UNIVERSITY OF CALIFORNIA
Santa Barbara

Climate Change, Megafaunal Extinctions, and Human Colonization of Madagascar

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Anthropology

by

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September 2021

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July 2021

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I thank B. Culleton, L. Eccles, and C. Ebert for their thoughtful training during sample analysis. The laboratory component of this research also greatly benefitted from work with A.I. Domic, J.H. Curtis, R. George, M. Brenner, R. Wood, B. Crowley, V. Atuderei, M. Buckley, J. Southon, S. Ivory, M. Velez, D. Evans, W. Kirleis, J. Wiethold, I. Bishop, T.

Lacourse, N. Riedel, A. Telka, and H. Birks, as well as from help from laboratory assistants such as M. Davis, L. Green, and S. Kielar. I am grateful for the support and intellectual contributions from my coauthors (L.M.A. Rakotozafy, J.F. Ranaivoarisoa, G. Clark, A. Anderson, L. Godfrey, H.T. Wright, A.I. Domic, J.H. Curtis, and M. Brenner) and particularly from D.J. Kennett, K.G. Douglass, and B.E. Crowley. I thank all members of my PhD committee for their support and feedback on my dissertation, and I thank those who provided outside comments on my dissertation papers (particularly D. Burney, L. Godfrey, and Z. Farris). I also thank members of my earlier PhD committee (S. Newsome, K. Freeman, and P.J. Perry) for their support and comments, which fostered earlier stages of my dissertation research. This research benefitted from a variety of funding sources that are mostly listed in my CV, but I particularly thank the National Science Foundation and multiple organizations within UC Santa Barbara and Pennsylvania State University. I must end by thanking my friends and family who consistently encouraged me to pursue my interests and who made the process both enjoyable and memorable.

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EDUCATION:

PhD in Anthropology (expected Jul 2021)
University of California at Santa Barbara, College of the Letters and Science, Santa Barbara, CA

MA in Anthropology (May 2017)
Pennsylvania State University, College of the Liberal Arts, State College, PA
Graduated with distinction (4.0 GPA)

BS in Geology and Anthropology (double major) with **Minor in Mathematics** (Sep 2015)
University of Oregon, College of Arts and Sciences, Clark Honors College, Eugene, OR
Graduated summa cum laude (4.15 GPA)

HONORS AND AWARDS:

Lambda Alpha National Anthropology Honor Society | 2018
PSU Center for Human Ecology Poster Award | 2017
Society for Archaeological Sciences R.E. Taylor Poster Award | 2017
Clark Honors College President’s Thesis Award | 2015
University of Oregon Anthropology Department Undergraduate Paper of the Year Award | 2015
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FELLOWSHIPS AND SCHOLARSHIPS:

National Science Foundation Graduate Research Fellowship | 2015-2020 | $96,000
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American Philosophical Society Lewis and Clark Fellowship | 2017 | $5,000
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Pennsylvania State University Graduate Fellowship | 2015-2016 | $26,250 + tuition
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M. Glockers Garner Scholarship | 2011 | $1,500
Benton County Foundation Scholarship | 2011 | $500

PUBLICATIONS:

Hixon S., Douglass K., Crowley B., Rakotozafy L., Clark G., Anderson A., Haberle S., Ranaivoarisoa J., Buckley M., Fidiarisoa S., Mbola B., Kennett D. "Late Holocene spread of pastoralism coincides with megafaunal extinction on Madagascar." *Proceedings of the Royal Society B* (accepted).

*Domic A., ***Hixon S.**, Velez M., Ivory S., Douglass K., Brenner M., Curtis J., Culleton B., Kennett D. "Influence of Late Holocene climate change and human occupation on terrestrial and aquatic ecosystems in southwest Madagascar." *Frontiers in Ecology and Evolution* (in review). *co-first authors

Hixon S., Douglass K., Godfrey L., Eccles L., Crowley B., Rakotozafy L., Clark G., Haberle S., Anderson A., Wright H., Kennett D. (2021): "Ecological Consequences of a Millennium of Introduced Dogs on Madagascar." *Frontiers in Ecology and Evolution,* https://doi.org/10.3389/fevo.2021.689559.

Bechert U., **Hixon S.**, Schmitt, D. "Diurnal variation in serum concentrations of cortisol in captive African (*Loxodonta Africana*) and Asian (*Elephas maximus*) elephants." *Zoo Biology* (2021).

*Douglass K., ***Hixon S.**, Wright H., Godfrey L., Crowley B., Manjakahery B., Rasolondrainy T., Crossland Z., Radimilahy C. "A critical review of radiocarbon dates clarifies the human settlement of Madagascar." *Quaternary Science Reviews* 221 (2019): 105878. *co-first authors

Hixon S., DiNapoli, R.J., Hunt T.L., Lipo C.P. "Historical accounts of freshwater use on Rapa Nui (Easter Island)." *Journal of the Polynesian Society* 129.2 (2019): 163-189.

DiNapoli, R.J., Lipo C.P., Brosnan T., Hunt T.L., **Hixon S.**, Morrison A.E., Becker M. "Rapa Nui (Easter Island) monument (*ahu*) locations explained by freshwater sources." *PLOS ONE* 14.1 (2019). e0210409.

Hixon S., Elliott Smith E., Crowley B., Perry G., Randrianasy J., Ranaivoarisoa J.F., Kennett D., Newsome S. "Nitrogen isotope (δ^{15}N) patterns for amino acids in lemur bones are inconsistent with aridity driving megafaunal extinction in southwestern Madagascar." *Journal of Quaternary Science* 33.8 (2018): 958-968.

Hixon S., Lipo C., Hunt T., Lee C. "Using structure from motion mapping to record and analyze details of the colossal hats (*pukao*) of monumental statues on Rapa Nui (Easter Island)." *Advances in Archaeological Practice* 6.1 (2018):42-57.

Hixon S., Lipo C.P., McMorran B., Hunt T.L. "The colossal hats (*pukao*) of monumental statues: an analysis of *pukao* variability on Rapa Nui (Easter Island)." *Journal of Archaeological Science* 100 (2018): 148-157.
https://www.nature.com/articles/d41586-018-05347-y
https://www.bbc.com/news/science-environment-44466163

PROFESSIONAL PRESENTATIONS:

"Aridification, Extinction, and the Colonization of SW Madagascar by Pastoralists" invited seminar at the Max Planck Institute for the Science of Human History (2021)

"Ecological Consequences of a Millennium of Dogs on Madagascar" oral presentation at the virtual General Assembly of the European Geophysical Union (2021)

"Late Holocene spread of pastoralism coincides with endemic megafaunal extinction on Madagascar" oral presentation at the virtual 86th Annual Society for American Archaeology Conference, San Francisco, CA (2021)

"Insight on trophic level estimation through amino acid $\delta^{15}N$ values from Madagascan megafauna" oral presentation at the virtual 80th Annual Society for Vertebrate Paleontology Conference, Cincinnati, OH (2020)

"Settlement and extinction chronologies of Madagascar" oral presentation at the Radiocarbon Universe webinar series of the Energy and Environmental Sustainability Laboratories, Pennsylvania Sate University (2020)
https://eesl.iee.psu.edu/radiocarbon-universe

"Past temporal and dietary overlap among introduced and extinct endemic herbivores in SW Madagascar" poster presentation at the 56th Annual Association for Tropical Biology and Conservation meeting in Antananarivo, Madagascar (2019)

"A critical review of radiocarbon dates clarifies the human settlement of Madagascar" oral presentation at the 84th Annual Meeting of the Society for American Archaeology in Albuquerque, NM (2019)

"Patterns in amino acid $\delta^{15}N$ values are inconsistent with aridity driving megafaunal extinction in southwestern Madagascar" oral presentation at the 2nd Annual Lembersky Conference in Human Evolutionary Studies in Rutgers, NJ (2018)

"Patterns in amino acid $\delta^{15}N$ values are inconsistent with aridity driving megafaunal extinction in southwestern Madagascar" poster at the 82nd Annual Meeting of the Society for American Archaeology in Vancouver, BC (2017)

"The colossal hats (*pukao*) of monumental statues: an analysis of shape variability among the *pukao* of Rapa Nui" poster at the 80th Annual Meeting of the Society for American Archaeology in San Francisco, CA (2015)
http://www.nbcnews.com/science/weird-science/giant-easter-island-hats-may-have-been-rolled-place-n347986

RESEARCH EXPERIENCE:

Isotope Geochemistry Lab, University of California, Santa Barbara, CA (Jan-Sep 2020)
Worked under the direction of Lab Director Dr. Douglas Kennett and Lab Manager Dr. Richard George. Prepared plant and bone samples for stable isotope analysis and compiled and analyzed stable isotope and radiocarbon datasets from California and Mesoamerica. Helped with radiocarbon pretreatment lab set up, including the assembly of equipment for bone collagen pretreatment and for the graphitization of micromolar samples through Zn reduction.

Isotope Geochemistry Lab, Pennsylvania State University, State College, PA (Aug 2015 – Dec 2018)
Worked under the direction of Lab Director Dr. Douglas Kennett and Lab Manager Dr. Brendan Culleton with sample pretreatment, quality control, and occasional AMS maintenance. Prepared bone and shell for stable isotope analysis and bone and charcoal for radiocarbon analysis. Radiocarbon sample preparation included graphitization on a vacuum line. Prepared bone collagen samples for measurement of $\delta^{15}N$ and $\delta^{13}C$ values in order to reconstruct the diets of past individuals. Also worked with carbonate samples from a marine shell midden to quantify $\delta^{18}O$ values in order to identify past changes in temperature and salinity of estuarine waters in the state of Washington.

Center on Teaching and Learning (CTL) Fellowship, University of Oregon, Eugene, OR (Sep 2014 – Jun 2015)
Selected as one of three undergraduates to participate in the University of Oregon Undergraduate Research Fellowship offered through the CTL. Project deliverables included a research plan, quarterly progress reports, and a final report and presentation. Research sought to understand the variability among topknots (*pukao*) that adorn many of the monumental Easter Island statues (*moai*). Used three dimensional computer models of *pukao* to evaluate which surface features are stylistic with related temporal and special variability and which are functional and relate to *pukao* construction and transport. Findings helped explain how prehistoric islanders designed *pukao* and placed them atop *moai*.

Geospatial Research and Mapping Field Program, Easter Island, Chile (May-Jun 2014)
Participated in an NSF-sponsored project under the direction of Dr. Terry Hunt, University of Oregon, and Drs. Carl Lipo, Christopher Lee, and Matt Becker, California State University at Long Beach. Project mapped the landscape and coastal springs of Easter Island. Applied knowledge of GIS to field research and gained experience with aerial image collection and processing. Collected aerial imagery over archaeological features using a DJI Phantom Quadcopter, learned photo collection using a Trimble Gatewing X100 drone, and generated and manipulated three dimensional models of both artifacts and archaeological features on the island using Agisoft Photoscan and MeshLab software. Also gained experience with a StellarNet spectrometer and SptectraWiz software in order to collect representative reflectance signatures from various rock types on the island for subsequent materials mapping in ERDAS IMAGINE

using multispectral WorldView2 imagery. Visited a local high school agronomics class, talked about spectroscopy, and demonstrated how to use a spectroscope.

Museum Intern, University of Pennsylvania, Philadelphia, PA (Aug-Sep 2013 and 2014)
Worked in the physical-biological anthropology laboratory at the Museum of Archaeology and Anthropology under the direction of Dr. Janet Monge. Learned to identify skeletal specimens for bar coding and creation of collections and inventory databases. Also served as a docent for mummy museum exhibits.

TEACHING EXPERIENCE:

Teaching Assistant, University of California, Santa Barbara, CA (Sep-Dec 2020, Mar 2021-present)
Worked under the direction of Dr. Stuart Smith to remotely teach Introduction to Archaeology to a section of ~50 undergraduate students. Worked under Dr. Douglas Kennett to remotely teach the same course in 2021. Prepared lectures, coordinated discussion, administered assignments, worked with students individually to improve writing, and graded multiple essays per student.

PROFESSIONAL DEVELOPMENT:

NSF Graduate Research Opportunities Worldwide, Australian National University (Jan-Mar 2019)
Worked with Drs. Simon Haberle, Geoffrey Clark, and Janelle Stevenson in the paleoecology laboratory of the ANU College of Asia and the Pacific. Learned sediment pretreatment protocols for pollen and charcoal analysis, microscope methods for automated microcharcoal identification, and the analysis of charcoal count data. Created a record of macrocharcoal through analysis of a swamp core from Yap, Federated States of Micronesia as part of an ongoing project to identify early human settlement of the island. Collected bone samples as part of my dissertation research and worked with Dr. Rachel Wood in the ANU Radiocarbon Laboratory to expand my knowledge of pre-screening techniques for the identification of bone samples that are suitable for ^{14}C analysis.

Isocamp Course in Stable Isotope Biogeochemistry, University of Utah (Jun 2017)
Attended the laboratory and lecture components of an intensive two-week course that was focused on the environmental and biological theory that underlies fractionation processes across a range of environmental applications. The laboratory component involved practice with research design, the collection and pretreatment of field samples, quality control, data analysis and visualization, and presentation. Laboratory sample pretreatment procedures included water extractions from leaves and soils through cryogenic vacuum distillation, soil carbonate extraction through acid digestion, leaf lipid extraction from leaves and soils through silica gel column chromatography, and leaf lipid identification and quantification through gas chromatography.

University of Antananarivo, Antananarivo Madagascar (Aug-Sep 2016, Jul-Oct 2017, Sep 2018, Oct 2019)
Photographed subfossil bone specimens and learned how to record three dimensional structures using the Artec Space Spider for detailed morphometric analysis of subfossil bone specimens. Identified and sampled bones under the direction of Dr. Lucien Rakotozafy and Dr. Steve

Goodman for radiocarbon and stable isotope analyses. Planned and led lake sediment coring with Drs. Mark Brenner and Jason Curtis (University of Florida) at three locations in SW Madagascar between Tulear and Morombe. Conducted regional pedestrian survey and excavated ten test units with members of the Morombe Archaeological Project in the vicinity of Lamboara and Ranobe. Set up monthly collection of coastal water samples and exported archaeological shell samples for measurement of $\delta^{18}O$ values in order to identify seasons of past human occupation at coastal archaeological sites.

Center for Stable Isotopes, University of New Mexico, Albuquerque, NM (Jun-Jul 2016, Jun-Jul 2018, Apr-May 2019)
Measured compound specific $\delta^{15}N$ values in bone collagen under the direction of Dr. Seth Newsome. Specifically broke down collagen into amino acids and used a gas chromatography combustion isotope ratio mass spectrometer (GC/C/IRMS) to obtain compound specific stable isotope measurements. Prepared bone collagen samples for $\delta^{2}H$ measurements and learned how to interpret stable nitrogen and hydrogen isotope values.

Geology Field School, University of Oregon, Central OR and Western MT (Jun-Jul 2015)
Participated in the University's geology field camp under the direction of Drs. Jim Watkins, Marli Miller, Samantha Hopkins, and Ray Weldon. Mapped various geological structures (in map view and geological cross section) such as lava flows and various deformation structures using self-directed pedestrian surveys and stereoviewers. Also created a couple of detailed stratigraphic columns with complete rock descriptions (mostly paleosols, siliciclastics, and carbonates).

Igneous Petrology Lab, University of Oregon, Eugene, OR (Mar-May 2014)
Worked in Dr. Paul Wallace's igneous petrology lab under the direction of Ph.D. student Madison Myers on research designed to expand understanding of the history of volcanism in southwestern Colorado. Crushed and sieved ash samples from the San Juan volcanic field, picked sanidine, quartz, and biotite using a stereomicroscope, mounted and polished individual grains on slides, and intersected melt inclusions in grains for analysis in a Fourier transform infrared spectrometer.

