J. Culleton and D. J. Kennett, Dept of Anthropology, Pennsylvania State Univ., PA, USA. – M. R. Sutherland, Data Science Program, New College of Florida, Sarasota, FL, USA. – K. E. Samonds, Dept of Biological Sciences, Northern Illinois Univ., Dekalb, IL, USA. – D. A. Burney, National Tropical Botanical Garden, Kalaheo, HI, USA.

Researchers are divided about the relative importance of people versus climate in triggering the Late Holocene extinctions of the endemic large-bodied fauna on the island of Madagascar. Specifically, a dramatic and synchronous decline in arboreal pollen and increase in grass pollen ca 1000 yr ago has been alternatively interpreted as evidence for aridification, increased human activity, or both. As aridification and anthropogenic deforestation can have similar effects on vegetation, resolving which of these factors (if either) led to the demise of the megafauna on Madagascar has remained a challenge. We use stable nitrogen isotope ($\delta^{15}N$) values from radiocarbon-dated subfossil vertebrates to disentangle the relative importance of natural and human-induced changes. If increasing aridity were responsible for megafaunal decline, then we would expect an island-wide increase in $\delta^{15}N$ values culminating in the highest values at the time of proposed maximum drought at ca 1000 yr ago. Alternatively, if climate were relatively stable and anthropogenic habitat alteration explains the palynological signal, then we would anticipate little or no change in habitat moisture, and no systematic, directional change in $\delta^{15}N$ values over time. After accounting for the confounding influences of diet, geographic region, and coastal proximity, we find no change in $\delta^{15}N$ values over the past 10 000 yr, and no support for a period of marked, geographically widespread aridification culminating 900–950 yr ago. Instead, increases in grasses at around that time may signal a transition in human land use to a more dedicated agro-pastoralist lifestyle, when megafaunal populations were already in decline. Land use changes ca 1000 yr ago would have simply accelerated the inevitable loss of Madagascar's megafauna.

Five thousand years ago, the island of Madagascar was teeming with a diversity of large-bodied endemic vertebrates including giant lemurs (some of which, i.e. *Archaeoindris fontoynontii*, *Megaladapis edwardsi*, and *M. grandidieri*, attained body masses on par with gorillas). By 1000 yr ago, populations of most megafaunal taxa had dwindled (Crowley 2010). Although there is evidence that some endemic Malagasy megafauna lived well into the past millennium and even, in a few cases, into the 19th or 20th century (Flacourt 1658, Godfrey 1986, Burney and Ramilisonina 1998, Douglass 2016), bones from extinct endemic taxa are notably absent from human settlement sites that spread rapidly during the first half of the second millennium AD (Radimilahy 1998, Parker Pearson et al. 2010, Dewar 2014, Douglass and Zinke 2015). The most recent undisputed radiocarbon dates for any of the now-extinct species are ca 500 calendar years before present (Cal BP; Simons 1997, Muldoon et al. 2009). A hippo skull from the Univ. of Antananarivo collections has produced remarkably young dates (130 and 155 Cal BP; Burney et al. 2004). These authors assumed (because of its large size) that this skull was from Mananjary, the type site for the largest of the extinct Malagasy hippos *H. laloumena*. However, the skull had neither provenience information nor a specimen label, and a recent study of its morphology (Faure et al. 2010) has confirmed that it is a *Hippopotamus amphibius* which was apparently brought to the Académie Malgache for comparative study. Another hippo specimen at the Académie Malgache, this one actually from Mananjary, yielded a much older radiocarbon date (2250 ± 100 Cal BP).

Factors that contributed to megafaunal demise continue to be debated. While some researchers have suggested that direct competition with introduced domesticated species or hypervirulent diseases may have killed the megafauna (Dewar 1984, MacPhee and Marx 1997), most have focused on climate change (increasing aridity), hunting by humans, or anthropogenic habitat alteration (Battistini 1971, Burney and MacPhee 1988, Burney 1993, 1999, Godfrey and Jungers 2003, Burney et al. 2004, Kaufmann 2004, Clarke et al. 2006, Godfrey and Irwin 2007, Virah-Sawmy et al. 2009, 2010, Crowley 2010, Crowley et al. 2012, Godfrey and Rasoazanabary 2012, Crowley and

Samonds 2013, Goodman et al. 2013, Goodman and Jungers 2014, Burns et al. 2016). Because aridification and anthropogenic deforestation can have similar effects on vegetation, resolving which of these factors (if either) triggered megafaunal extinctions in Madagascar has remained a challenge. Episodes of local vegetation change and shifts in lake levels are evident throughout the Holocene (Table 1); those within the human period have been interpreted alternatively as evidence of widespread aridification (Goodman and Rakotozafy 1997, Virah-Sawmy et al. 2010), increased human activity (Burney 1987b, Matsumoto and Burney 1994, Gasse and Van Campo 1998, Bartlett et al. 2016, Burns et al. 2016), or both (Burney 1993, 1999, Clarke et al. 2006, Crowley 2010, Goodman et al. 2013). In particular, widespread evidence for a decline in arboreal pollen and increase in grass pollen ca 1000 yr ago has been interpreted as evidence for a severe island-wide drought that resulted in the demise of the megafauna (Virah-Sawmy et al. 2010).

Nitrogen isotope (δ^{15}N) data from terrestrial vertebrates may provide a vehicle for differentiating Late Holocene aridification and anthropogenic deforestation (Gröcke et al. 1997, Newsome et al. 2011, Rawlence et al. 2012, Lohse et al. 2014). In addition to reflecting trophic level (Ambrose 1991), nitrogen isotope values in animals (and in the plants they consume) are strongly influenced by environmental parameters such as precipitation, temperature, and soil nitrogen cycling. Moisture availability exerts a primary control on plant δ^{15}N values (Schulze et al. 1998, Handley et al. 1999, Amundson et al. 2003, Aranibar et al. 2004, Swap et al. 2004, Craine et al. 2009, Crowley et al. 2011), and consumers living in moist habitats typically have lower δ^{15}N values than those inhabiting drier localities, even if they feed at a similar trophic level (Ambrose 1991, Cormie and Schwarcz 1994, Murphy and Bowman 2006, Crowley et al. 2011, Hartman 2011, Symes et al. 2013). Nitrogen isotope values are also influenced by soil acidity and salinity (Mariotti et al. 1980, Wooller et al. 2005). Plants and consumers from localities with more acidic soils may exhibit lower δ^{15}N values (Mariotti et al. 1980, Rodière et al. 1996, Gröcke et al. 1997), and those from coastal settings, which are exposed to marine nitrates and salts, tend to have particularly elevated δ^{15}N values (Heaton 1987, Ambrose 1991, Muzuka 1999, Crowley et al. 2012). Conversely, forest loss does not have a systematic influence on plant or consumer δ^{15}N values (Högberg 1997, Schulze et al. 1998, Nakagawa et al. 2007, Wang et al. 2007, Darling and Bayne 2010, Crowley et al. 2013, Schillaci et al. 2014). This likely reflects inconsistent alterations in the availability of various nitrogen sources to plants, as well as variable responses of consumers to forest loss. Whereas some species may simply retreat into remaining forested habitat, others may exploit disturbed habitats and consume novel resources. The fact that vegetation changes per se are unlikely to systematically impact consumer nitrogen isotope values means that δ^{15}N values in animal tissues can be used to track temporal changes in moisture once variation related to diet, geographic region, and coastal proximity is taken into account, and can thus be used as an indirect test of causes of vegetation change.