African Archaeology Lab, University of Oregon, Eugene, OR (Oct-Dec 2013)
Volunteered with Dr. Stephen Dueppen in the African Archaeology Lab to better understand the subsistence strategies and patterns evident in his West African study sites. Sorted and labeled bone fragments from an Iron Age cultural deposit in Burkina Faso and learned about contemporary butchery practices as well as their traces in the archaeological record.

Kualoa Field School, University of Hawaiʻi at Mānoa, Honolulu, HI (Jun-Jul 2013)
Participated in the first Kualoa Field School in Kaʻaʻawa Valley and Kualoa, Oʻahu, under the direction of Dr. Terry Hunt, Dean of the Clark Honors College at the University of Oregon. Conducted pedestrian surveys, assisted in work with ground penetrating radar, gained experience using GPS and a total station for topographic mapping, and mapped several stone features using the tape and compass mapping technique. Learned basic augering methods, participated in the excavation of a 2 m x 2 m test unit to a depth of 0.7 m, and applied my knowledge of stratigraphic profiling and soil description.

Geology and Archaeology Club, University of Oregon, Eugene, OR (2013-2014 academic year)
Served as the Vice President (2013-14) and helped organize fundraising events and host faculty colloquia (member since Jan 2011). Participated in a club field trip led by Dr. Dave Blackwell, professor of geology, to Escalante National Park in UT during Spring Break 2012.

SERVICE:

Collaborator on the development of a Research Topic for *Frontiers in Ecology and Evolution* (2020-2021)
https://www.frontiersin.org/research-topics/16622/early-human-colonization-of-remote-indian-ocean-islands-and-its-ecological-impacts
Reviewer for:

- *The Holocene* (2021)
- *Quaternary Science Reviews* (2020-21)
- *Malagasy Nature* (2020)

Co-Editor of SAA Island & Coastal Archaeology interest group newsletter "The Current" (Spring 2018-present)
Volunteered in State College Community Education Extended Learning (CEEL) Program (Spring 2018)

OUTREACH:

Radio Interview:
"Easter Island explanation" interview with Wendyl Nissen of RadioLIVE, NZ (Jun 12th, 2018). https://www.radiolive.co.nz/home/articles/long-lunch/2018/06/the-long-lunch--in-case-you-missed-it-12-06-18.html

Oral Presentations:
"Extinction, Drought, and the Spread of Pastoralism in Madagascar" presented at the University of California at Santa Barbara, Department of Ecology, Evolution, and Marine Biology (May 5th, 2020).

"Radiocarbon and the Chronology of Past Species Turnover in SW Madagascar" presented at the University of Antananarivo's Museum of Art and Archaeology, Antananarivo, Madagascar (Oct 15th, 2019).

"Past Construction and Transport of Stone Monuments on Rapa Nui (Easter Island)" presented at the University of Western Australia, Perth (Mar 21st, 2019).

"Introduction to Madagascar and Its Prehistory" presented at the Australian National University, Canberra in guest lecture for Prof. Geoffrey Clark's "Past Human Expansions" undergraduate course (Mar 12th, 2019).

"Past Megafaunal Extinction and Species Introductions in Madagascar" presented at the Australian National University College of Asia and the Pacific, Canberra, Australia (Feb 6th, 2019).

“Carbon Isotope Analyses in Plant and Bone” presented at University of Antananarivo Department of Paleontology and Biological Anthropology, Antananarivo, Madagascar (Sep 14th, 2018).

“Past Construction and Transport of Stone Monuments on Rapa Nui (Easter Island)” presented at Darwin Research Station, Puerto Ayora, Santa Cruz, Ecuador (Jul 9th, 2018).

Bulletin Publications:
Hixon S., Elliott Smith E., Crowley B., Perry G., Randrianasy J., Ranaivoarisoa J.F., Kennett D., Newsome S. “Nitrogen isotope values of amino acids in lemur bone help disentangle the history of recent extinction in southwestern Madagascar.” *SAS Bulletin* 42.1 (2019): 11-14.

OTHER ACTIVITIES AND SKILLS:

Software – ArcGIS, ERDAS IMAGINE, Agisosft Photoscan, Meshlab, Fusion LiDAR, Spectrawiz, Artec Space Spider, and SigmaPlot

Field and Laboratory Equipment – GPS, Quadcopter, GC/IRMS, graphitization line

Open Water SCUBA – PADI certification acquired in June 2011

Languages –German; 3 years of Spanish

Other:
Attended virtual “Science Communication Workshop” organized by the British Ecological Society’s Palaeoecology Special Interest Group (Spring 2020)
Associate Member of Sigma Xi (Spring 2019-present)
Attended Society for American Archaeology online seminar “Outreach, Engagement, and Advocacy: The Importance of Reaching the Public through Media” (Spring 2018)
Participated in PSU Anthropology pedagogy interest group (Fall 2017-Spring 2018)
Member of the:

- Conservation Paleobiology Research Coordination Network (Winter 2020-present)
- European Geophysical Union (2021)
- Society for Vertebrate Paleontology (2020)
- Association for Tropical Biology & Conservation (2019)
- Quaternary Research Association (Spring 2019-present)
- Society for Archaeological Science (Spring 2017-present)
- Society for American Archaeology (Spring 2015-present)

ABSTRACT

Climate Change, Megafaunal Extinctions, and Human Colonization of Madagascar

by

Sean Wolf Hixon

Biodiversity provides us with a host of cultural, scientific, and economic benefits, and highly biodiverse islands such as Madagascar are the focus of many conservation efforts. History provides essential context to the current biodiversity crisis and can influence how conservation groups engage with local communities. On Madagascar, environmental history narratives since the French colonial era have emphasized past human contributions to deforestation and species extinctions. However, these inferred contributions, and even the time of initial human arrival on Madagascar, are based on limited data and subject to ongoing archaeological debate. I use chemical analyses of subfossil bone and lake sediments recovered from archaeological fieldwork and museum collections to test ideas that past animal introductions and drought contributed to the disappearance of endemic megafauna in arid SW Madagascar.

Radiocarbon data from introduced ungulates (cattle, sheep, goats, and bushpigs, n=59) and endemic megafauna (pygmy hippopotamuses, giant tortoises, elephant birds, and giant lemurs n=213) demonstrate 1) that the spread of pastoralism in SW Madagascar coincided with a pulse of megafaunal extinction ~1,000 years ago and 2) that this turnover occurred hundreds to possibly thousands of years after the first directly ^{14}C-dated trace of human activity on the island. Directly ^{14}C-dated butchered bone suggests that humans hunted extinct Malagasy megafauna for thousands of years, yet the spread of pastoralism likely heightened the impact of this hunting as pastoralism aided expanding human populations. Moreover, stable carbon and nitrogen isotope data suggest that sheep, goats, tortoises, and hippos had broadly similar diets or exploited similar habitats, which left

potential for direct forms of competition between sheep and goats and endemic megaherbivores. Introduced domestic dogs also share a mutualism with pastoralists who occasionally hunt, and ^{14}C-dated dog bone collected from across Madagascar suggest that dogs at least briefly co-occurred with the island's extinct megafauna ~1,000 years ago. Dogs could have facilitated human-led hunts of forest-dwelling extinct megafauna, yet relatively high stable carbon isotope values in dog collagen suggest few individuals consumed primarily forest bushmeat. The distinct isotopic niches of dogs and the endemic forest predator known as the fosa (*Cryptoprocta ferox*) suggest that any negative interaction between the two follows from something other than predation and exploitation competition (e.g., interference competition and disease transmission).

Ongoing aridification is a major concern for agropastoralists in southern Madagascar, and it is unclear the degree to which introduced livestock and endemic megafauna were sensitive to drought. Geochemical analysis of a sediment core from SW Madagascar revealed a succession of dry intervals during the last ~1600 years. The driest interval coincided with the appearance of livestock and the disappearance of endemic megafauna around the lake. Coupled lake sediment and bone stable carbon isotope records suggest that pygmy hippos and cattle coped with vegetation changes associated with past aridification and forest clearance by consuming more xerophytic C4 and CAM plants during drier times. However, unlike the endemic megafauna, cattle may have been more sensitive to drought, as their bone collagen stable isotope values suggest they survived by strategically exploiting wet habitat during dry intervals of the past millennium. I worked with members of the Morombe Archaeological Project to excavate three additional coastal ponds in SW Madagascar (Tampolove, Ankatoke, and Andranobe), which revealed different lengths of co-occurrence among humans, introduced vertebrates, and extinct endemic

megafauna during the past six millennia. Although the modification of a bone from an extinct pygmy hippo and the deposition of human subsistence remains (e.g., cutmarked fish bones and processed mangrove whelk shells) recovered from these ponds likely span only the past millennium, a directly dated introduced bushpig tooth from ~4,000 years ago may help confirm that humans were present on the island by the mid Holocene. The disappearance of extinct megafauna (particularly giant tortoises and pygmy hippos) in the vicinity of these three sites matches regional extinction patterns in SW Madagascar. Together, these data clarify species-specific responses to past ecological and climatic stressors and suggest that the spread of pastoralism, rather than simply the presence of human hunters or occurrence of drought, contributed to past megafaunal extinction on Madagascar.

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“The beauty and genius of a work of art may be reconceived, though its first material expression be destroyed; a vanished harmony may yet again inspire the composer, but when the last individual of a race of living things breathes no more, another heaven and another earth must pass before such a one can be again.”

William Beebe, *The Bird: Its Form and Function*, (1906:18)

I. CH. 1: INTRODUCTION

Insular settings contribute to both speciation and extinction, and the material record within the well-defined boundaries of islands often captures fascinating traces of past evolutionary change. Remote islands were one of the last places that humans colonized, and, as geographically-bounded “laboratories,” these islands can provide convenient settings to study human cultural diversity and environmental impacts (Burney 1997; Fitzhugh and Hunt 1997; Kirch 1980). While island archaeological records reflect remarkable histories of skillful human voyaging (Goodwin, et al. 2014; Johns, et al. 2014) and perseverance in extreme environments (Lipo, et al. 2013), it is often noted that “Islands are where species go to die” (Quammen 2012:258). Approximately 95% of the ~200 bird and mammal species that have gone extinct since AD 1500 were island endemics (Loehle and Eschenbach 2012).

Questions regarding the human contribution to extinction form part of a grand challenge in archaeology to identify how “human activities have shaped Earth’s biological and physical systems” (Kintigh, et al. 2014). The modern global biodiversity crisis has given a recent sense of urgency to research on human-environment interactions that define the Anthropocene (Crutzen 2002; Dirzo, et al. 2014) and what is considered Earth’s sixth mass extinction (Barnosky, et al. 2011). Academic concepts like these form part of a widespread warning by scientists to humanity regarding accelerating environmental degradation (Ripple, et al. 2017). However, questions on human environmental impacts are as old as our recognition of species extinction itself. As early as the mid-19th century, 50 years before the death of the last known passenger pigeon, writers such as American diplomat George Marsh observed that “Man is everywhere a disturbing agent. Wherever he plants his foot, the harmonies of nature are turned to discords” (Marsh 1885 [1864]:33). With the same observation in mind, Charles Lyell and others considered if environmental factors or humans contributed to the disappearance of animals in the fossil record (Lyell 1863; Owen 1846). Today, archaeological research can help reconstruct past environmental baselines to set goals for conservation planning (Armstrong, et al. 2017; Nogué, et al. 2017b) and archaeologists continue to debate the relative importance of human hunting versus climate change in driving past extinction in a variety of times and places (Grayson 2008; Haynes 2007; Martin 1973). For example, in New Zealand, the disappearance of the endemic moa shortly followed the arrival of Polynesians, and numerous kill sites contribute to a consensus that human hunting drove moa extinction (Anderson 2003; Perry, et al. 2014). Meanwhile, in mainland Africa, megaherbivore diversity started to decline in the mid Pliocene (~4.6 million years ago). This predates the expansion of hominins into carnivore niche space by millions of years and is better explained by the expansion of C4 grasslands (Faith, et al. 2018). Given strong evidence that human disturbance contributed to some past extinctions and not others, what is the value of using new tools to continually address century-old questions on extinction? There are several reasons, which are outlined below:

1. Old environmental history narratives have modern consequences. In many cases, early environmental history narratives are based on speculation or limited data, yet they have been used to disenfranchise people from ancestral homeland as part of “fortress” conservation efforts (Brockington 2002). The archaeological record

can give a more accurate sense of how humans have shaped and are part of modern ecosystems.

2. It is useful to identify and learn from exceptions to the judgement that humans are everywhere a negative “disturbing agent.” It is true that humans and domesticated animals have flourished as we replace wild biomass and homogenize Earth’s ecosystems (Bar-On, et al. 2018; McKinney and Lockwood 1999). However, there are also many important cases in which human subsistence behavior has promoted biodiversity in somewhat unexpected ways (Bird, et al. 2008; Castilla 1999; Codding, et al. 2014; Grayson 2001).
3. Every extinct organism was unique. Pulses of extinction that punctuate Earth’s history suggest shared extinction drivers (Alvarez, et al. 1980), yet details on the causes and consequences of recent species extinctions can’t be generalized. Each case gives useful context to our understanding of modern ecosystems (Doughty, et al. 2013; Federman, et al. 2016; Godfrey, et al. 2008).
4. Research with recently “extinct” species can reveal taxa that are merely cryptic. This exciting possibility doesn’t entail cryptozoology or require Conan Doyle’s “Lost World.” For example, human hunting contributed to the extinction of giant tortoises in the Galapagos after Darwin’s historic visit in 1835, yet the analysis of DNA from extinct tortoise museum specimens and extant tortoises suggests that one genetic lineage still exists in an intermixed population (Poulakakis, et al. 2008). Additionally, on Madagascar, an endemic carnivoran known from the island’s subfossil record may still exist in remote parts of the far north (Nomenjanahary, et al. in press).

Given that Madagascar is Earth’s oldest island and home to a diverse array of threatened species (Ganzhorn, et al. 2001), it is a useful place to learn how past human activity shaped the island’s ecosystems. As is often noted, what Madagascar has in common with all other islands is that it is unique. Until the past millennium, the island’s “megafauna” included not only Earth’s most massive bird (*Vorombe titan*, ~650 kg, Hansford and Turvey 2018) but also multiple species of diminutive pygmy hippo that were only ~1 m tall (Stuenes 1989). Even Madagascar’s status as “island” is somewhat misleading (Wit 2003), for its size (about 1.4 times larger than the state of California) and ancient basement rock justify its nickname as the “Eighth Continent” (Tyson 2000). Indeed, it is often useful to consider Madagascar as an island of islands because its diverse ecoregions range widely from humid forests to xerophytic thicket, and its river networks define boundaries between microendemic species (Vences, et al. 2009). This dissertation is focused on the spiny thicket and succulent woodland of SW Madagascar because the aridity of this region has left relatively well preserved archaeological and paleontological deposits. The region includes early examples of human-modified megafaunal bone (Hansford, et al. 2018; MacPhee and Burney 1991), and the current inhabitants of the countryside rely on fishing and agropastoralism. Though introduced zebu cattle outnumbered people on the island in the early twentieth century (Kaufmann and Tsirahamba 2006), the arrival time of zebu and other introduced animals on the island is not well-documented (Douglass, et al. 2019). Consequently, it is unknown when and how past pastoralists successfully came to exploit Madagascar’s diverse ecoregions and whether they contributed to the disappearance of the island’s endemic large herbivores. I have used archaeological field work and chemical analyses of bones and lake sediments to address the following questions:

- Did the spread of pastoralism coincide with the growth of human populations, and was there potential for negative ecological interactions between introduced livestock and now extinct megaherbivores?
- What was the potential for introduced predators, such as dogs, to contribute to the hunting of megafauna, and was there potential for competition between dogs and endemic carnivorans?
- How did climate change during the past spread of pastoralism, and how did the drought tolerance of livestock compare to that of endemic megafauna?
- How long did people, livestock, and extinct megafauna cooccur in coastal SW Madagascar during the second half of the Holocene?

A. Archaeology of Madagascar

The material record of Madagascar reflects a history of population movements and species translocations from across the Indian Ocean (Boivin, et al. 2013; Pierron, et al. 2017). For example, people introduced zebu cattle of South Asia to Madagascar, possibly via East Africa (Hanotte, et al. 2002). The coastal middens of SW Madagascar include traces of zebu and other introduced animals (Douglass, et al. 2018), and bones of introduced livestock and other terrestrial animals are particularly abundant at inland sites such as Rezoky, Asambalahy, and Andranosoa (Rasamuel 1984; Vérin and Battistini 1971). These inland archaeological deposits are typically shallow (<50 cm) and include some traces of iron working (e.g., slag), remains of extant hunted game (e.g., lemur and tenrec bone), and imported ceramics (e.g., sgraffito) that attest to trade networks that clearly spanned the Indian Ocean during the early centuries of the past millennium (Vérin and Battistini 1971). The potential social interactions among the pastoralists who colonized inland Madagascar and any preexisting human populations are unknown, and the interactions between inland pastoralists and traders at coastal entrepôts (particularly at Mahilaka in NW Madagascar, Radimilahy 1998) are poorly known (Dewar and Wright 1993). Coastal entrepôts undoubtedly served as conduits that spread Malagasy resources across the Indian Ocean (e.g., chlorite schist, timber, and textiles) and brought a series of introduced plants and animals to the island (e.g., zebu, goats, sheep, dogs, cats, rats, mice, and chickens, Boivin, et al. 2013). However, it is unclear whether all human-introduced animals arrived on Madagascar during the expansion of Indian Ocean trade networks around the start of the last millennium. Less is known about how the spread of pastoralism and commensal species interacted with climate change and shaped the island's existing biodiversity.

B. Theoretical framework

"Endless queries can be addressed in nature. The key to success lies in choosing from the myriads of possibilities those particular questions that are both important and answerable."

Steven Stanley, *The New Evolutionary Timetable,* (1981:80)

The question, "Did human hunting or climate change cause past extinction?" is an interesting one that has been considered in many times and places by archaeologists, paleontologists, conservation workers, and the curious public. However, scientific answers to this question are complicated for a couple of reasons. First, causation in the historical sciences is difficult to infer merely from a sequence of events, and historical storytelling that may follow regular narrative forms, glosses over the incomplete material record, and include untestable components (discussed by Terrell 1990) that sometimes give rise to the judgement that "…no science can ever be historical" (Gee 2001). Still, causation can be difficult to identify even in modern experimental work (nicely illustrated in Stephen Jay Gould's discussion of Sir Ronald Fisher's reluctance to infer that smoking causes cancer when given the observed association of smoking and lung cancer (Gould 2011:296-308)). This dissertation is based on the idea that historical science does exist (in disciplines that range from archaeology to astronomy) and that it should involve data gathered to test competing falsifiable hypotheses (Cleland 2001). A second and more specific challenge to identifying extinction causes follows from the observation that relatively small and isolated populations are relatively susceptible to extinction in the face of stochastic environmental and demographic processes (Lande 1998; Ovaskainen and Meerson 2010). This makes the ultimate cause of extinction almost unknowable and not particularly interesting. For example, even the ultimate time and cause of the recent extinction of the Tasmanian thylacine (a carnivorous marsupial) are poorly known despite historical information (Carlson, et al. 2018). Past extinctions on Madagascar are similarly shrouded in mystery. Here, a suite of anthropogenic and climatic stressors might have negatively impacted endemic pygmy hippo populations (reviewed by Burney, et al. 2004), yet it is possible that a single landslide in a lonely inland drainage killed the last fertile group and doomed the species to extinction. This dissertation does not address questions on this landslide or similarly complicated questions regarding the first person to set foot on Madagascar. Instead, my dissertation research addresses basic questions on the potential for certain types of interactions between animals and the potentially divergent responses of animals to past environmental change.

These questions are inspired by theory from community ecology. Though it is often noted that the historical sciences are “somewhat depauperate in theory” and must borrow from related disciplines (Jackson and Blois 2015:4915), even data from the historical sciences can help adjudicate theory. As noted by Steven Jay Gould, “theory and observation are Siamese twins, inextricably intertwined and continually interacting”

(Gould 2011:148). Community ecology is useful for studying the past spread of pastoralism and the decline of endemic megafauna because it focuses on how species interact and communities are formed. This body of theory provides "an informed set of tools that allows us to understand, predict, and synthesize the variability that is seen among communities in both pattern and process" (Chase and Leibold 2003:142).

In a place like Madagascar, where a limited number of traces of past human activity have been reliably and directly dated (Douglass, et al. 2019), basic questions regarding the past spread of pastoralism must be addressed with theory that is empirically friendly. The conclusion of this dissertation will leave many unanswered questions regarding the behavior of past pastoralists and extinct megafauna. These questions may be addressed through increasingly fine-grained future research informed by additional bodies of theory from evolutionary ecology. However, this does not diminish the value of the present research, just as it does not diminish the value of the earliest paleontological and archaeological work on Madagascar, which focused on establishing useful taxonomic units. As noted by Steven Stanley, "Practicing scientists must operate at those levels that, during their particular lifetimes, bear fruit" (Stanley 1981:185).

Within community ecology, the niche concept has a long history of application and is particularly useful for addressing the basic questions of this dissertation. In the early 20th Century, Joseph Grinnell focused on how the environment affects animal behavior and defined the ecological niche based on the where an organism can live (Grinnell 1917). Conversely, Charles Elton focused on how animal behavior affects the environment and defined the ecological niche based on the animal's role within a community (Elton 1927). More recently, G. Evelyn Hutchinson distinguished physical space from the environment when he attributed niches to species and defined niches as hypervolumes with *n* independent axes that define the numerous conditions required for survival (e.g., temperature and aspects of diet, Hutchinson 1957). The distinction between the Hutchinsonian niche and the actual physical environment continues to give a foundation for ecological thinking by enabling spatially-explicit species distribution modelling that captures conditions that favor range expansion, speciation, and extinction (Colwell and Rangel 2009; Holt 2009).

An organism's ecological niche influences its chemical composition, and the stable isotope content of hard tissue preserved in the material record can give insight on the "isotopic niche" of past organisms. To be ecologically meaningful, isotopic niches must be considered in terms of the environmental gradients that they reflect (reviewed in Newsome et al. 2007). In some cases, this can be done explicitly by using mixing models to infer proportions of different resources that contributed to an organism's diet (Parnell et al. 2011). Isotopic niches are useful to consider, because they are sensitive to a wide range of niche dimensions and conveniently integrate ecological information over different amounts of time depending upon which tissue is analyzed (Bearhop et al. 2004). However, all analytical approaches have limitations, and the primary limitation of the isotopic niche is that organisms with dissimilar ecological niches may have indistinguishable isotopic niches. To help resolve such issues of equifinality, researchers can turn to analyses of behavior and gut content of modern organisms and to the analysis of other physical traces left by long-dead organisms (e.g., coprolites and dental calculus).

Species-specific niches determine which species interact and how they interact. Negative interactions may threaten species with extinction, and even positive interactions may indirectly threaten individuals and populations when we consider networks of interspecific interaction. For example, an introduced predator may threaten an endemic herbivore by consuming it (predation), it may threaten another predator through niche overlap that creates harassment or exploitation of a shared resource (exclusion or exploitation competition), and it may even disadvantage a relatively small animal bystander in a way that neither benefits nor harms the predator (e.g., by stepping on the bystander, ammensalism, Fig. 1). If the introduced predator interacts with yet another organism in a way that confers a benefit to both (mutualism), then this creates an indirect negative effect on the predator's prey because the mutualism enhances the predation preesure. All of these interactions define communities (Mougi and Kondoh 2012) and can leave traces in the archaeological record (Jackson and Blois 2015), but predation is perhaps the easiest to recognize given that it often leaves punctured and cutmarked bone.

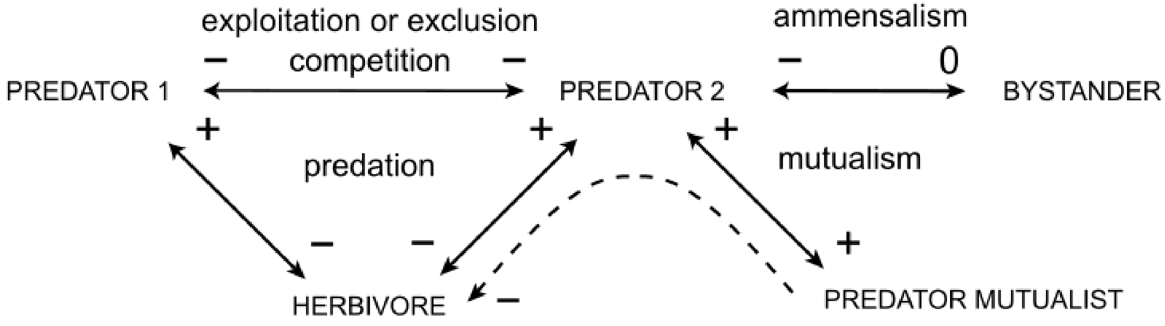

Figure 1. Hypothetical interaction web illustrating various types of direct interactions and one indirect effect, with signs marking net benefit or harm. As illustrated by the dashed arrow, the mutualist of predator 2 limits the herbivore population even though the mutualist and herbivore may never interact directly. This gives a small sample of known ecological interactions that maintain modern communities and affected the composition of past communities.

The morphology, chemical content, dental microwear, and dental calculus of skeletal remains enable us to infer multiple aspects of the niches of past people and other animals, yet competition remains relatively difficult to recognize in the subfossil record. This is because we know from modern work that all animals that compete directly for resources have niche overlap but not all animals with overlapping niches compete. This follows from the fact that niche overlap in one dimension (e.g., diet) does not exclude the possibility that organisms partition their niches in another dimension (e.g., activity pattern, Fig. 2). Almost any case of multiple paleodiet proxies applied to the fossil record can illustrate this quality of multidimensional niches. For example, the similar stable carbon isotope content of subfossil bone protein of an extant lemur (*Propithecus verreauxi*) and an extinct giant lemur (*Pachylemur insignis*) from SW Madagascar suggest that these animals exploited a similar dietary niche, yet amino acid specific stable nitrogen isotope values document spatial partitioning among these co-occuring species (Hixon, et al. 2018).

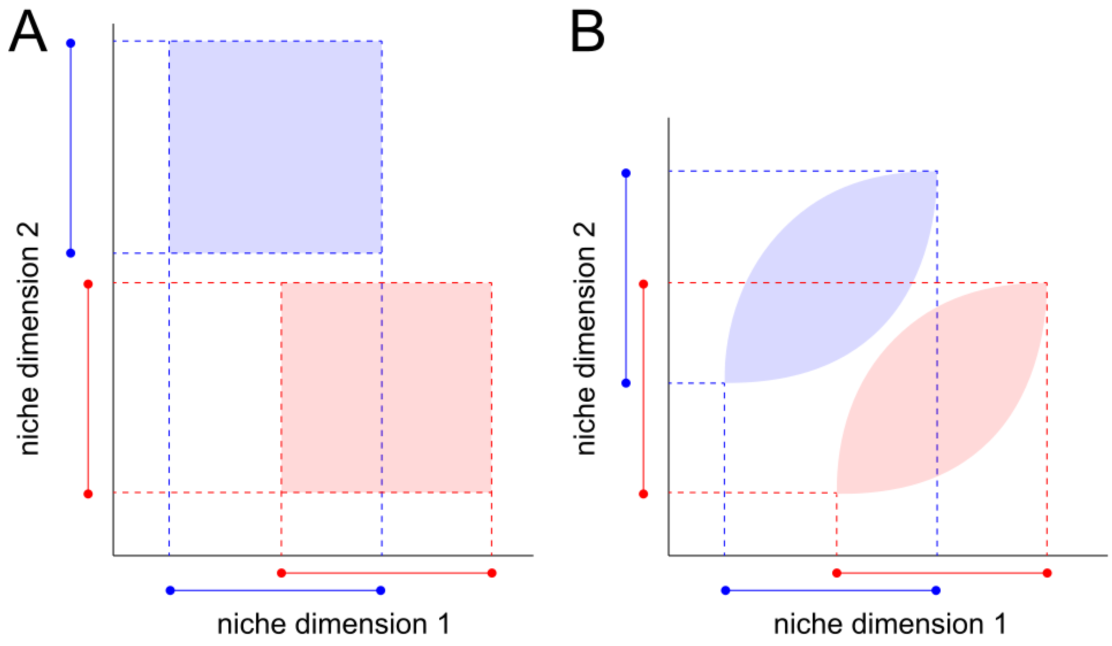

Figure 2. Conceptual examples of how two organisms (red and blue) can partition their niches despite niche overlap in one or more niche dimensions. As discussed in the text, multiple paleodiet proxies can reveal niche overlap along one dimension and niche partitioning along another (A). Also, the potential dependence of niche attributes on one another complicates the inference of multidimensional niche overlap based on projections along individual axes (i.e., dietary proxies, B).

Competition is difficult to recognize from niche overlap, because competition depends also on 1) resource supply, 2) the impacts of each potential competitor on the given resource, and 3) the sensitivity of each competitor to resource depression (reviewed by Chase and Leibold 2003). Constrasting examples of potential herbivore competitors from mainland Africa and the Galapagos help illustrate certain aspects this important point. Goats flourished in the Galapagos after people introduced them to multiple islands during the 19th and early 20th Century, and the broad diets of these goats overlapped with endemic land iguanas and giant tortoises. It was this dietary overlap, combined with limited supply of plant resources during dry intervals and the extreme negative impacts of goat grazing on native plants, that created competition between goats and endangered endemic herbivores (Coblentz 1978; MacFarland, et al. 1974). On Pinta Island, vegetation used by endemic herbivores rapidly recovered following the removal of goats, and this helped make it feasible for giant tortoises to maintain a sustainable population (Hamann 1993). The situation is strikingly different in the Serengeti of East Africa, which supports a diverse community of endemic grazers. Despite exploiting similar plants, grazers such as wildebeest, zebra, and Thomson’s gazelle coexist rather than unsustainably compete because their impacts on the vegatation can in fact facilitate the grazing of each other (Arsenault and Owen-Smith 2002; McNaughton 1976, 1979). In general, the effects of herbivores on each other via their impacts on plants are diverse (Foster, et al. 2014; McClure 2015), so past dietary overlap among potential competitors raises more questions than it answers.

Competition is just one of a series of interactions that define how an organism’s way of life transforms its environment, and we as humans are remarkable with the number of ecological connections we forge. This behavior contributes to human niche construction, which is an important topic in archaeology given its association with past plant and animal domestication (Smith 2016) and lasting environmental legacies (McClure 2015). Niche construction theory explicitly recognizes that organisms both alter their environment through behavior (i.e. construct niches) and respond to alterations in the environment (i.e. respond to the development their own niches and those of others). Beavers and their dammed pools are often considered classic examples of niche construction, but the most striking example of niche construction behavior (NCB) may be the cyanobacteria of ~2.3 billion years ago that produced enough oxygen both to precipitate the iron ions in the ancient sea and make respiration possible for the vast majority of extant organisms (Cloud 1973). The recognition of NCB in humans is not new. As Karl Marx stated: "It is as clear as noon-day that man, by his industry, changes the forms of materials furnished by Nature, in such a way as to make them useful to him" (Marx 1961 (1844)). Also, for over eighty years, human ecologists have studied NCB in humans (under various labels of environmental engineering, manipulation, and management) in small-scale human societies (Smith 2015:230). Niche construction theory (NCT) may be considered distinct from standard evolutionary theory given that NCT considers two adaptive processes in evolution (natural selection and niche construction) and two general forms of inheritance (genetic and ecological, Odling-Smee 1988). What NCT lacks is "a general theory of behavior that is required to explain why humans would construct niches" (Mohlenhoff, et al. 2015:E3093). Consequently, those who advance NCT do not present it as something radically new, but instead hope that it will enable "a more general evolutionary framework within which other theories [e.g. those in evolutionary biology, developmental biology, and the human sciences] can be subsumed" (Kendal, et al. 2011:785).