We use δ^{15}N values derived from bone collagen of 238 radiocarbon-dated individuals belonging to 24 extant and extinct vertebrate genera from 17 subfossil sites across Madagascar (Fig. 1) to quantify the degree to which proposed island-wide aridity versus anthropogenic habitat alteration may have affected vertebrates during the Late Holocene. Under widespread natural aridification, we would expect to see an increase in δ^{15}N values over time in all geographic regions. Specifically, we would expect to see elevated values around 1000 yr ago when there is evidence for an increase in grass pollen in southeastern, central, and northwestern Madagascar (Table 1). If, on the other hand, anthropogenic habitat alteration were primarily responsible for previously observed changes in plant communities, then we would expect to see no systematic change in δ^{15}N values over time.

Material and methods

Sample preparation and analysis

Detailed information about each specimen, including stable isotope data, radiocarbon age, and data source, is provided in Supplementary material Appendix 1, Table A1. Radiocarbon dates and δ^{15}N values are previously published for 217 and 167 of these specimens respectively (Burney et al. 2004, Karanth et al. 2005, Crowley 2010, Samonds et al. 2010, Crowley et al. 2012, Crowley and Godfrey 2013, Crowley and Samonds 2013, Kistler et al. 2015, Godfrey et al. 2015).

The collagenous residue for 20 new specimens (Supplementary material Appendix 1, Table A1) was isolated. Twelve of these samples were demineralized in 0.5 M EDTA, gelatinized at 70°C for 20 h in 0.01 N HCl, filtered through 1.5 μm glass-fiber filters, and dried under vacuum in the Quaternary Paleoecology Laboratory at the Univ. of Cincinnati. Nitrogen isotope data were analyzed on a Carlo Erba Elemental Analyzer connected to a Finnigan Thermo Electron Delta XP continuous flow system at the Univ. of California, Santa Cruz Stable Isotope Laboratory, and normalized using IAEA acetanilide and an internal gelatin standard. The remaining eight samples (all *Pachylemur insignis* from Tsirave) were demineralized in 0.5 N HCl at 5°C for 24–72 h, briefly soaked (< 1 h) in 0.1 N NaOH at room temperature to extract humic acids, rinsed twice with NanoPure water, gelatinized in 0.01 N HCl at 60°C for 10 h, and lyophilized in the Pennsylvania State Univ. Human Paleoecology and Isotope Geochemistry lab. Four high-quality samples (UA3047, UA3088, UA3093, and UA3133) were selected for further collagen purification using the modified Longin (1971) method with ultrafiltration (Brown et al. 1988). These samples were passed through 30 kDa Centriprep® ultrafilters that had been thoroughly cleaned by centrifuging to eliminate contaminants (Bronk Ramsey et al. 2004). Collagen from the four remaining samples (UA3629, UA3610, UA3695, UA3619) was purified with an XAD-hydrolysis method modified from Stafford and colleagues (1988). Nitrogen isotope data were analyzed on a Costech Elemental Analyzer (ECS4010) connected to a Thermo DeltaPlus Advantage continuous flow mass spectrometer at the Yale Earth Systems Center for Stable Isotopic Studies facility.

Table 1. Reconstructed vegetation change and inferred climate during the Holocene.

Site	Ecoregion	Type of evidence	Vegetation/habitat change with dates	Source
Lake Tritrivakely	Central Highlands	Diatoms and pollen	Cool, dry conditions; transition from ericoid heath vegetation to wooded grassland at ca 9800 Cal BP.	Burney 1987a, Gasse and Van Campo 1998
Anjohibe Cave	Dry Deciduous Forest	Speleothem and pollen	Wet throughout the early and middle Holocene, punctuated by a ca 100-yr drought roughly 7500 yr ago. Pollen suggest that ca 7000–8000 yr ago the savanna surrounding Anjohibe may have been more densely wooded than in the late Pleistocene.	Burney et al. 1997, Wang and Brook 2013
Ste-Luce	Humid Forest (coastal SE)	Diatoms and pollen	Decline in fire-sensitive woody taxa and increase in open *Myrica*-ericoid grassland between ca 5900 and 3000 Cal BP; continued dominance of open-thicket forest closer to the coast. Lower water levels at ca 5800, 4600, and 3000 Cal BP.	Virah-Sawmy et al. 2009, 2010
Lake Tritrivakely	Central Highlands	Diatoms and pollen	Decrease in aquatic plants and increase in Gramineae ca 4000 Cal BP.	Gasse and Van Campo 1998
Anjohibe Cave	Dry Deciduous Forest	Speleothem	Transition to a drier climate beginning ca 4000 yr ago.	Wang and Brook 2013
Andolonomby marsh (Ambolisatra)	Spiny Thicket (coastal SW)	Pollen	Transition from dry forest to palm savanna between ca 3500 and 2500 Cal BP.	Burney 1993, 1999[a]
Lake Tritrivakely	Central Highlands	Diatoms and pollen	Increased moisture and lower temperatures between 3500 and 2800 Cal BP.	Gasse and Van Campo 1998
Lake Mitsinjo	Dry Deciduous Forest	Pollen	Relatively stable woodland-savannah between ca 3590 (3420 ± 120 ^{14}C yr BP) and 2000 Cal BP. Drying of the lake prevents paleoecological interpretation between ca 2000 and 800 Cal BP.	Matsumoto and Burney 1994
Lake Ihotry	Spiny Thicket	Diatoms and pollen	Wet episode between ca 3300 and 2050 Cal BP; increase in salinity (indicating drying) and decline in dominant forest pollen starting ca 2050 Cal BP.	Vallet-Coulomb et al. 2006
Ste-Luce	Humid Forest (coastal SE)	Diatoms and pollen	Pulsed increases in pioneer species and low water levels between 1900 and 950 Cal BP.	Virah-Sawmy et al. 2009, 2010
Lake Kavitaha	Central Highlands	Pollen	Decline in woody vegetation beginning ca 1400 Cal BP (530–780 Cal AD).	Burney 1987b
Andolonomby (Ambolisatra)	Spiny Thicket (coastal SW)	Pollen	Dramatic decline in arboreal vegetation and appearance of ruderal vegetation ca 1500 Cal BP.	Burney 1993, 1999, Burney et al. 2003[a]
Lake Amparihibe	Dry Deciduous Forest	Lake sediments	Eutrophication of lake at ca 1000 Cal BP (1130 ± 50 ^{14}C yr BP).	Burney 1999
Anjohibe Cave	Dry Deciduous Forest	Speleothem	Shift from C_3 plant-dominated to C_4 plant-dominated landscape ca 1100–1000 yr ago (890–990 CE) without a reduction in rainfall.	Burns et al. 2016
Ste-Luce	Humid Forest (coastal SE)	Diatoms and pollen	Low water levels and rapid reduction in most woody taxa between 1000 and 900 Cal BP.	Virah-Sawmy et al. 2009, 2010
Lake Tritrivakely	Central Highlands	Diatoms and pollen	Increase in temperature and transition from woody savanna to grass-dominated savanna between 1000 and 700 Cal BP.	Gasse and Van Campo 1998
Lake Mitsinjo	Dry Deciduous Forest	Pollen	Transition from woody savanna to grass-dominated landscape shortly before 790 Cal BP (890 ± 80 ^{14}C yr BP); shift to ruderal pollen around 500 Cal BP.	Matsumoto and Burney 1994
Lake Ihotry	Spiny Thicket	Pollen	Abrupt decline in tree pollen at 650 Cal BP.	Vallet-Coulomb et al. 2006
Lake Kavitaha	Central Highlands	Pollen	Decline in woody vegetation to $<15\%$ total pollen ca 600 Cal BP.	Burney 1987b