Niche construction changes the environment and can help explain consistent associations among taxa. However, the realized niches of organisms also track environmental change to different extents, which creates novel communities. For example, the diversity of fossil mammals at sites in the U.S. shifted dramatically during late Quaternary environmental fluctuations and justifies the observation that “Mammal communities are continually, and unpredictably, emergent” (Graham, et al. 1996:1605). This does not deny the fact that interspecific interactions structure communities and that “Species and populations are not billiard balls knocked around the landscape by changing climate” (Jackson and Blois 2015). However, considering how niches respond to long-term environmental change is essential for answering questions about past extinction and current threats to biodiversity.

How different niche dimensions respond to long-term environmental change has been studied on different scales in different disciplines, which has given rise to a wide range of terminology with somewhat different meaning. For example, on time scales of seasons and lifespans, archaeologists have considered how organisms move to track resource availability or stay in place and buffer environmental change (Cashdan 1992). Paleontologists have considered how niches are conserved through range shifts on continental scales and over the scale of millions of years (DeSantis, et al. 2012). Resource tracking and niche conservativism may also be considered in terms of “specialization” (Simpson 1952:205), “ecological flexibility” (Pianka 2011:239) and “ecological and climatic tolerances” (Meltzer 2015:45). As noted since at least Lyell (1835), species with narrow or inflexible niches are relatively prone to extirpation and extinction in the face of an environmental perturbation.

C. Dissertation organization

This dissertation is organized into four co-authored journal articles. Each chapter presents new data to build on previous research and addresses questions on the past spread of pastoralism and extinction of endemic megafauna in SW Madagascar. Chapter 2 uses ^{14}C and stable isotope data from the subfossil bones of livestock and extinct megafauna from archaeological and paleontological deposits to identify the potential for negative interactions between introduced and extinct megaherbivores. This builds on the past work of many researchers to refine chronologies of species extinction and introduction (most recently Crowley 2010; Douglass, et al. 2019), and it tests the idea that past shifts in human land use contributed to loss of endemic megaherbivores (Dewar 1997; Godfrey, et al. 2019). Chapter 3 uses a similar approach to identify whether dogs could have aided human hunting of endemic megafauna and interacted negatively with endemic predators. This gives historical context to the current antagonistic relationship between dogs and endemic fosa (Farris, et al. 2017; S. Merson, et al. 2019). Also, because the ancestry of introduced animals can be inferred through future DNA analyses, chronologies of past species introductions can contribute to an understanding of when different groups from around the Indian Ocean arrived in Madagascar (Boivin, et al. 2013; Crowther, et al. 2016; Dewar and Wright 1993). Chapter 4 uses coupled stable isotope records from bones found in archaeological deposits and associated lake sediments to identify how livestock and endemic megafauna responded to dry intervals during the past ~1,600 years. These data are used to test the old assumption that endemic megafauna were relatively drought sensitive and prone to extinction in the face of Late Holocene aridification (Mahé and Sourdat 1972). It also provides some long-term context to how pastoralists currently move across SW Madagascar in response to aridification and other stressors (Feldt, et al. 2017). Lastly, Chapter 5 uses ^{14}C-dated excavated bone from a relatively long period of time (the past 6,000 years) to identify past patterns of local co-occurrence among humans, human introduced species, and extinct megafauna. This expanded time depth is confined to the vicinity of three coastal ponds north of the Chapter 4 study site. Coupled occurrence and paleohydrological data from these three ponds test elements of both Chapters 2 and 4. Faunal occurrence and stratigraphic data also give context to important traces of early interactions between humans and extinct megafauna (MacPhee and Raholimavo 1988; MacPhee and Burney 1991) that were collected during the early 20th Century (G Grandidier 1905; White 1930). The thesis concludes with a summary of key findings, limitations, and areas for future work.

II. CH. 2: Late Holocene spread of pastoralism coincides with endemic megafaunal extinction on Madagascar[1]

A. *Abstract*

Recently expanded estimates for when humans arrived on Madagascar (up to ~10,000 years ago) highlight questions about the causes of the island's relatively late megafaunal extinctions (~2000-500 years ago). Introduced domesticated animals could have contributed to extinctions, but the arrival times and past diets of exotic animals are poorly known. To conduct the first explicit test of the potential for competition between introduced livestock and extinct endemic megafauna in southern and western Madagascar, we generated new radiocarbon and stable carbon and nitrogen isotope data from the bone collagen of introduced ungulates (zebu cattle, sheep, goats, and bushpigs, n=66) and endemic megafauna (pygmy hippopotamuses, giant tortoises, and elephant birds, n=68) and combined these data with existing data from other endemic megafauna (n=282, including giant lemurs). Radiocarbon dates confirm that introduced and endemic herbivores briefly overlapped chronologically in this region between 1000 and 800 calibrated years before present (cal BP). Moreover, stable isotope data suggest that goats, tortoises, and hippos had broadly similar diets or exploited similar habitats. These data support the potential for both direct and indirect forms of competition between introduced and endemic herbivores. We argue that competition with introduced herbivores, mediated by opportunistic hunting by humans and exacerbated by environmental change, contributed to the late extinction of endemic megafauna on Madagascar.

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[1] This chapter has been accepted for publication in *Proceedings of the Royal Society*

B. Introduction

Until quite recently, Madagascar's diverse endemic fauna included gorilla-sized lemurs (*Archaeoindris fontoynontii*), giant tortoises (*Aldabrachelys* spp.), three-meter-tall elephant birds (*Vorombe titan*), and one-meter-tall pygmy hippos (*Hippopotamus* spp.). However, all of the island's endemic animals >10 kg are now extinct, and introduced zebu cattle (*Bos indicus/taurus*) are currently the largest animal on the island. A wide range of potential stressors, including overhunting, drought, fire, disease, and biological invasion could have contributed to extinctions on Madagascar (Burney, et al. 2004). To test extinction hypotheses that involve competition between endemic and introduced herbivores, we integrate radiocarbon dating with stable isotope analysis of introduced ungulate and extinct endemic megaherbivore bone collagen.

A debate regarding when humans first arrived on Madagascar is ongoing. Some researchers favor early human arrival 10,000-4,000 years ago based on rare stone tools and cutmarks on ancient elephant bird bone (Dewar, et al. 2013; Hansford, et al. 2018), while others favor recent arrival 1,600-1,000 years ago based on broader cultural considerations (Anderson, et al. 2018). Here, we accept that people were on the island 2,000-1,600 years ago based on a recent review of radiocarbon (^{14}C) data associated with traces of human activity (Douglass, et al. 2019). However, it was not until ~1,000 years ago that most populations of endemic megafauna crashed (Crowley 2010). These extinctions coincided with drought in parts of southern Madagascar (Faina, et al. in press; Vallet-Coulomb, et al. 2006). Still, the idea that island-wide aridification drove extinctions is inconsistent with: 1) the persistence of diverse Malagasy megafauna during relatively severe Pleistocene climate fluctuations; 2) megafaunal bone stable isotope records that suggest few directional changes in habitat aridity (Crowley, et al. 2017;

Hixon, et al. 2018); and 3) paleoclimate records that reveal asynchronous changes in regional climate during the Late Holocene (Faina, et al. in press; Scroxton, et al. 2017). While Madagascar's Late Holocene fossil record is rich, the early Holocene and Pleistocene records in particular are sparse and limited to <20 ^{14}C-dated individuals from central and northern Madagascar (Crowley 2010).

An alternative hypothesis is that the spread of pastoralism and farming onto the island ~1,000 years ago triggered megafaunal extinctions (Dewar 1997; Godfrey, et al. 2019). Paleoenvironmental records document vegetation change in multiple regions of Madagascar during the past millennium (Burns, et al. 2016; Virah-Sawmy, et al. 2016), but there are very few data from directly ^{14}C-dated introduced animals (Douglass, et al. 2019). Today in southern and western Madagascar (SW Madagascar), the foddering needs of livestock currently influence the movement of pastoralists; these people modify both grasslands and forests through selective clearance and the propagation of introduced succulents to sustain livestock (Kaufmann and Tsirahamba 2006).

We consider potential for interactions among humans, livestock, and endemic megafauna that may be direct (e.g., resource competition or hunting) or indirect (e.g., mediated by hunting/predation, as in apparent competition, see below). Direct competition between introduced and endemic animals resulting from overlap in diet or habitat use can be partially inferred through stable isotope analysis of consumer tissue. Evidence for hunting comes from butchery marks on Malagasy megafaunal bone (Anderson, et al. 2018; Hansford, et al. 2018). Hunting could have acted in concert with regional aridification to drive megafaunal extinction (an early formulation of the "synergy hypothesis," Fig. 1, Burney 1999). Alternatively, hunting could have occurred alongside pastoralism to create apparent competition between introduced and endemic herbivores ("subsistence shift hypothesis," Fig. 1; Godfrey, et al. 2019). Apparent competition occurs between two species that are prey for the same predator/hunter (Holt and Bonsall 2017), and it disadvantages prey that are more sensitive to predation (e.g., slowly-reproducing megafauna that are not part of animal husbandry). By definition, apparent competition does not depend on overlapping resource use of potential competitors (as inferred from stable isotope and other data). Instead, support for apparent competition comes from evidence of: 1) contemporaneous shared predation/hunting pressure (as inferred through cutmarked and ^{14}C-dated bone); and 2) different impacts on prey populations (surmised in our case due to differences in animal husbandry versus bushmeat hunting). Regardless of direct competition among herbivores, livestock could have devastated endemic megafauna simply by facilitating human population growth and overhunting.

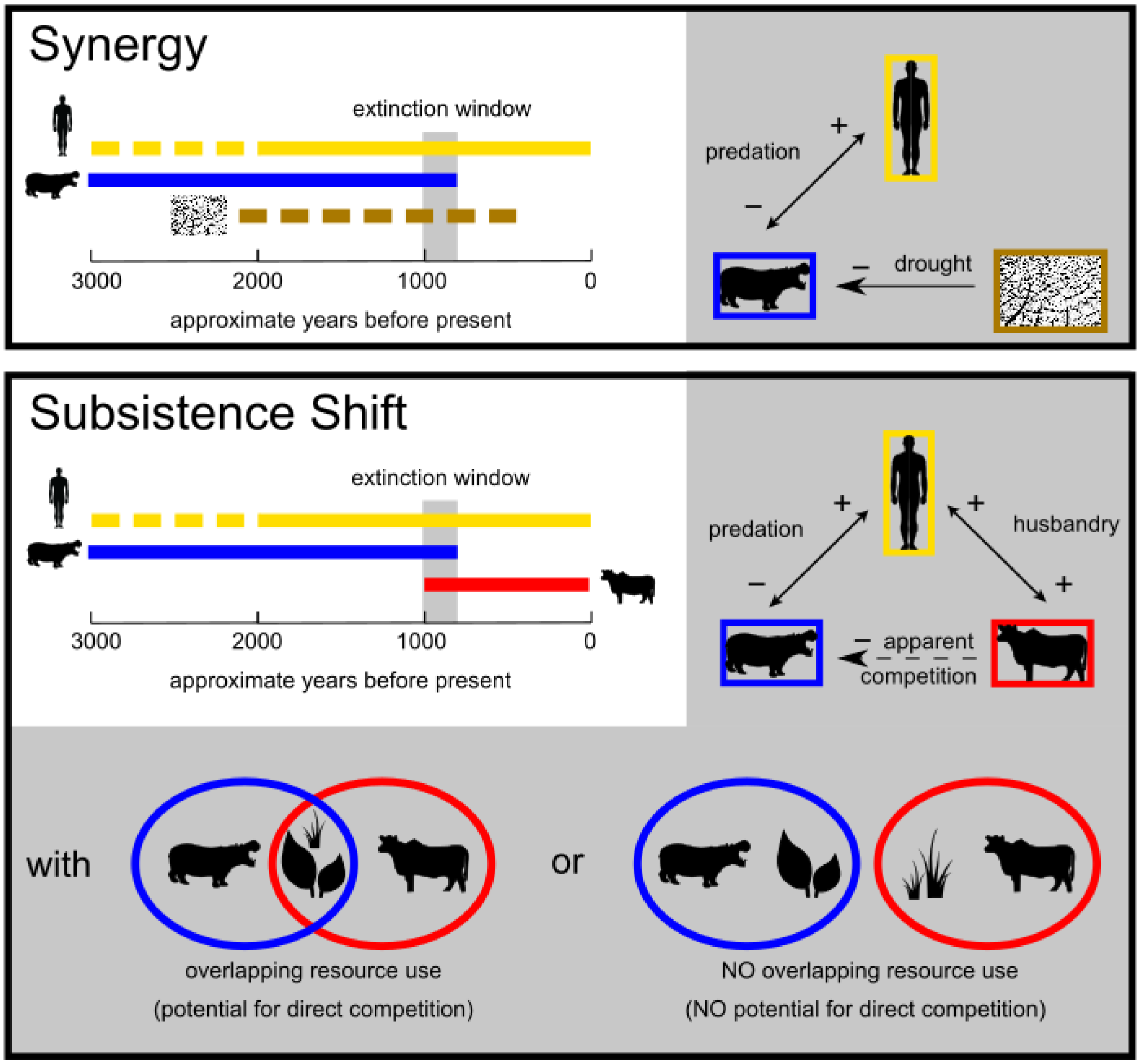


Figure 1. Two possible scenarios for megafaunal extinction, with human arrival and megafaunal extinction estimates drawn from ^{14}C reviews (Crowley 2010; Douglass, et al. 2019). Dashed lines represent uncertain timing of human introduction and aridification, blue represents extinct endemic megafauna, and red represents introduced herbivores. The “synergy” hypothesis involves impacts of drought and overhunting, and the “subsistence shift” hypothesis involves apparent competition and possibly direct competition between introduced livestock and endemic megafauna. These versions of the “synergy” and “subsistence shift” hypotheses are not mutually exclusive: Negative synergistic effects involving drought and introduced livestock could have contributed to megafaunal extinction.

A precise chronology of pastoralism and species extinctions on Madagascar is needed to test the “synergy” and “subsistence shift” hypotheses: lack of temporal overlap between introduced and endemic megaherbivores is inconsistent with the latter hypothesis (Fig. 1). Here, we directly ^{14}C date exotic ungulates from SW Madagascar to test the possibility that biological invasion contributed to a pulse of megafaunal extinction. We report data from ovicaprids (goats, *Capra hircus*, and/or sheep, *Ovis aries*), bushpigs (*Potamochoerus larvatus*), and zebu (*Bos indicus/taurus*). We focus on the relatively abundant and well-preserved bone deposits of SW Madagascar. Based on reports of mixed megafaunal and introduced herbivore bones (Dewar 1984), we predict that the arrival of livestock preceded megafaunal extinction.

Direct competition can follow from niche overlap, and stable carbon isotope ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) values of bone collagen give unique insight into the past niches (diet and habitat) of individuals and groups. The photosynthetic pathway of plants strongly influences their $\delta^{13}C$ values and those of consumer tissue (Crowley and Samonds 2013): Plants that use the C_3 photosynthetic pathway (primarily trees, shrubs, and herbs) tend to be depleted in ^{13}C relative to plants that use the C_4 pathway (primarily grasses) or CAM pathway (primarily succulents). Relatively open soil nitrogen cycling in arid environments drives relatively high ecosystem $\delta^{15}N$ values (Austin and Vitousek 1998). To a lesser extent, local environmental conditions, including canopy cover and coastal proximity can also influence $\delta^{13}C$ and $\delta^{15}N$ values (Crowley, et al. 2011). Existing data suggest that endemic megaherbivores were browsers (Godfrey and Crowley 2016), so we predict that they had overlapping $\delta^{15}N$ and $\delta^{13}C$ values with browsing goats and not with introduced grazers such as zebu and sheep. While similar isotope values may reflect overlaps in resource use that create direct competition (Fig. 1), direct competition does not necessarily follow from overlaps in resource use. This is because: 1) animals may partition resources by foraging on different plants, at different times, or in different areas with similar isotope values (McNaughton 1976); and 2) the impacts of herbivory on plant communities are diverse (Foster, et al. 2014). In contrast, nonoverlapping $\delta^{15}N$ and

δ^{13}C values suggest distinct diets and habitat use and leave little potential for direct competition (Fig. 1).