[a] Original date ranges presented in Burney 1993 were corrected and reinterpreted in Burney (1999) and Burney et al. (2003).

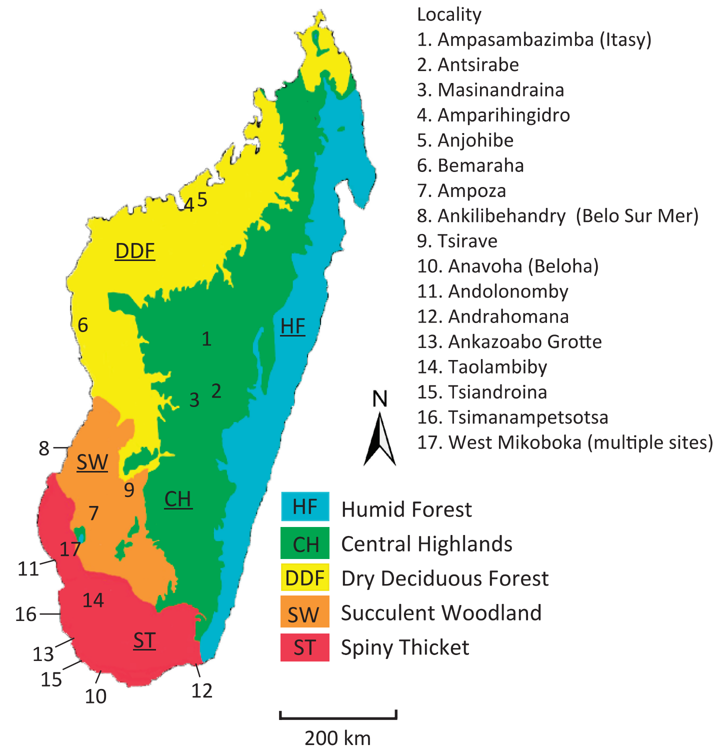

Figure 1. Map of Madagascar showing ecoregions and subfossil localities included in this study. For some statistical analyses, the Spiny Thicket and Succulent Woodland are combined into a single geographic region called the Subarid Bioclimatic Zone (SBZ). Map adapted from Burgess et al. (2004) and Cornet (1974).

Collagen preservation was evaluated using sample yield, isotope values, and elemental ratios (van Klinken 1999). Twelve radiocarbon dates were obtained at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory (CAMS), and the remaining eight *Pachylemur* were obtained at the Keck-Carbon Cycle Accelerator Mass Spectrometry Facility at the Univ. of California, Irvine (KCCAMS). Conventional radiocarbon age estimates are based on a 5568 year half-life, ^{13}C-corrected, and include a background subtraction based on simultaneously prepared modern and ^{14}C-free bone standards. We calibrated individual ^{14}C ages to calendar years before present (Cal BP) using the Southern Hemisphere calibration curve, SHCal13, in Calib 7.1 (Stuiver and Reimer 1993, Hogg et al. 2013). Ages were calibrated using a 20-yr moving average, and 2σ calibrated ages were rounded to the nearest 10 yr. We use mean Cal BP ages $\pm 1\sigma$ in figures, tables, and statistical tests.

Data analysis

All specimens have mean calibrated ages between 501 and 10 000 calendar years before present (Cal BP). These date ranges securely bracket previously observed regional vegetation changes (Table 1). We accounted for variable rainfall among sites by controlling for ecoregion (Fig. 1). Specimens come from a variety of subfossil localities in four ecoregions defined on the basis of climate and vegetation (Burgess et al. 2004): the Central Highlands (CH), Dry Deciduous Forest (DDF), Spiny Thicket (ST), and Succulent Woodlands (SW). The ST and SW are quite similar in climate and, to a slightly lesser extent, vegetation; both are characterized by prolonged dry seasons, <1300 mm annual rainfall, and an abundance of spiny and succulent plants. Madagascar can also be divided into Bioclimatic Zones on the basis of climate variables alone (Cornet 1974). Using this classification, the ST and SW ecoregions are collapsed into a single geographic region called the Subarid Bioclimatic Zone. We adopt this classification here (referring to the region as 'SBZ') to increase statistical power in several of the statistical tests outlined below. We also controlled for potential isotopic effects associated with proximity to the coast by designating sites as 'coastal' (<10 km from the coast) or 'inland' (Fig. 1). Finally, we used genus as a proxy for trophic level, as animals belonging to different genera tend to have differing diets.

We used general linear models (GLM) to determine which explanatory variables (time, genus, ecoregion, coastal proximity) best explain variation in δ^{15}N values for 1) all taxa from all ecoregions, 2) all taxa from each ecoregion, 3) all taxa from just coastal or inland sites in the SBZ, 4) lemurs from all ecoregions, 5) lemurs from the CH or SBZ, and 6) lemurs from just coastal or inland sites in the SBZ. We focused on lemurs because they are our best-represented taxonomic group. We also used analysis of variance (ANOVA) coupled with pairwise Tukey post-hoc tests of honestly significant differences (HSD) to check for differences in δ^{15}N values among time bins for each of these datasets.

We divided the data into eight time bins. We used 500-yr bins between 501 Cal BP and 3500 Cal BP when there is asynchronous evidence for regional desiccation of lakes, declines in forest pollen, and increases in grass pollen

Table 2. General linear models for collagen $\delta^{15}N$ values that incorporate ecoregion, coastal proximity (coastal or inland), time (binned time intervals), and genus.

Selected data	n	Included variables	r^2[a]	Regression statistics	Significant explanatory variables and interactions
All taxa All ecoregions Coastal and inland	238	Ecoregion Coastal proximity Time Genus	0.73	F = 6.2 DF = 120, 116[b] $p < 0.001$	Genus ($p < 0.001$) Ecoregion ($p < 0.001$) Genus × Ecoregion ($p = 0.001$)
All taxa CH only	39	Time Genus	0.92	F = 20.5 DF = 23, 15 $p < 0.001$	Genus ($p < 0.001$) Time ($p = 0.001$) Genus × Time ($p = 0.001$)
All taxa SBZ only Coastal and inland	184	Coastal proximity Time Genus	0.50	F = 3.4 DF = 74, 109 $p < 0.001$	Genus ($p < 0.001$) Time ($p = 0.033$) Coastal proximity ($p = 0.014$)
Lemurs only All ecoregions Coastal and inland	187	Ecoregion Coastal proximity Time Genus	0.69	F = 5.6 DF = 88, 98 $p < 0.001$	Genus ($p < 0.001$) Ecoregion ($p = 0.002$) Genus × Ecoregion ($p = 0.001$)
Lemurs only CH only	34	Time Genus	0.86	F = 11.6 DF = 19, 14 $p < 0.001$	Genus ($p < 0.001$) Time ($p = 0.002$) Genus × Time ($p = 0.001$)
Lemurs only SBZ only Coastal and inland	148	Coastal proximity Time Genus	0.46	F = 3.4 DF = 52, 95 $p < 0.001$	Genus ($p < 0.001$) Coastal proximity ($p = 0.005$)
Lemurs only SBZ only Inland only	80	Time Genus	0.26	F = 2.1 DF = 26, 53 $p = 0.01$	Genus ($p = 0.004$)
Lemurs only SBZ only Coastal only	68	Time Genus	0.21	F = 1.7 DF = 25, 42 $p = 0.059$	Genus ($p = 0.015$)

[a] Reported r^2 values are adjusted coefficients of determination for each corrected model.

[b] Reported degrees of freedom are model (first) and error (second).

(Table 1). We created a single time bin to accommodate our small sample from 3501 to 10 000 Cal BP. With the exception of a few brief intervals of aridity, Madagascar's climate throughout this time is reported to have been wet (Table 1; Burney 1993, Burney et al. 1997, Gasse and Van Campo 1998, Virah-Sawmy et al. 2009, Goodman et al. 2013, Wang and Brook 2013).

Finally, using linear regressions and Pearson correlation coefficients, we examined the relationship between individual calibrated radiocarbon ages and $\delta^{15}N$ values for datasets with more than five individuals. These included: 1) all taxa from each ecoregion, 2) lemurs from the CH or SBZ, 3) lemurs from just coastal or just inland sites in the SBZ, 4) specific lemur genera from the CH or SBZ, and 5) lemurs at selected subfossil sites with sufficient sample size to be examined independently. All analyses were performed using SPSS 22 and JMP Pro 11.2. Significance was set at $\alpha = 0.05$ for all tests.

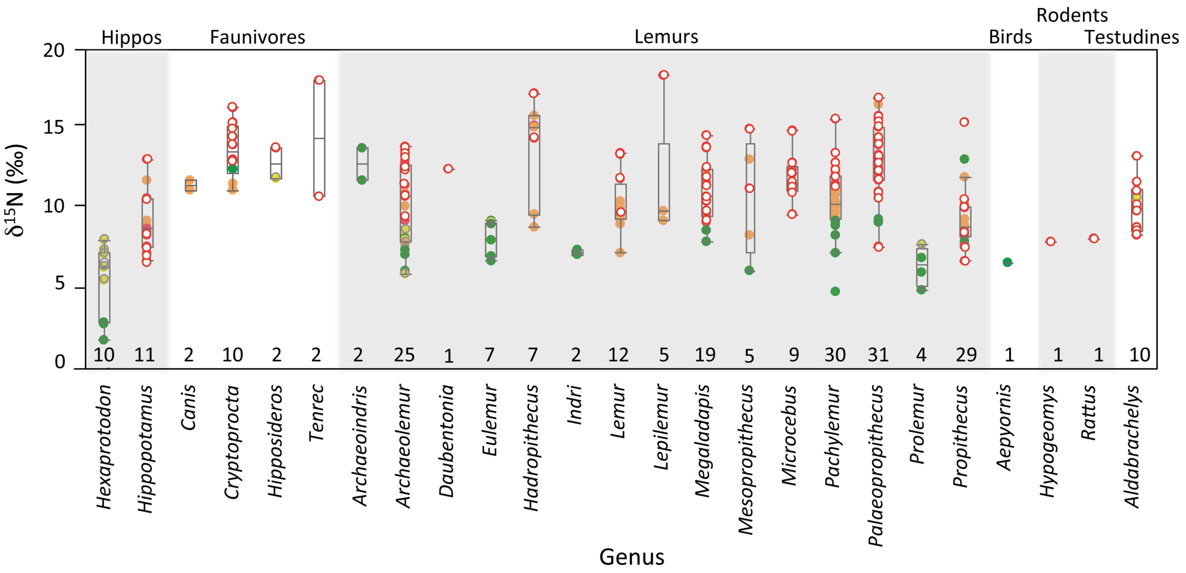

Figure 2. Boxplots summarizing isotope data for subfossil genera included in this study. Boxes include median, 1st and 3rd quartiles, and whiskers extend 1.53 the interquartile range from boxes. Numbers below boxes indicate sample sizes. Colors correspond to ecoregions presented in Fig. 1. Open circles are used for the spiny thicket.