C. Methods

Study area/regional overview

SW Madagascar experiences a prolonged dry season and receives only a brief rainy season during the southern hemisphere's winter. Regional vegetation is dominated by deciduous C_3 trees and CAM succulents, as well as some C_4 grasses (Crowley and Godfrey 2013). Riparian forests dissect this otherwise dry landscape, but relatively high δ^{15}N values in subfossil lemur collagen suggest that these animals did not prefer wet corridors (Crowley, Godfrey, et al. 2012). The similar environmental conditions across SW Madagascar justify the comparison of stable isotope data from plants and animals across the region (Crowley, et al. 2011). To make relatively fined-grained comparisons of stable isotope data, we also used two approaches to group data from multiple sites: (1) Five ecogeographic site groups defined by coasts and drainages with comparable aridity (Fig. 2); and (2) simple inland versus coastal groups.

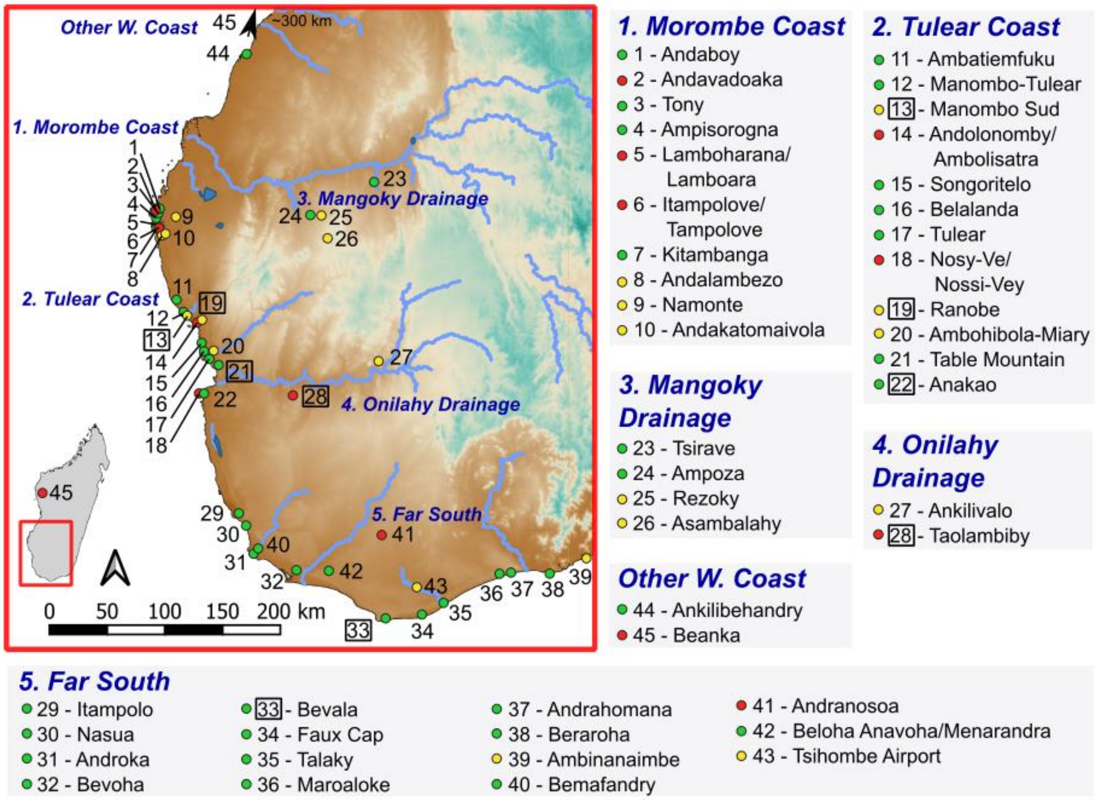


Figure 2. Map of 45 study sites in SW Madagascar included in this study. Sites marked in green include bones of only endemic animals, those in yellow include only introduced animal bone, and those in red include both. We used sites grouped along the Morombe coast (1-10), Tulear coast (11-22), Mangoky drainage (23-26), and Onilahy drainage (27-28), and sometimes the Far South (29-43) for comparisons of stable isotope values among taxa (Appendix "Data Analysis – Radiocarbon & Stable Isotopes"). Specimens from two other west coast sites (44 & 45) contribute ^{14}C data to our analyses but are not considered in comparisons of stable isotope data given their relatively wide geographical spread. Plant stable isotope data comes from specimens collected in the vicinity of sites outlined in black.

Data collection

Details regarding all aspects of sample selection, laboratory analysis, data review, and data analysis are provided in the Appendix. We sampled skeletal remains from 66 introduced zebu, sheep, goats, and bushpigs as well as 71 endemic tortoises, hippos, and elephant birds from 21 sites in SW Madagascar (Fig. 2, Appendix Datasets S1 & S2). We extracted and purified bone collagen at the Pennsylvania State University (PSU), gathered stable carbon and nitrogen isotope data at the Yale Analytical and Stable Isotope

Center, and submitted 111 ancient samples with sufficient preservation for analysis at the PSU AMS ^{14}C Laboratory or the UC Irvine W.M. Keck Carbon Cycle AMS Laboratory (Appendix “Sample Collection” & “Laboratory Analyses”). We co-analyzed these new data with previously published regional ^{14}C data from 155 megafaunal bones and eggshells, as well as stable isotope data from 261 specimens belonging to five endemic taxa (see Appendix “Additional Data”). The published dataset includes data from two extinct lemur taxa: the giant ruffed lemur (*Pachylemur insignis*) and monkey lemur (*Archaeolemur majori*). The giant monkey lemur had a semi-terrestrial locomotor strategy (Jungers 1980) that would have made it more likely to interact with introduced ungulates, and a relatively large number of giant ruffed lemur bones have been directly ^{14}C dated. We ultimately excluded 39 specimens due to data quality issues. The final co-analyzed dataset includes reliable ^{14}C dates (n=238), $\delta^{13}C$ values (n=374), and $\delta^{15}N$ values (n=293) from 45 sites (Fig. 2).

Data analysis

We estimated introduction and extinction times based on sequences of ^{14}C data using both classical and Bayesian approaches to control for differences in sample size (Fig. 3, Appendix Table S1). General linear models (Appendix Tables S2 & S3) compared stable isotope values among taxa, across space, and through time. We fitted Bayesian ellipses to stable isotope data for each taxon to visualize overlap in isotopic niche space (Fig. 4, Appendix Fig. S6 & Table S4). Stable isotope mixing models informed by modern plant $\delta^{13}C$ data (Appendix Dataset S3 & Fig. S2-3) expanded dietary inference (Appendix Fig. S4). To establish endmembers for our mixing model, we combined published data from the region (n=492) with new $\delta^{13}C$ data for 242 plant samples collected at three sites in the vicinity of Tulear/Toliara, SW Madagascar and analyzed at the University of Cincinnati (Appendix Dataset S3).

D. Results

Chronological overlap

Radiocarbon-dated bone and eggshell suggest comparable introduction times among herbivores and a brief overlap between introduced and extinct endemic megafauna in SW Madagascar. Reliable ^{14}C dates from endemic megafaunal bone and eggshell (n=186) span the Holocene, yet ~95% of the specimens are younger than 4000 calibrated years before present (cal BP). All ^{14}C-dated introduced animals (n=52) are younger than 1020 cal BP. The earliest ^{14}C-dated introduced animals are a sheep from Andranosoa (Fig 2., PSUAMS-8684, 1165±25 ^{14}C BP, 1060-960 cal BP) and a contemporaneous zebu from the same site (PSUAMS-8685, 1150±15 ^{14}C BP, 1060-960 cal BP). These individuals predate the last known individuals of the giant ruffed lemur *P. insignis* (from Tsirave, CAMS-167930, 940±20 ^{14}C BP, 900-740 cal BP) and hippo (from Lamboharana/Lamboara, PSUAMS-5629, 1100±15 ^{14}C BP, 980-930 cal BP). Both the earliest ^{14}C-dated bushpig (PSUAMS-5619, 975±15 ^{14}C BP, 910-790 cal BP) and what is possibly the earliest ^{14}C-dated goat (an ovicaprid tentatively identified as *Capra hircus*, PSUAMS-3764, 900±20 ^{14}C BP, 800-730) come from Andavadoaka, and these animals also likely overlapped temporally with the last known *P. insignis* in the region. The last securely dated giant tortoise (from Lamboharana/Lamboara, PSUAMS-5131, 1155±15 ^{14}C BP, 1060-960 cal BP) and elephant bird (from Ambolisatra/Andolonomby, OxA-33535, 1237±24 ^{14}C BP, 1180-1000 cal BP) likely overlapped temporally with the zebu and sheep at Andranosoa and predate the earliest introduced bushpigs and goats by possibly less than 100 years.

Classical and Bayesian 95% confidence/credible intervals suggest that all regional extinctions and introductions occurred over the course of less than 500 years between 1200 and 700 cal BP (Fig. 3, Appendix "Data Analysis – Radiocarbon," Table S1). During this interval, individuals of all nine endemic and introduced taxa could have briefly co-occurred and interacted. The Bayesian and classical approaches suggest that the maximum temporal overlap between introduced and endemic herbivores was ~500-600 years (shared between zebu and *P. insignis*).

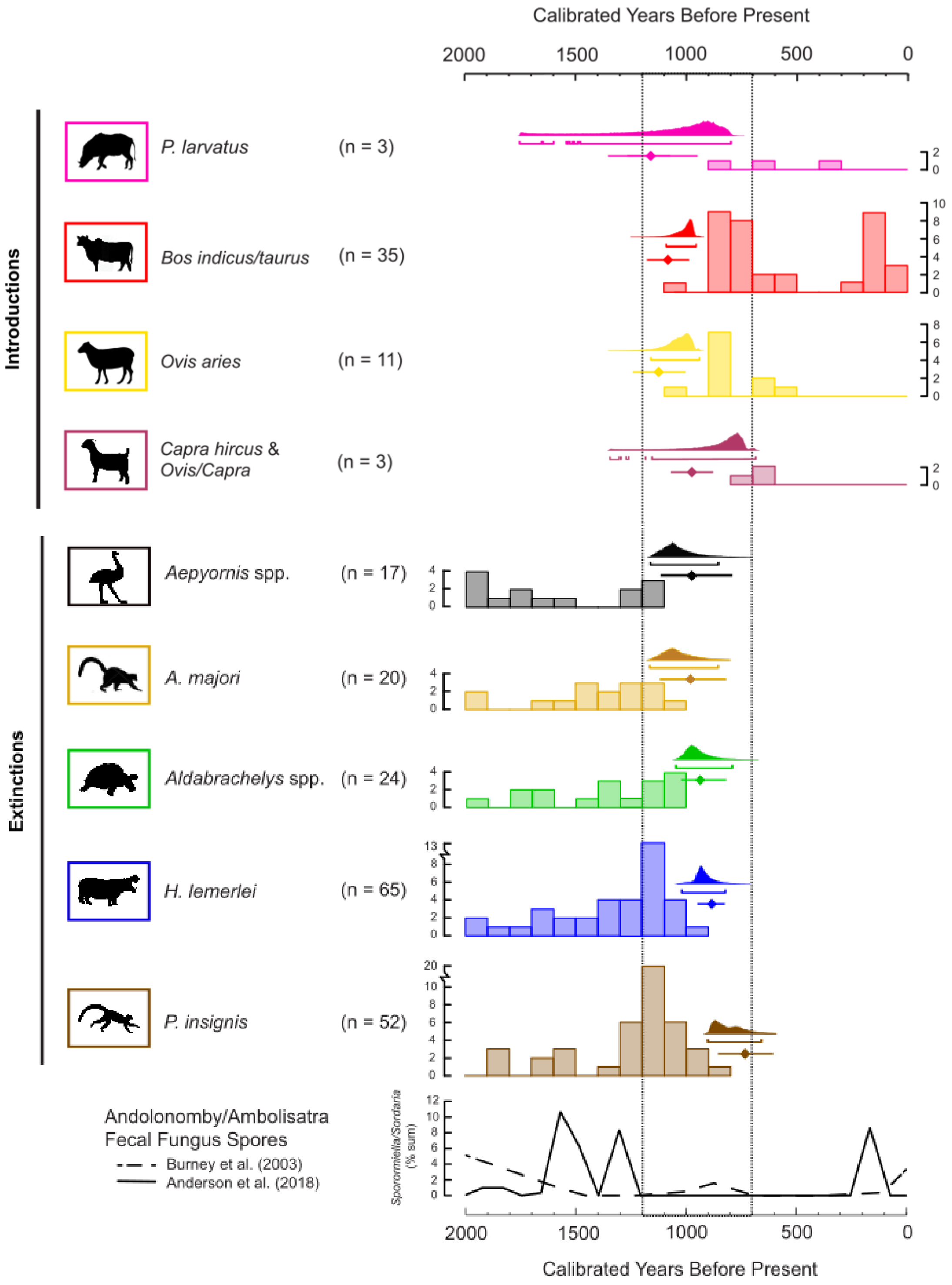


Figure 3. Taxon-specific ^{14}C date histograms (unsaturated color) and confidence/credible intervals (saturated color) for extinction and introduction event estimation. Bayesian posterior probability distributions with 95% brackets give the probability that a species is not present at a certain time given that it was not sampled. Lines with median estimates marked as diamonds give the 95% confidence intervals produced from the application of a classical frequentist approach to the problem of event estimation. Estimates from the

classical approach give the probability that a species was not sampled at a certain time given that it was not present. Note that two ^{14}C-dated unspecified *Ovis/Capra* are approximately contemporary with a ^{14}C-dated *Capra hircus* (PSUAMS-3693), and these three specimens are grouped to create confidence/credible intervals for goat introduction. The dashed line highlights a 500-year period that likely included the depicted series of introductions and extinctions. Published records of faecal fungus spores in Andolonomby sediment may reflect local megaherbivore abundance and are included for comparison (Anderson, et al. 2018; Burney, et al. 2003).

Niche overlap

Herbivore δ^{13}C and δ^{15}N values demonstrate various degrees of potential niche overlap among hippos, giant tortoises, both giant lemur species (*A. majori* and *P. insignis*), and ovicaprids (Fig. 4). For example, *Archaeolemur majori* and *P. insignis* share ~80% of their isotopic niche space with goats, yet this overlap accounts for <45% of the isotopic niche space occupied by goats. Isotopic overlap between introduced and endemic herbivores appears to have been greater at coastal sites (n=144 individuals from 17 sites), yet this could be a product of relatively limited sampling at inland sites (n=139 individuals from 9 sites, Appendix Fig. S6).

Six general linear models based on multiple approaches to grouping data according to collection site suggest that taxon, age, location, and interactions among all variables typically best explain variability in faunal δ^{13}C and δ^{15}N values (Appendix Table S2 & S3, See Appendix "Data Analysis – Stable Isotopes" for full discussion of models). These models highlight differences in δ^{13}C values between coastal and inland individuals, which creates greater similarity in δ^{13}C values among herbivores at coastal sites.