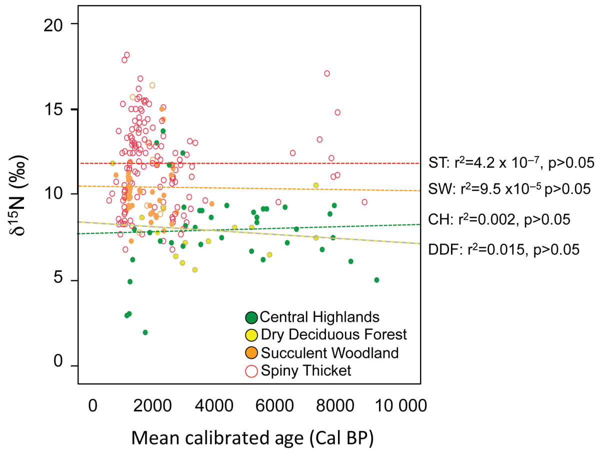

Figure 3. Scatterplot showing changes in δ^{15}N from 10 000 to 500 Cal BP, with regressions of nitrogen isotope values on calibrated radiocarbon age for individuals from each ecoregion. Colors correspond to ecoregions presented in Fig. 1. Open circles are used for the spiny thicket.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.s5s2n> (Crowley et al. 2016).

Results

Eight general linear models were used to determine the relative importance of genus, ecoregion, time and coastal proximity in explaining variation in vertebrate consumer δ^{15}N values (Table 2). Genus is a significant predictor of δ^{15}N values for all eight GLMs, and ecoregion is a significant predictor for analyses across different geographic regions. There is also a significant interaction between genus and ecoregion when all taxa are included, reflecting the geographically uneven distribution of some genera (Fig. 2). Time, on the other hand, is only significant in three models: all taxa from the CH, lemurs only from the CH, and all taxa from the SBZ. Lastly, coastal proximity is only significant in the GLM for SBZ lemurs, and there is a significant interaction between genus and coastal proximity for all taxa in the SBZ (Table 2).

Both genus and time are significant predictors of δ^{15}N values in the CH when all taxa are included as well as when only lemurs are considered, and there is a significant interaction between genus and time. Both of these GLMs are highly significant ($p < 0.001$), explaining 92% and 86% of the variation in δ^{15}N values, respectively. GLMs for the SBZ do not explain as much variation in δ^{15}N values as those for the CH. A model that includes time, genus, and

Table 3. Relationship between δ^{15}N values and calibrated ^{14}C age for lemurs from the Central Highlands (CH), Spiny Thicket (ST), and Succulent Woodland (SW). Regressions were calculated only when samples exceeded 5 individuals.

Taxon	n	Ecoregion and coastal proximity	Age range (Cal BP)	δ^{15}N range (‰)	Trend over oime	Inferred environmental shift
All lemurs	34	CH inland	1175–9090	4.9–13.8	$r = -0.22$, $p > 0.05$	No change
All lemurs	148	SBZ (all)	505–8700	6.8–17.2	$r = +0.11$, $p > 0.05$	No change
All lemurs	68	SBZ coastal	505–8700	7.7–17.2	$r = -0.12$, $p > 0.05$	No change
All lemurs	80	SBZ inland	605–3800	6.8–15.4	$r = +0.30$, $p = 0.008$	Becoming wetter
Pachylemur	7	CH inland	1175–7730	4.9–9.4	$r = +0.91$, $p = 0.004$	Becoming wetter
	23	SBZ (all)	1010–3800	9.0–15.6	$r = +0.15$, $p > 0.05$	No change
	19	SBZ inland	1010–3800	9.0–12.9	$r = +0.21$, $p > 0.05$	No change
Megaladapis	17	SBZ (all)	1460–5935	9.2–14.6	$r = -0.67$, $p = 0.003$	Becoming drier
	10	SBZ coastal	1460–5935	9.3–14.6	$r = -0.75$, $p = 0.01$	Becoming drier
	7	SBZ inland	2140–3165	9.2–11.7	$r = +0.05$, $p > 0.05$	No change
Archaeolemur	18	SBZ (all)	1150–2555	7.8–13.9	$r = -0.56$, $p = 0.02$	Becoming drier
	12	SBZ coastal	1150–2255	7.8–13.9	$r = -0.33$, $p > 0.05$	No change
	6	SBZ inland	1175–2555	7.9–13.0	$r = -0.66$, $p > 0.05$	No change
Palaeopropithecus	29	SBZ (all)	1010–3095	7.7–16.9	$r = -0.30$, $p > 0.05$	No change
	19	SBZ coastal	1010–2550	7.7–16.9	$r = -0.24$, $p > 0.05$	No change
	10	SBZ inland	1245–3095	10.7–14.5	$r = +0.11$, $p > 0.05$	No change
Propithecus	24	SBZ (all)	605–2020	6.8–15.4	$r = -0.07$, $p > 0.05$	No change
	23	SBZ inland	605–2020	6.8–15.4	$r = -0.07$, $p > 0.05$	No change
Microcebus	9	SBZ coastal	505–7835	9.7–14.9	$r = +0.41$, $p > 0.05$	No change

Table 4. Relationship between δ^{15}N values and calibrated ^{14}C age for lemurs from localities with > 5 individuals.

Site	Ecoregion	Coastal proximity	n	Age range Cal BP	δ^{15}N range (‰)	Trend over time	Inferred environmental shift
Ampasambazimba[1]	CH	Inland	34	1175–9090	4.9–13.8	$r = -0.22$, $p > 0.05$	No change
Taolambiby	ST	Inland	42	605–3165	6.8–15.4	$r = +0.46$, $p = 0.002$	Becoming wetter
Tsirave	SW	Inland	36	1010–3800	7.3–15.1	$r = -0.19$, $p > 0.05$	No change
Andolonomby	ST	Coastal	33	1075–5935	9.3–16.9	$r = -0.54$, $p = 0.001$	Becoming drier
Andrahomana	ST	Coastal	13	505–8700	9.6–17.2	$r = +0.17$, $p > 0.05$	No change

[1] Ampasambazimba is the only site in the Central Highlands. Therefore values for Ampasambazimba match those presented for the CH in Table 1.

coastal proximity explains 50% of the variation in δ^{15}N values for all taxa, and 46% of the variation in δ^{15}N values for lemurs only. Both of these models are highly significant ($p < 0.001$). Whereas time, genus, and coastal proximity are significant explanatory variables when all taxa are considered, only genus and coastal proximity are significant when just lemurs are considered. GLMs that include time and genus for inland and coastal lemurs from the SBZ only explain 26 and 21% of the variation in δ^{15}N values, and the coastal GLM is only marginally significant. Only genus emerges as a significant explanatory variable in either of these models. Genus is clearly an important driver of variation in δ^{15}N values. Faunivores and some lemurs have higher δ^{15}N values than elephant birds, hippopotami, and rodents from the same ecoregion (Fig. 2).

Linear regressions fail to indicate any significant relationships between individual calibrated radiocarbon ages and δ^{15}N values when ecoregions are considered independently (Fig. 3). There is also no relationship between age and δ^{15}N for lemurs from the CH, the SBZ (including both coastal and inland sites), or coastal sites in the SBZ, and a trend towards wetter conditions is observed for individuals from inland sites in the SBZ (Table 3).

In order to control for generic differences in diet and physiology, we must examine relationships between δ^{15}N values and radiocarbon age for specific lemur genera in specific regions or at particular sites. Nitrogen isotope data for CH *Pachylemur* suggest a trend towards feeding in wetter habitats. No relationship exists between δ^{15}N values and age for any of the lemur genera from inland sites in the SBZ, and *Megaladapis* is the only lemur genus from coastal sites to exhibit a significant relationship between δ^{15}N values and age, suggesting exploitation of drier habitats (Table 3).

In addition to there being no evidence of region-wide trends, there is no evidence of consistent temporal trends for lemurs at specific subfossil sites (Table 4). When all extinct lemur genera are considered, no change in δ^{15}N values is observed over time for Ampasambazimba, Tsirave, or Andrahomana; δ^{15}N data suggest Taolambiby became wetter and Andolonomby became drier (Table 4). Figure 4 and 5 further illuminate differences among sites and species. At Andolonomby, *Archaeolemur*, *Megaladapis*, and *Palaeopropithecus* all exhibit increasing δ^{15}N values over time (Fig. 4a). At Tsirave, δ^{15}N values increase for *Archaeolemur*, but not for *Pachylemur* (Fig. 4b), and at Ampasambazimba, δ^{15}N values are stable over time for *Archaeolemur*, *Pachylemur*, and *Palaeopropithecus*, but decrease for *Megaladapis* (Fig. 4c). There is no change in δ^{15}N values over time for extant *Microcebus* at Andrahomana or for *Propithecus* at Taolambiby (Fig. 5).

ANOVA results further demonstrate variable changes in δ^{15}N values through time (Table 5). When all taxa are considered, there are significant isotopic differences among time bins when all ecoregions are included. Tukey's post-hoc tests indicate that values are highest from 1001–1500 and 1501–2000 Cal BP and lowest for 3501–10 000 Cal BP. There are also significant isotopic differences among time bins for just the CH or the SBZ. In the CH, δ^{15}N values are highest from 2001–2500 Cal BP, and lowest from 1001–1500 and 1501–2000 Cal BP (Table 5). In the SBZ, δ^{15}N values are highest from 1001–1500 and 1501–2000 Cal BP and lowest from 2501–3000 Cal BP (Table 5). There are no differences in δ^{15}N values among time bins when coastal and inland sites are examined independently.

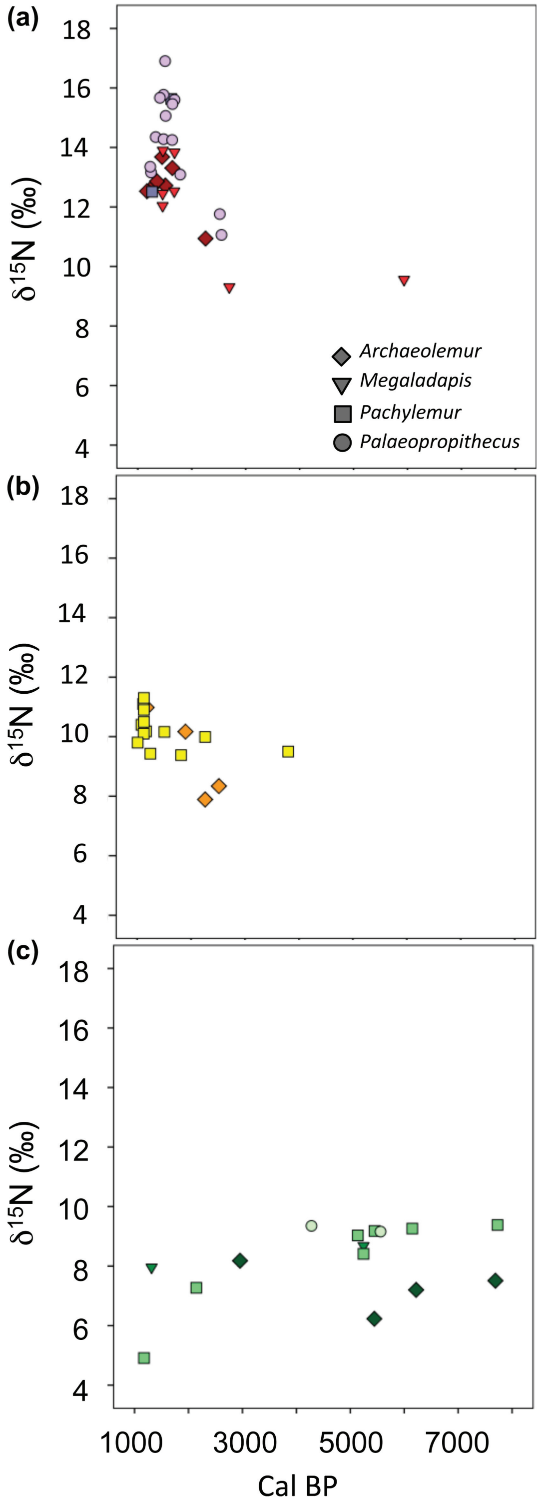

Figure 4. Scatterplots showing the relationship between δ^{15}N and calendar ages for selected extinct subfossil lemurs from subfossil sites Andolonomby (a), Tsirave (b), and Ampasambazimba (c).

Patterns are broadly similar when only lemurs are considered (Table 5). There are differences among time bins when all ecoregions are included, as well as when regions are considered independently. Tukey's post-hoc tests indicate

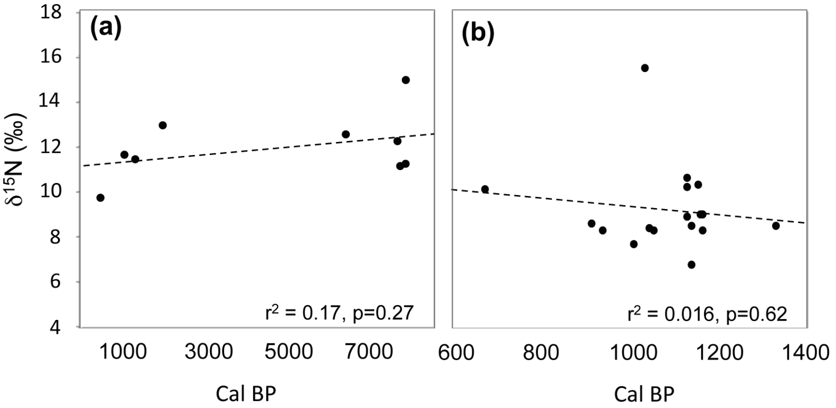

Figure 5. Scatterplots showing the relationship between δ^{15}N and calendar ages for *Microcebus* spp. from Andrahomana (a), and *Propithecus verreauxi* from Taolambiby (b).

that values are again highest from 1001–1500 and 1501–2000 Cal BP and lowest for 3501–10 000 Cal BP when all ecoregions are included. In the CH, δ^{15}N values are highest from 2001–2500 Cal BP, and lowest from 1001–1500, 2501–3000, and 3501–10 000 Cal BP (Table 5). In the SBZ, δ^{15}N values are highest from 1501–2000 Cal BP, and lowest from 501–1000 Cal BP (Table 5). There are no differences in δ^{15}N values among time bins when coastal and inland sites are examined independently.