Because there are no widespread and consistent effects of site group or coastal proximity on δ^{13}C or δ^{15}N values across herbivore taxa, we feel secure in considering isotopic niche overlap among taxa from all site groups. The relatively large areas of isotopic niche space occupied by goats, sheep, zebu, hippos, and giant tortoises (sample size corrected standard ellipse areas [SEAc]≥15‰^{2}, Fig. 4) suggest that these animals all exploited more varied resources and habitats than elephant birds or giant lemurs (SEAc≤10‰^{2}). To some extent, SEAc values are sensitive to the amount of time and space (i.e. number of sites) integrated in each group (Appendix Table S4). However, predictor variables of temporal spread (defined as the period spanning 50% of the mean calibrated dates) and number of sites sampled within each taxonomic group cannot fully account for the variance in SEAc values (Appendix "Data Analysis – Stable Isotopes"). The inability of temporal and geographic spread to explain variation in SEAc values suggests that differences in these values correspond to dietary differences among taxa. Goats and sheep are noteworthy because they have one of the shortest temporal spreads (≤200 years) and come from one of the smallest number of sites (n=2 for sheep, n=4 for goats), yet each occupies a relatively large isotopic niche space (SEAc≥15‰^{2}). In contrast, elephant bird samples also come from a similarly limited number of sites (n=3, including two inland sites) yet form a relatively small isotopic niche (SEAc=6.8‰^{2}) despite having the largest temporal spread (>10,000 years).

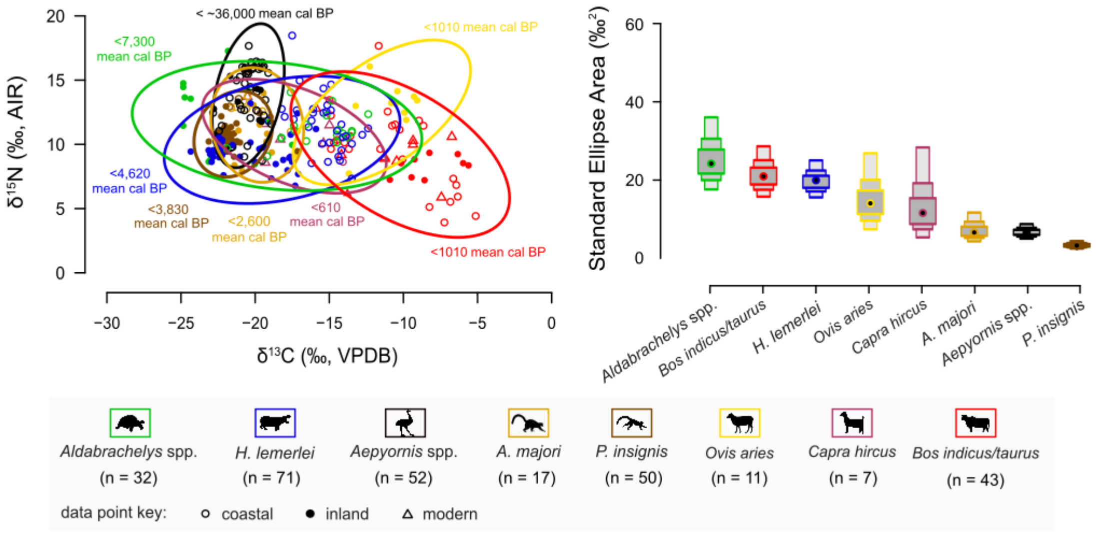


Figure 4. Taxon-specific stable isotope values in bone collagen space (left, n=283), with bolded ellipses that outline approximately 95% of the data from each group. All data are from site groups 1-5. Solid points represent individuals from inland sites, and hollow points represent individuals from coastal sites. Modern individuals of *Capra hircus* and *Bos indicus/taurus* are marked as triangles. Stable carbon isotope data from *Aepyornis* spp. eggshell organics are corrected so that they are comparable to bone collagen values (SI "Data Analysis –Stable Isotopes"). Only one *Aepyornis* spp. individual on this figure is represented by bone collagen data (UCIAMS-224190, $\delta^{13}C=-22.7‰$, $\delta^{15}N=10.7‰$). Mean calibrated date ranges next to ellipses specify the range of ages for samples in each group. Sample size corrected standard ellipse areas (SEAc, containing approximately 40% of the data from each group, right) give relative estimates for the similarity of stable isotope values between individuals of the same taxon. SEAc estimates for each taxonomic group appear as modes (points) surrounded by shaded boxes that span 50%, 75%, and 95% of the estimates (from dark to light). See Appendix Fig. S6 for ellipses fitted to coastal and inland data separately.

Plant $\delta^{13}C$ values document expected patterns among photosynthetic groups, with significantly lower values in C_3 plants (n=537, $\bar{x}=-27.1‰$) than in CAM succulents (n=136, $\bar{x}=-13.3‰$) or C_4 grasses (n=61, $\bar{x}=-12.3‰$, Dataset S3, See Appendix "Data Analysis – Stable Isotopes" for additional discussion of plant $\delta^{13}C$ data.). Large $\delta^{13}C$ ranges for zebu (n=45, 10.7‰, from −15.9‰ to −5.2‰) and ovicaprids (n=20, 11.9‰, from −20.5‰ to −8.6‰) are consistent with modern observations that these animals consume a diversity of grasses, shrubs, and endemic succulents (Feldt, et al. 2017; Randriamalala, et al. 2016). Elevated $\delta^{13}C$ values for zebu and sheep suggest that these animals generally consumed more CAM or C_4 plants (succulents and grasses) than did other introduced livestock and endemic megafauna. Indeed, the results of a mixing model involving all $\delta^{13}C$ values from modern plants in the region suggest that CAM or C_4 plants comprised ~90% of zebu diet and ~80% of sheep diet on average (Appendix "Data Analysis – Stable Isotopes," Fig. S4). All other herbivores (including goats and possibly introduced bushpigs) likely consumed more C_3 plant material than CAM and C_4 plant material. Of the extinct megaherbivores, hippos consumed the most CAM or C_4 plant material (~35% of hippo diet).

For those taxa with sufficient sample sizes and temporal spreads (zebu, hippos, giant tortoises), we can observe site-group specific changes through time in collagen stable isotope values (Fig. 5, Appendix Fig. S5). There are no significant increases in megafaunal $\delta^{13}C$ values over time, despite pollen records from the coastal site of Andolonomby/Ambolisatra (site group 2) that document the decline of arboreal plant taxa over the last 2,000 years (Fig. 5C, Virah-Sawmy, et al. 2016). As forests declined, hippo $\delta^{13}C$ values apparently decreased at coastal site groups 1 and 2 (Appendix Fig. S5A), and giant tortoise $\delta^{13}C$ values significantly decreased at site group 1 ($n=9$, $r_s=0.66$, $p=0.05$). Meanwhile, zebu $\delta^{13}C$ values apparently increased at site groups 1 and 2 (Appendix Fig. S5A).

Megafauna $\delta^{15}N$ values and a contemporary record of the salinization of Lac Ihotry (near site group 1, Fig. 5B & D, Vallet-Coulomb, et al. 2006) suggest that at least the coastal animals may have tracked local aridification. Hippo collagen $\delta^{15}N$ values significantly increased at coastal site group 2 ($n=15$, $r_s=-0.55$, $p=0.03$) and apparently increased at coastal site group 1 and inland site group 4 (Appendix Fig. S5B). Tortoise collagen $\delta^{15}N$ values also apparently increased at site group 1. Despite this drying trend, zebu collagen $\delta^{15}N$ values significantly decreased at site groups 1 and 2 ($n=15$ and 16, respectively, and $r_s\geq0.54$, $p\leq0.03$, Appendix Fig. S5B).

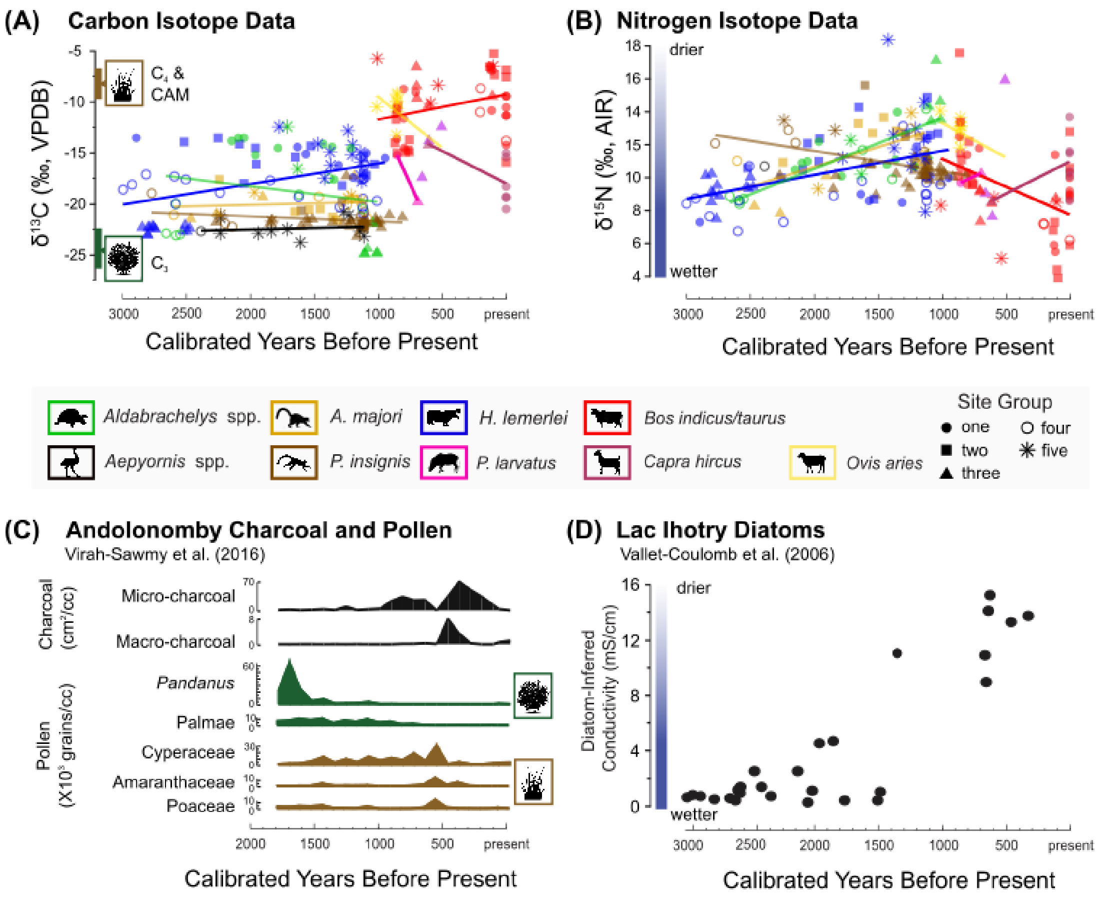


Figure 5. Stable carbon (5A, n=228) and nitrogen (5B, n=212) isotope values through time, with points colored according to taxon (following Figs. 3-4), points shaped according to site group (following Fig. 2), regression lines for all data from each taxon, and published regional records of vegetation change (5C) and aridity (5D) for comparison (Vallet-Coulomb, et al. 2006; Virah-Sawmy, et al. 2016). C_3 and C_4 & CAM plant $\delta^{13}C$ ranges are based on modern data from SW Madagascar in collagen space. Note that uneven sampling across sites through time can explain some of the region-wide changes in taxon-specific isotope records. See Appendix Fig. S5 for temporal trends in $\delta^{13}C$ and $\delta^{15}N$ values plotted separately and according to both site group and taxon for taxa with relatively large sample sizes and temporal spreads.

E. Discussion

Brief temporal overlap between introduced livestock and endemic megafauna is consistent with a key component of the “subsistence shift” hypothesis for megafaunal extinction (Godfrey, et al. 2019). Isotopic niche overlap among coastal goats, hippos, and giant tortoises indicates that direct forms of competition could have existed in some cases between introduced and endemic herbivores. Regardless of when humans first arrived on the island, multiple lines of evidence suggest that the spread of pastoralism in SW Madagascar contributed to megafaunal extinction.

Radiocarbon data suggest that zebu, sheep, goats, and bushpigs all became established in SW Madagascar between 1,200 and 700 years ago. This timing coincided with significant growth and movement of Malagasy populations (Pierron, et al. 2017), the rise of the island's earliest urban center (Radimilahy 1997), and the expansion of trade along the Swahili Coast (Boivin, et al. 2013). Here we have shown that species introductions also coincided with the regional extinction of five endemic herbivore taxa. The co-occurrence of livestock and endemic megafauna that we document was possibly brief and is not visible in records of large herbivore fecal fungus spores from lake sediments (Burney, et al. 2003). However, chronological overlap is consistent with mixed archaeological/paleontological deposits and historic accounts of endemic megafauna (Dewar 1984).

During the brief co-occurrence of livestock and endemic megafauna, pastoralists both relied on their livestock and hunted endemic animals (Anderson, et al. 2018; Godfrey, et al. submitted). Predation impacts populations of prey species to different extents, which likely put introduced and endemic herbivores into apparent competition that negatively affected endemic species (Fig. 1). The impact of human predation on livestock populations was minimal. Pastoralists kill livestock, and ovicaprids are sometimes considered pests because of their diverse and voracious appetites, yet animal husbandry typically gives a net benefit to both humans and domesticates. This is particularly true for zebu, which are currently repositories of wealth for pastoralists in SW Madagascar and are used in a variety of ceremonies and rites. Pastoralists expand their zebu herds by protecting them from predators, modifying vegetation to create a reliable supply of fodder, and moving to track suitable habitat (Feldt and Schlecht 2016; Kaufmann and Tsirahamba 2006). Zebu outnumbered people on Madagascar by as much as 2:1 in the early 20th century (Kaufmann and Tsirahamba 2006), and ~55% of Madagascar's surface was dedicated to pastoralism in 2000 (Anonymous 2003). The expansion of zebu populations likely contributed to human population growth, which indirectly facilitated the hunting of endemic animals. Endemic herbivores likely did not benefit from animal husbandry and became increasingly susceptible to predation as humans transformed forests for livestock. Small-bodied lemurs, such as the endemic sifaka *P. verreauxi*, have sustained hunting pressure from humans for at least a millennium, and this pressure may have caused reductions in body size (Sullivan, et al. 2020). Extinct endemic herbivores with long lifespans, relatively slow reproductive rates, and few ways to escape terrestrial predators (e.g. giant tortoises) were also butchered (Anderson, et al. 2018; Godfrey, et al. submitted) and likely suffered the greatest from the increase in hunting pressure that livestock husbandry facilitated (Johnson 2002).

Isotopic niche overlap among goats, hippos, and giant tortoises indicates that there was some potential for direct forms of competition between introduced and endemic herbivores. Elephant birds likely had a relatively distinct isotopic niche from introduced herbivores, yet our results suggest that overlaps in collagen stable isotope values among taxa varied both temporally and spatially, so identifying niche overlap at a particular time and site group remains challenging. Nevertheless, existing data suggest that isotopic niche overlap may have been greater at coastal than inland sites. Future research should compare the vegetation histories of coastal and inland SW Madagascar and expand faunal datasets to identify any lags between coastal human settlement and inland extinctions. Particular attention should be given to goats, which are notorious invaders of other island ecosystems that can browse some endemic plants to near extinction (Coblentz 1978). Perhaps the most extreme impact of goats on vegetation and other herbivores comes from the Galápagos, where goats are known to decimate vegetation during the dry season and leave little browse for endemic giant tortoises (MacFarland, et al. 1974). On Madagascar, people may have encouraged ovicaprids to forage on a wide range of plant types in deference to the grazing preferred by zebu. The tolerance of Malagasy giant tortoises to resource depression could have been high (Braithwaite 2016), but our findings underscore that the potential for direct competition must be considered during ongoing efforts to reintroduce giant tortoises and maintain local human livelihoods (Pedrono, et al. 2013; Randriamalala, et al. 2016).