Discussion

Decades of research have led to two competing hypotheses about what triggered the Late Holocene extinctions of Madagascar's megafauna. Some lines of evidence, including spikes in *Sporormiella* spore counts prior to palynological evidence of habitat change (Burney et al. 2003), butchered bones (MacPhee and Burney 1991, Pérez et al. 2005, Godfrey et al. 2011, Cox et al. 2013, Mathena et al. 2015), body size bias in the extinction process (Godfrey and Irwin 2007), and ethnographic accounts of megafauna and megafaunal hunting (Godfrey 1986, MacPhee and Burney 1991, Burney and Ramilisonina 1998, Godfrey and Jungers 2003), suggest that humans were involved. Alternatively, decreases in woody pollen counts from sediment cores have been used to suggest increasing aridification was responsible (Virah-Sawmy et al. 2009, 2010). Aridification has been posited for the island beginning 4000 yr ago in the north and sweeping southward over the next several centuries (Burney 1993, 1999, Gasse and Van Campo 1998, Wang and Brook 2013). More dramatic and synchronous desiccation has been reported beginning 1200 yr ago and peaking around 900–950 Cal BP (Virah-Sawmy et al. 2009, 2010). Indeed, the temporal coincidence of transitions from predominately arboreal to non-arboreal pollen in southeastern, central, and northern Madagascar led Virah-Sawmy and colleagues (Virah-Sawmy et al. 2010) to argue that a severe island-wide drought approximately 1000 yr ago was the primary trigger of megafaunal extinction.

Researchers favoring a larger role for humans point to evidence of human impacts prior to the posited island-wide drought. There is definitive evidence of human butchery of now-extinct species in southwestern Madagascar more than 2000 yr ago (Pérez et al. 2005) and contested evidence of butchery by humans in the northwest over 4000 yr ago (Gommery et al. 2011, Dewar 2014). Burney and colleagues (2003) showed that precipitous declines in the spores of the dung fungus *Sporormiella* preceded spikes in charcoal microparticles and changes in pollen profiles at sites across Madagascar during the Late Holocene. These authors used this evidence to argue that hunting by humans severely impacted the megafauna starting ca 2000 yr ago, and that the loss of these creatures facilitated extensive fire-induced habitat modification (Burney et al. 2003). Additionally, the overlap in timing of apparent aridification and human presence also led Burney (1999) to propose a 'Synergy hypothesis', which posits that the combination of increasing human presence and dwindling water resources negatively impacted the native fauna. This hypothesis was developed further by Clarke and colleagues (2006) to suggest that human settlements around receding water resources in the southwest may have made native fauna more vulnerable to human predation in the Late Holocene.

Humans may have arrived on Madagascar by 4000 or 5000 yr ago (Dewar 2014), but there is no indication of widespread human presence until after 2500 yr ago (Burney et al. 2004), and no evidence of large settlement sites until near the end of the first millennium of the Common Era, CE. The first major settlement sites in the west and south (Sarodrano on the west coast and Enijo on the Menarandra River in the extreme south) date to between the 7th and the 10th century CE (Parker Pearson et al. 2010, Douglass and Zinke 2015). In the north, the large Arab trading posts of Irodo and Mahilaka date from the 9th century CE and later (Radimilahy 1998, Dewar 2014). All of these sites lack evidence of endemic megafaunal consumption but *Bos indicus* (the humped zebu cow) was present at each (Andrianaivoarivony 1987). Additionally, a femur attributed to *Bos indicus* was found in a level at an archaeological site at Velondriake Marine Protected Area (southwest coast, Andavadoaka) dated to the 11th to 13th century CE (Douglass 2016). Humped cattle are also depicted in the rock art of the Upper Onilahy River in the southwest

Table 5. Summary statistics for each time bin and one-way analysis of variance comparing $\delta^{15}N$ values among time bins for selected datasets. For each test, time bins that share the same superscript letter are statistically indistinguishable [Tukey's honestly significant difference (HSD) test; $\alpha = 0.05$].