Vegetation change and aridification likely affected interactions among humans and herbivores. Our isotopic data suggest that vegetation change was likely the primary stress for endemic populations while aridification could have been a greater stress for introduced livestock. Forest cover declined in coastal SW Madagascar during the last 2,000 years (Faina, et al. in press; Virah-Sawmy, et al. 2016), yet C_4 grasses and CAM succulents remained a minor component of hippo and tortoise diet before their extinction, and carbon isotope data suggest that elephant birds and giant lemurs (*A. majori* and *P. insignis*) may have relied exclusively on C_3 vegetation. Dwindling patches of forest left less browse for endemic megafauna but likely involved the spread of herbaceous and succulent vegetation that introduced herbivores generally prefer. Forest clearance during this time was widespread and may have been anthropogenic; similar transitions to a grassy biome occurred in the absence of drought in northern and central Madagascar (Burney 1987; Burns, et al. 2016). At the same time, increases in collagen $\delta^{15}N$ values of hippos and possibly other taxa indicate that these animals tracked aridification in SW

Madagascar by persisting in increasingly arid habitat. Meanwhile, relatively low $\delta^{15}N$ values in zebu collagen suggest that they may have exploited relatively moist habitat. Modern Malagasy herders move their animals in pursuit of freshwater and succulent fodder during the dry season (Feldt and Schlecht 2016). In this light, consistent past reliance on relatively moist habitat by ancient zebu may reflect their sensitivity to drought, which is an ongoing concern in southern Madagascar.

Understanding past changes in herbivory on Madagascar is important for conservation efforts. We observe that introduced ungulates are unique in their isotopic niche breadth and reliance on C_4 or CAM vegetation. Despite the mixed woodlands and C_4-dominated grasslands that currently exist in many regions on the island, our expanded $\delta^{13}C$ data are consistent with previous work that suggests Madagascar lacked a group of endemic grazers (Godfrey and Crowley 2016). Extinctions of large herbivores can have cascading negative effects on remaining plant and animal species due to the various ways in which large herbivores consume vegetation, redistribute resources, and modify the physical environment (Owen-Smith 1987). For example, experimental data suggest that the Malagasy giant tortoises aided the dispersal and germination of baobab (*Adansonia* spp.) seeds (Andriantsaralaza, et al. 2014), and extant hippos from Africa play important roles in both cycling nutrients (Schoelynck, et al. 2019) and maintaining the structural heterogeneity of riparian vegetation (Kanga, et al. 2013). Likewise, introduced bushpigs on Madagascar may help disperse large seeds, but the full extent to which introduced species and extant endemic species have continued the ecosystem services of now-extinct megafauna is unknown. Introduced ruminants are poor candidates for facilitating large seed dispersal, particularly given that zebu had limited dietary overlap with endemic megafauna.

Combined stable isotope and radiocarbon data give us unique insight into Late Holocene pulses of biodiversity loss in SW Madagascar and contribute to a growing body of evidence that indicate that climate change or hunting pressure alone rarely drive extinction (e.g., Bird, et al. 2016; Nogué, et al. 2017a). In SW Madagascar, direct and indirect interactions between introduced and endemic herbivores, which involved an increase in human population, likely contributed to megafaunal extinction to a greater extent than novel hunting pressure or regional aridification. This pattern is not unique to Madagascar. Indeed, shifts in human subsistence also may help explain lags between human presence and extinction elsewhere. For example, relatively late changes in stone tool technologies and patterns of human subsistence may help explain a prolonged period of coexistence (30,000 years) between humans and megafauna in the Indian subcontinent (Jukar, et al. 2020). Also, in North America, the introduction of a novel hunting pressure alone cannot explain the Late Holocene extinction of California's flightless sea duck that occurred only after a protracted (8,000 years) period of coexistence and hunting (Jones, et al. 2008). However, increasing human reliance on marine resources during the Late Holocene, associated with the proliferation of sedentary coastal human communities, might explain the sea duck's late extinction (Jazwa, et al. 2012). In Eurasia, Koch and Barnosky (2006) suggest that hominins who specialized in pursuing large-bodied prey tracked booms and busts in prey populations on timescales of 100,000 years and that it was the arrival and proliferation of anatomically modern humans with broad diets that ultimately contributed to megafaunal extinctions. The similarity in these cases follows from the general observation that a predator population that specializes in one type of prey will track changes in the prey population, while one that relies on a diversity of prey can easily overexploit the prey species that cannot sustain heavy predation (Winterhalder and Lu 1997). These interactions among hunters and potential competitors must be considered when drawing parallels between recent overkill on islands and earlier extinctions in continental settings (Martin 1984). We identify Madagascar as an ideal place to further study this mechanism of extinction due to the potentially early arrival of people, the island's short extinction chronology, and the relatively recent arrival of pastoralism.

F. Supplementary Material - Appendix

Sample Collection. The 242 plant samples analyzed for this study were collected during September 2019 from three sites in the vicinity of Tulear/Toliara (Fig. 2):

- Ambohimahavelo (23.43461°S, 43.80446°E, immediately south of Table Mountain), an inland site (>10 km from the coast) covered by dry spiny forest thicket (see Madagascar Vegetation Mapping Project) on Eocene clayey limestone (see Madagascar Ministry of Mines Mapping Project).
- Andrevo (23.02903°S, 43.54540°E, near Manombo Sud), an active coastal dune of carbonate sand covered by degraded forest.
- Ranobe (23.01533°S, 43.61035°E), in a mix of spiny forest thicket and cultivated land near a coastal pond.

We sampled leaves from three types of C_4 grasses (Poaceae, n=53), one species of CAM succulent (*Euphorbia stenoclada*, n=38), and five species of C_3 shrubs and trees (*Cedrelopsis grevei*, n=46, *Stereospermum nematocarpum*, n=49, *Terminalia ulexoides*, n=16, *Ziziphus spina-christi*, n=30, and *Phragmites mauritianus*, n=10). For each group, we collected leaves from three different individual plants within 2 m of the ground.

The 137 bones sampled for this study are housed in museum collections in Madagascar, Europe, Australia, and the United States (Dataset S1). Our sample includes specimens from four introduced groups: zebu cattle (*Bos indicus/taurus,* n=43), sheep (*Ovis aries*, n=11), goats (*Capra hircus*, n=7), and bushpigs (*Potamochoerus larvatus*, n=3). These came from 17 archaeological and paleontological sites spread throughout southern and western Madagascar (Fig. 2). To compare stable isotope values through time, we collected modern samples from ten *Bos indicus/taurus* and six *Capra hircus* from five sites in the region. Most bones were readily identifiable, but taxonomic assignment for six introduced animal bones was confirmed through Zooarchaeology by Mass Spectrometry (ZooMS) in the laboratory of M. Buckley at the University of Manchester (see below "Chemical pre-treatment and analysis of bones"). Two ovicaprid (*Ovis/Capra*) bones could not be identified to species level through ZooMS due to limited remaining sample.

Our sample also includes specimens from four extinct taxa of endemic megafauna: pygmy hippopotamuses (*Hippopotamus lemerlei*, n=51), giant tortoises (*Aldabrachelys* spp., n=17), and two different elephant birds (*Aepyornis* spp., n=2 & *Mullerornis modestus* n=1). These specimens come from ten paleontological sites, five of which also contain ancient introduced animal bones: Ambolisatra/Andonolomby, Andavadoaka, Andranosoa, Itampolove/Tampolove, and Lamboharana/Lamboara (Fig. 2). At least three species of extinct pygmy hippo have been identified in Madagascar, and the taxonomic distinctions between hippo postcranial remains are minimally described. Following the assessment of Malagasy pygmy hippo taxonomy by Stuenes (Stuenes 1989), we assume that all of the sampled pygmy hippos from southern and western Madagascar belong to *H. lemerlei*. Multiple extinct species of *Aldabrachelys* are known from SW Madagascar, including *A. abrupta* and *A. grandidieri,* which cannot be distinguished based on carapace thickness alone (Burleigh and Arnold 1986). We therefore only identify tortoises to genus level. Lastly, we also only identified *Aepyornis* to the genus level because eggshell is difficult to assign to species. Although the majority of skeletal material belongs to *A. maximus* in southwestern Madagascar, *A. hildebrandti* is not unknown (Goodman, et al. 1997).

Laboratory Analyses.

Preparation and analysis of plants: The plant samples were dried, ground, and weighed for stable isotope analysis in the Human Paleoecology and Isotope Geochemistry Laboratory at Pennsylvania State University. Samples were analyzed on a Costech Elemental Analyzer connected to a Thermo Fisher Delta V Advantage Isotope Ratio Mass Spectrometer (EA-IRMS) at the Stable Isotope Biogeochemistry Laboratory at the University of Cincinnati. Data were normalized for drift and size using caffeine, and for scale using caffeine and corn starch. The precision and accuracy of $\delta^{13}C$ measurements across runs was 0.04‰ and 0.12‰, respectively.

Chemical pre-treatment and analysis of bones: Chemical pre-treatment of the 137 bone samples took place in the Human Paleoecology and Isotope Geochemistry Laboratory at Pennsylvania State University. Prior to demineralization, bones sampled from museum collections suspected of using conservants went through solvent washes that involved 20 minute sonicated baths in 20 mL of methanol (MeOH), acetone, dichloromethane (DCM), and nanopure water (France, et al. 2011). For the 16 modern bone samples, we extracted lipids using 3× sonication in 2:1 DCM:MeOH followed by rinses in DI water (as in Bligh and Dyer 1959; Guiry, et al. 2016 but substituting DCM for chloroform). Collagen extraction for both modern and ancient samples involved demineralization in 0.5 N hydrochloric acid (HCl) followed by gelatinization in 0.01 N HCl at 60°C for 10 hours. We purified crude collagen extracts from ancient samples through ultrafiltration (Beaumont, et al. 2010; Fernandes, et al. 2021) and/or XAD resin column chromatography (Lohse, et al. 2014, see "Pretreatment" column in Dataset S1; Stafford, et al. 1988; Stafford, et al. 1991). Intact collagen has a high yield and was mechanically separated from the smaller (<30 kDa) fraction of exogenous contaminants and degraded collagen through ultrafiltration. For stained collagen or degraded collagen with low yield, the relatively less polar contaminants (humates, in particular) can be separated chromatographically by passing the hydrolyzed sample through a column of XAD resin. Of the 122 ancient samples that we prepared, we purified 72 (~59%) through ultrafiltration and 50 (~41%) through XAD.

As mentioned above, we confirmed the taxonomic assignment of six introduced animal bones through Zooarchaeology by Mass Spectrometry (ZooMS, Fig. S1, Chase and Leibold 2003). ZooMS collagen fingerprints were collected from pre-prepared collagen (as above) following Guiry & Buckley (Guo 2006). In brief, this involved digesting ~1-2 mg collagen with 0.4 µg sequencing grade trypsin (Promega, UK) overnight at 37°C. The digests were then purified and fractionated on solid phase extraction Varian C18 tips (OMIX, UK), into 10% and 50% acetonitrile (ACN) in 0.1% trifluoroacetic acid (TFA), and dried down to completion. Following resuspension in 10 µL 0.1% TFA, 1 µL of each sample was co-crystallized with an equal volume of 10 mg/mL alpha-cyano-hydroxycinnamic acid matrix (in 50% ACN/0.1% TFA), allowed to dry and then analyzed by Matrix Assisted Laser Desorption Ionization Time of Flight Mass Spectrometry collecting up to 2,000 laser acquisitions over the mass range m/z 700-3,700. The resulting spectra were then compared with reference material from Buckley et al. (Chase and Leibold 2003).

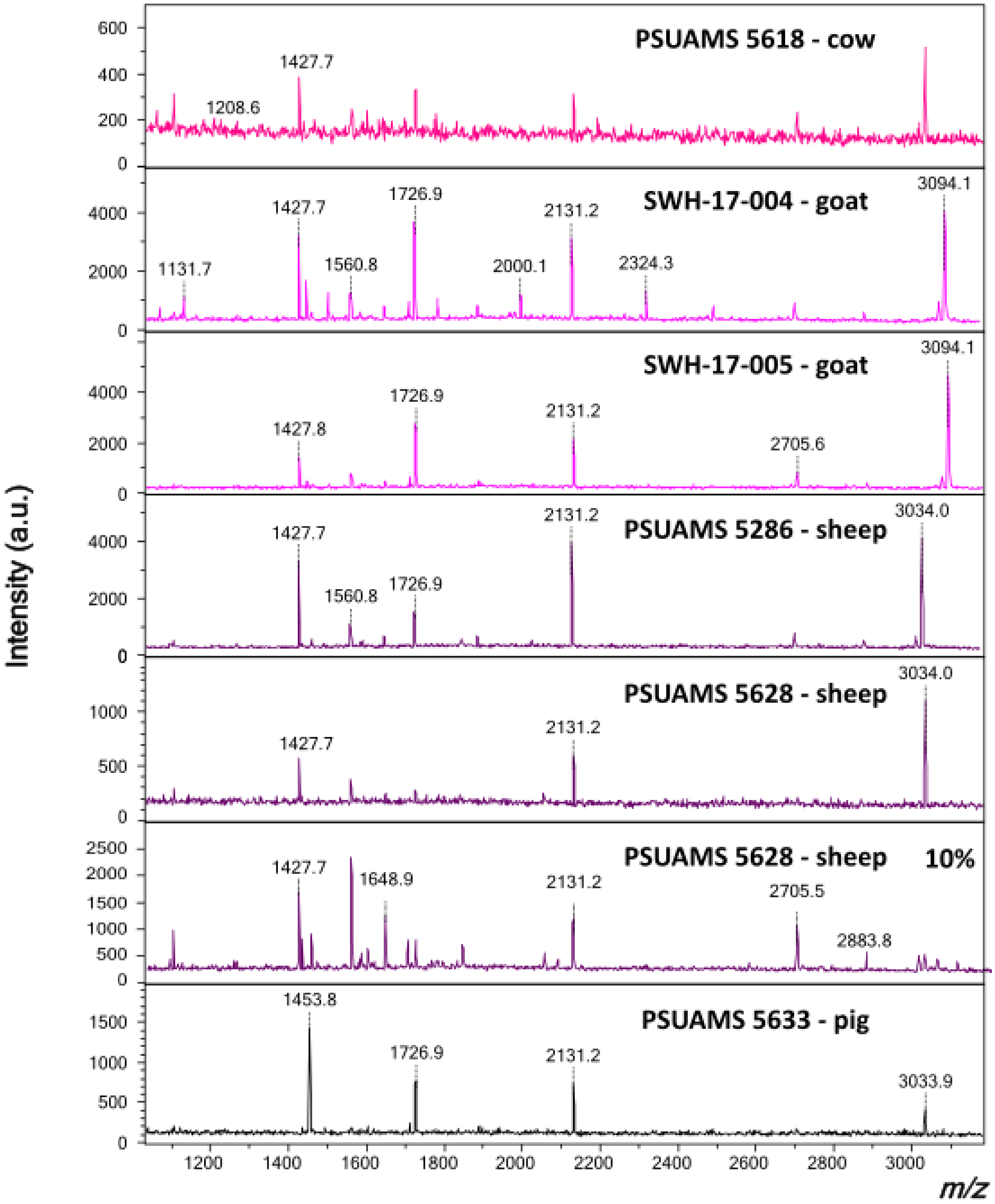


Figure S1. Mass spectra for proteins from six introduced animal bones. Ancient specimens are marked with their corresponding ^{14}C lab numbers, and modern specimens are marked with museum numbers. The 50% fractions for all specimens except PSUAMS 5628 provided identifiable spectra, and the spectrum from the 10% fraction confirmed that PSUAMS 5628 is a sheep.

We obtained $\delta^{13}C$ and $\delta^{15}N$ data from purified collagen with a Thermo DeltaPlus Advantage EA-IRMS at the Yale Analytical and Stable Isotope Center, where the long-term precision of $\delta^{13}C$ and $\delta^{15}N$ measurements is 0.2‰ and accuracy of $\delta^{13}C$ and $\delta^{15}N$ values is 0.1‰ and 0.2‰, respectively. We assessed indicators of sample quality and collagen preservation using percent collagen yield, C:N ratios, $\delta^{13}C$ values, and $\delta^{15}N$ values prior to AMS ^{14}C measurement according to standard procedures (Beaumont, et al. 2010; DeNiro 1985; D. Kennett, et al. 2017; Van Klinken 1999). In many cases, residual contaminants have distinct C:N ratios and stable isotope values, and this was the case for 3 samples from Taolambiby (Dataset S1). This left 119 purified samples with an absence of detectable contaminants. Of these, 102 were submitted as graphite to the PSU AMS ^{14}C Laboratory, 9 were submitted as graphite to the UC Irvine W.M. Keck Carbon Cycle AMS Laboratory for ^{14}C analysis, and 8 were left with only stable isotope data (see Dataset S1 "^{14}C Analysis Lab Number" column entries for dates from PSU AMS and UCI AMS).