Selection	Time bins (Cal BP)	n	Mean $\delta^{15}N$ $\pm 1\sigma$ (‰)	ANOVA Results[a]
All taxa	3501–10000	36	9.2 ± 2.5^{B}	$F_{6, 231} = 5.2$
All ecoregions	3001–3500	11	9.8 ± 2.4^{AB}	$p < 0.001$
Coastal and inland	2501–3000	34	9.5 ± 2.0^{B}	
	2001–2500	27	11.1 ± 2.4^{AB}	
	1501–2000	36	11.9 ± 3.2^{A}	
	1001–1500	73	11.3 ± 2.9^{A}	
	501–1000	21	10.6 ± 2.6^{AB}	
All taxa	3501–10000	19	8.0 ± 1.3^{B}	$F_{5, 33} = 6.7$
CH only	3001–3500	4	8.4 ± 1.0^{ABC}	$p < 0.001$
	2501–3000	5	8.8 ± 2.3^{AB}	
	2001–2500	4	11.5 ± 2.9^{A}	
	1501–2000	2	4.9 ± 4.2^{BC}	
	1001–1500	5	5.0 ± 2.2^{C}	
	501–1000	0	–	
All taxa	3501–10000	11	11.9 ± 2.5^{AB}	$F_{6, 178} = 3.4$
SBZ only	3001–3500	6	11.8 ± 1.6^{AB}	$p = 0.003$
	2501–3000	26	10.0 ± 1.7^{B}	
	2001–2500	21	11.3 ± 2.4^{AB}	
	1501–2000	33	12.4 ± 2.6^{A}	
	1001–1500	68	11.7 ± 2.3^{A}	
	501–1000	20	10.5 ± 2.6^{AB}	
All taxa	3501–10000	1	9.5^{A}	$F_{6, 101} = 2.9$
SBZ only	3001–3500	6	11.4 ± 1.6^{A}	$p = 0.7$
Inland only	2501–3000	22	10.0 ± 1.7^{A}	
	2001–2500	15	11.0 ± 2.2^{A}	
	1501–2000	28	12.3 ± 2.7^{A}	
	1001–1500	37	10.5 ± 2.0^{A}	
	501–1000	17	10.2 ± 2.7^{A}	
All taxa	3501–10000	10	12.1 ± 2.5^{A}	$F_{5, 71} = 2.2$
SBZ only	3001–3500	0	–	$p = 0.06$
Coastal only	2501–3000	4	10.1 ± 1.7^{A}	
	2001–2500	6	12.0 ± 2.7^{A}	
	1501–2000	23	13.4 ± 2.4^{A}	
	1001–1500	31	13.2 ± 1.8^{A}	
	501–1000	3	12.0 ± 2.1^{A}	
Lemurs only	3501–10000	29	9.3 ± 2.5^{B}	$F_{6, 181} = 4.8$
All ecoregions	3001–3500	8	9.7 ± 2.0^{AB}	$p < 0.001$
Coastal and inland	2501–3000	17	10.1 ± 2.1^{AB}	
	2001–2500	23	11.4 ± 2.5^{AB}	
	1501–2000	30	12.0 ± 2.8^{A}	
	1001–1500	65	11.4 ± 2.5^{A}	
	501–1000	16	9.8 ± 1.9^{AB}	
Lemurs only	3501–10000	18	8.0 ± 1.3^{B}	$F_{5, 28} = 4.6$
CH only	3001–3500	4	8.4 ± 1.0^{AB}	$p = 0.004$
	2501–3000	4	7.9 ± 1.1^{B}	
	2001–2500	4	11.5 ± 2.9^{A}	
	1501–2000	1	7.8^{AB}	
	1001–1500	3	6.4 ± 1.6^{B}	
	501–1000	0	–	
Lemurs only	3501–10000	10	11.8 ± 2.6^{AB}	$F_{6, 141} = 2.3$
SBZ only	3001–3500	4	11.0 ± 1.1^{AB}	$p = 0.04$
Coastal and inland	2501–3000	12	11.1 ± 1.2^{AB}	
	2001–2500	17	11.6 ± 2.4^{AB}	
	1501–2000	28	12.3 ± 2.7^{A}	
	1001–1500	62	11.5 ± 2.1^{AB}	
	501–1000	16	9.8 ± 1.9^{B}	
Lemurs only	3501–10000	1	9.5^{A}	$F_{6, 74} = 1.5$
SBZ only	3001–3500	4	11.0 ± 1.8^{A}	$p = 0.2$
Inland only	2501–3000	9	11.3 ± 1.3^{A}	
	2001–2500	12	11.3 ± 2.2^{A}	
	1501–2000	8	9.6 ± 1.1^{A}	
	1001–1500	33	10.4 ± 2.0^{A}	
	501–1000	14	9.6 ± 1.9^{A}	
Lemurs only	3501–10000	9	12.0 ± 2.6^{A}	$F_{5, 61} = 1.5$
SBZ only	3001–3500	0	–	$p = 0.2$
Coastal only	2501–3000	3	10.7 ± 1.3^{A}	
	2001–2500	5	12.6 ± 2.6^{A}	
	1501–2000	20	13.4 ± 2.4^{A}	
	1001–1500	29	13.0 ± 1.7^{A}	
	501–1000	2	11.1 ± 2.0^{A}	

[a] Reported degrees of freedom are model (first) and error (second).

(Rasolondrainy 2012), which appears to have been earlier yet, but has not been radiocarbon dated.

If drought were largely responsible for the demise of the megafauna, and if the inferred extreme drought culminating 900–950 Cal BP were particularly important, then we would expect to see an increase in $\delta^{15}N$ values after 3500 yr ago, and peaking during the most recent time bins (500–1000 or 1000–1500 Cal BP) in all ecoregions. We find little evidence to support this scenario. There are no consistent trends in $\delta^{15}N$ values among ecoregions, sites, or taxa. Nitrogen isotope data suggest that the Central Highlands were driest between 2001 and 2500 Cal BP. In the SBZ, $\delta^{15}N$ values are highest between 1001 and 2000 Cal BP for all taxa and between 1500 and 2000 Cal BP for lemurs when both inland and coastal sites are pooled. There are no significant differences among time bins when coastal and inland sites are considered separately. Whereas there is some evidence for increasingly drier conditions at some sites (e.g. Andolonomby), other sites exhibit no trends through time, or even suggest moister conditions (e.g. Ampasambazimba). High $\delta^{15}N$ values between 1000 and 2000 yr ago in the SBZ may reflect increasingly arid conditions. However, there is no isotopic evidence that habitat change across ecoregions ca 1000 yr ago was triggered by aridification.

An alternative scenario is that the previously observed declines in pollen of woody taxa and increases in grass pollen were driven by humans. Strong evidence of a simultaneous increase in grasses ca 1000 yr ago in southeastern, central, and northwestern Madagascar (coeval with the spread of large settlements throughout Madagascar; Radimilahy 1998, Dewar 2014) may signal a change in land use by people largely abandoning extractive foraging practices, including bushmeat hunting, in favor of a more dedicated agro-pastoralist lifestyle dependent particularly on zebu husbandry (Burns et al. 2016). Such a shift in subsistence strategy may explain why there is virtually no evidence of the consumption of endemic megafauna more recently than 1000 yr ago (Godfrey 1986, Godfrey et al. 2011, Douglass 2016). If Burney and colleagues (2003) are correct in their interpretation that declines in *Sporormiella* spores reflect megafaunal population demise starting ca 2000 yr ago, then the megafauna would have been in severe decline before the beginning of the last millennium. Burning of landscapes 1000 yr ago would have simply accelerated their inevitable extinction.

Acknowledgements – We thank G. Gunnell at The Division of Fossil Primates at the Duke Univ. Lemur Center, UMass Amherst Natural History Collections (Anthropology), and the Dept of Paleontology and Biological Anthropology and Laboratory of Vertebrate Paleontology at the Univ. of Antananarivo for providing subfossil material. Thanks also to the late G. Randria and L. Ranivoharimanana for facilitating sample export, and to D. Andreasen at the Univ. of California, Santa Cruz, T. Guilderson and P. Zermeño at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory, J. Southon at the Keck-Carbon Cycle Accelerator Mass Spectrometry Facility at the Univ. of California, and Irvine and B. Erkkila at the Yale Earth Systems Center for Stable Isotopic Studies for assistance with isotopic and radiocarbon analysis. NSF funding provided partial support sample collection and dating (BCS-1317163 to GHP) and laboratory support (BCS-1460369 to DJK and BJC).

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Supplementary material (Appendix ECOG-02376 at <www.ecography.org/appendix/ecog-02376>). Appendix 1.