Additional Data. We supplemented our plant dataset with previously-published data from 492 plants from two additional sites in SW Madagascar (Dataset S3, Crowley and Godfrey 2013; Crowley, et al. 2014; Crowley, et al. 2011; Godfrey, et al. 2016). Previously published data come from Beza Mahafaly (Fig. 2, in the Onilahy Drainage near Taolambiby) and Cap Sainte-Marie (Fig. 2, in the Far South near Bevala). Our new plant $\delta^{13}C$ data enable comparison of coastal versus inland plants from approximately the same latitude and expand our sample from C_4 grasses in the region (from n=8 to n=61 specimens).

We combine previously published $\delta^{13}C$ and $\delta^{15}N$ data from megafaunal bone and eggshell (n=262, 136 of which have associated ^{14}C data) with our new dataset (Anderson, et al. 2018; Braje, et al. 2017; Burleigh and Arnold 1986; Burney 1999; Clarke, et al. 2006; Coblentz 1978; Crowley and Godfrey 2013; Crowley, et al. 2017; Crowley, Godfrey, et al. 2012; Godfrey, et al. 2016; Godfrey, et al. submitted; Ramsey, et al. 2002; Stanlay 1981). The previously published stable isotope dataset includes pygmy hippos (n=26), giant tortoises (n=26), elephant birds (*Aepyornis* spp., n=128 & *Mullerornis modestus* n=2), *Pachylemur insignis* (n=54), and *Archaeolemur majori* (n=26). We exclude previously published $\delta^{13}C$ and $\delta^{15}N$ data from 23 of the 262 previously published individuals, because they have signs of contamination (atomic C:N>3.6) or uncertain pre-treatment information (Dataset S1).

We also compiled previously published ^{14}C data from megafaunal bone and eggshell collected in southern and western Madagascar (Anderson, et al. 2018; Arsenault and Owen-Smith 2002; Battistini, et al. 1963; Braje, et al. 2017; Burleigh and Arnold 1986; Burney 1999; Clarke, et al. 2006; Crowley 2010; Crowley, et al. 2017; Dewar 1984; Douglass, et al. 2019; Godfrey, et al. submitted; Hansford, et al. 2018; Mahé and Sourdat 1972; Perez, et al. 2005; Ramsey, et al. 2002; Stanlay 1981; Stanley 1981). The previously published literature from these regions includes a total of 156 ^{14}C-dated specimens from six extinct taxa of endemic megafauna: pygmy hippos (n=25), giant tortoises (n=16), elephant birds (*Aepyornis* spp., n=33 & *Mullerornis modestus* n=2), giant ruffed lemurs (*Pachylemur insignis,* n=54), and monkey lemurs (*Archaeolemur majori*, n=26). Because of concerns regarding the reliability of ^{14}C data, we exclude 30 dates (~14% of the endemic ^{14}C dataset) from analysis. These data come from samples that lack pre-treatment information, were not purified before analysis, or have signs of contamination (atomic C:N>3.6). This excludes the last published occurrence datum for giant tortoises, pygmy hippos, and elephant birds (Dataset S1):

- One *Aldabrachelys* spp. carapace (Ambolisatra/Andolonomby, BM 2125 750±370 ^{14}C BP (Burleigh and Arnold 1986)), which has a mean calibrated age that is ~290 years younger the youngest confidently dated individual (Ampoza left femur, PSUAMS 5131 1155±15 ^{14}C BP).
- One *Hippopotamus lemerlei* unknown element (Itampolo, GaK 1506 980±200 ^{14}C BP (Mahé and Sourdat 1972)), which has a mean calibrated age that is about ~60 years younger than the youngest confidently dated individual (Lamboharana/Lamboara atlas, PSUAMS 5629 1100±15 ^{14}C BP).
- Eggshell calcite for two *Aepyornis* spp. (Talaky GaK 276 840±80 ^{14}C BP (Battistini, et al. 1963) and Andrahomana, UCLA 1893 1000±150 ^{14}C BP (Braje, et al. 2017)) which have mean calibrated ages that are ~230-380 years younger than the youngest confidently dated individual (Talaky eggshell calcite, OxA 8270 1240±35 ^{14}C BP (Ramsey, et al. 2002)).

Data Analysis.

Radiocarbon: We calibrated radiocarbon dates in OxCal 4.4 using the Southern Hemisphere calibration curve SHCal20 (Hogg, et al. 2020). To estimate the timing of introductions and extinctions based on existing ^{14}C data, we used both classical frequentist and Bayesian statistical approaches (Crowley 2010). The latest date for an extinct animal and the earliest date for an introduced animal are the maximum likelihood estimators of the true regional extinction and introduction events, respectively, but these estimators are biased due to the Signor-Lipps effect (lags between a last recorded occurrence and extinction and between an introduction and first recorded occurrence that follow from an imperfect skeletal record (Strauss and Sadler 1989)). Approaches to the problem of event estimation build inference about true extinction event times based on the attributes of the series of ^{14}C dates that precedes these events, as well as the true introduction event times based on the attributes of the series of ^{14}C dates that follow.

To construct classical confidence intervals for extinction and introduction times, we used the Gaussian-resampled inverse-weighted McInerny (GRIWM) approach of Bradshaw et al. (2012) in R. In a sensitivity analysis of eight classical frequentist statistical approaches to the problem of event estimation based on radiometric dates, Saltré et al. (2015) found that the GRIWM approach had the highest accuracy. This approach starts with the assumptions that 1) radiometric errors are approximately normally distributed and 2) sample record density is a proxy for population density. Based on the first assumption, the GRIWM approach incorporates measurement uncertainty by resampling dates from the probability distributions associated with each measurement. Nonlinear calibration curves yield nonnormal calibrated age distributions, yet normal distributions can reasonably approximate the spread of calibrated distributions for most dates that we consider. The second assumption is problematic due to variation through time in both bone preservation and the ^{14}C calibration curve. However, the practical implication is that dates relatively close to an event of interest are relatively more important for estimating the time of the given event. Thus, the GRIWM weights observations inversely according to their temporal distance from the event of interest. In the case of an extinction event, the confidence interval produced through the GRIWM approach reflects the probability that a species was not sampled at a certain time because it was no longer present.

By using the “Boundary” function in OxCal, we followed the Bayesian approach of Buck and Bard (2007). This flexible approach incorporates calibrated measurement uncertainty and, in our case, starts with the assumptions that 1) extinct animals are truly extinct, and 2) dateable material was deposited uniformly during the interval of interest. The Bayesian prior assumption of uniform deposition rate tends to underestimate the true degree of temporal overlap between introduced and extinct taxa, because, in reality, extinction tends to involve a period of declining population (and decreasing rate of deposition), while introduction tends to involve a period of expanding population (and increasing rate of deposition). In the case of an extinction event, the posterior probability represents the probability that a species is extinct at a certain time given that it was not sampled. For both the GRIWM and Bayesian approaches, we follow Crowley (2010) by using endemic herbivore ^{14}C dates that span only the past 4,000 years to estimate extinction events (Table S1), and we treat the confidence/credible intervals for bushpig and *Ovis/Capra* introduction with caution due to the limited ^{14}C dated sample from these taxa (n=3 each). Due to limited sample size, we group the two *Ovis/Capra* specimens with the single directly ^{14}C-dated *Capra hircus* specimen. These specimens all fall within a temporal window of ~150 years, so the *Ovis/Capra* confidence/credible intervals may accurately reflect the time of *Capra hircus* introduction.

Table S1. Classical and Bayesian estimation for extinctions (†) and introductions corresponding to Fig. 3. The existing post-4000 cal BP sample of *Mullerornis modestus* (n=2) is too small to permit analysis, and the confidence/credible intervals for *P. larvatus* and combined *Capra hircus* & unspecified *Ovis/Capra* introduction should be treated with caution due to limited sample size (n=3 each).

Taxa	n	Event Estimation (cal. BP)			
		Classic 95% CI	Classic m	Bayes 95% CI	Bayes μ±σ
†*Aepyornis* spp.	17	1110-790	980	1160-860	1030±90
†*Archaeolemur majori*	20	1120-810	990	1160-850	1030±90
†*Aldabrachelys* spp.	24	1010-810	920	1040-780	930±70
†*Hippopotamus lemerlei*	65	950-830	890	1020-830	920±40
†*Pachylemur insignis*	52	860-610	740	900-670	810±70
Potamochoerus larvatus	3	1360-960	1170	1760-800	1110±250
Bos indicus/taurus	35	1180-990	1090	1090-940	1000±40
C. hircus & Ovis/Capra	3	1070-810	940	1340-690	870±140
Ovis aries	11	1240-1000	1130	1160-940	1040±60

Stable Isotopes: New plant $\delta^{13}C$ data from three sites in SW Madagascar document few differences between sympatric C_4 and CAM plants but significantly lower values in C_3 plants (Fig. S2). We used general linear models (R package glmulti) with our combined dataset of 734 plant $\delta^{13}C$ measurements to identify variables that influence plant stable isotope values (i.e. photosynthetic pathway and site). Photosynthetic pathway, site, and interactions between the two variables explain variation in $\delta^{13}C$ values in the best fit model (AIC=2951.99). When controlling for site, both C_3 and CAM plants have significantly lower $\delta^{13}C$ values than C_4 plants ($p<0.0001$ and $p=0.003$, respectively, Fig. S3). We observed a site-specific difference between C_4 and CAM plants only at Andrevo, where CAM plant $\delta^{13}C$ values ($n=15$, $\bar{x}=-14.8$‰) are significantly lower than C_4 plant values ($n=17$, $\bar{x}=-13.3$‰; $t(30)=-9.4$, $p<0.001$). When controlling for photosynthetic pathway, plants from Cap Sainte-Marie have significantly higher mean $\delta^{13}C$ values than those from all other sites ($p\leq0.001$), yet the magnitude of this difference is small (~1‰). For example, the difference in mean $\delta^{13}C$ values between C_3 plants from Cap Sainte-Marie ($n=51$, $\bar{x}=-27.5$‰) and other sites in the region ($n=486$, $\bar{x}=-28.6$‰) is significant (Mann-Whitney $U=7192.5$, $p<0.001$) but on the order of 1‰. Water scarcity likely explains the relatively high plant $\delta^{13}C$ values in plants from Cap Sainte-Marie. Coastal proximity might increase plant $\delta^{13}C$ values (Sparks and Crowley 2018), yet coastal proximity is not consistently associated with higher plant $\delta^{13}C$ values at other sites. For example, when controlling for photosynthetic pathway, plants from the coastal site of Ranobe have apparently (but insignificantly) lower $\delta^{13}C$ values than those from the inland site of Ambohimahavelona ($p=0.24$) and apparently (but again insignificantly) higher $\delta^{13}C$ values than those from the inland site of Beza Mahafaly ($p=0.92$).

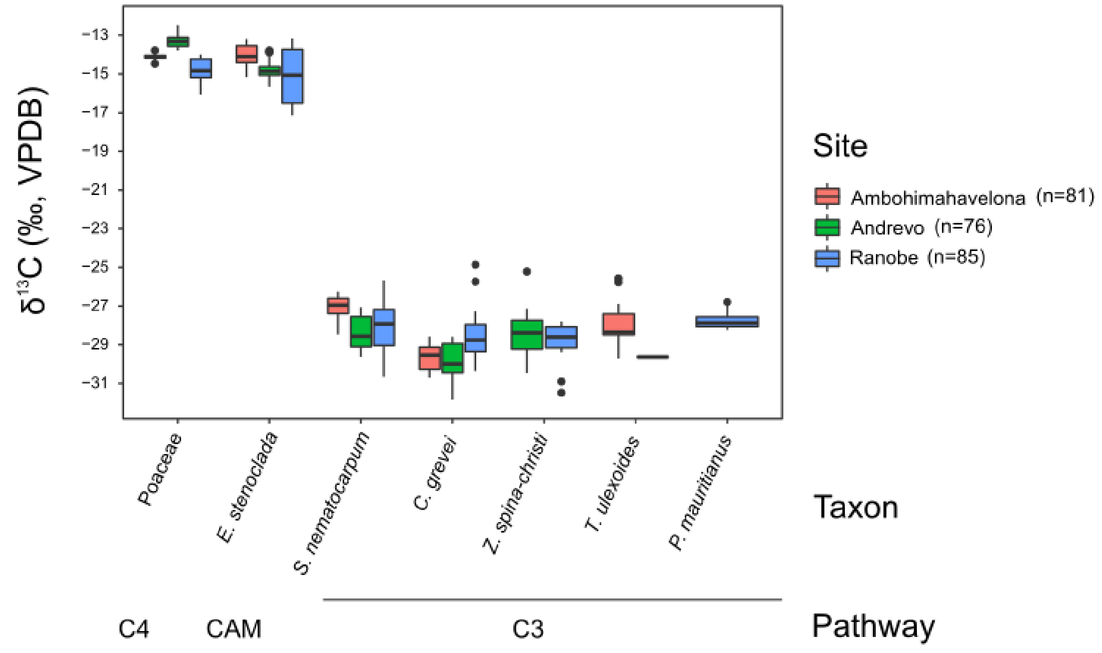


Figure S2. New plant δ^{13}C data from SW Madagascar according to site, taxon, and photosynthetic pathway. Plant δ^{13}C values vary between sites but most significantly between C_3 and C_4 + CAM photosynthetic pathways.

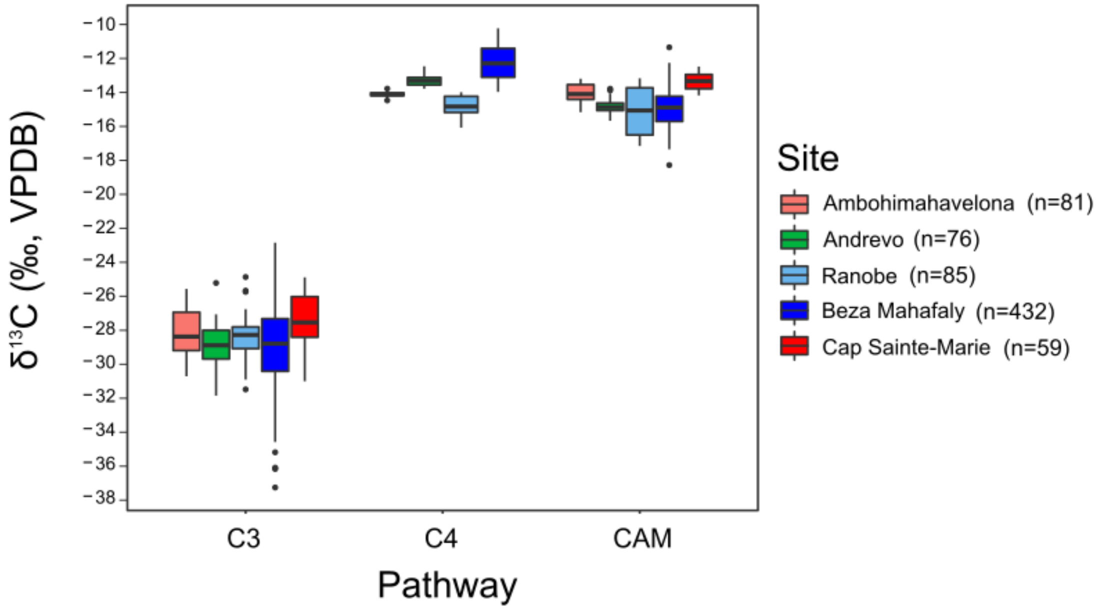


Figure S3. New and previously published plant δ^{13}C data from SW Madagascar according to site and photosynthetic pathway.

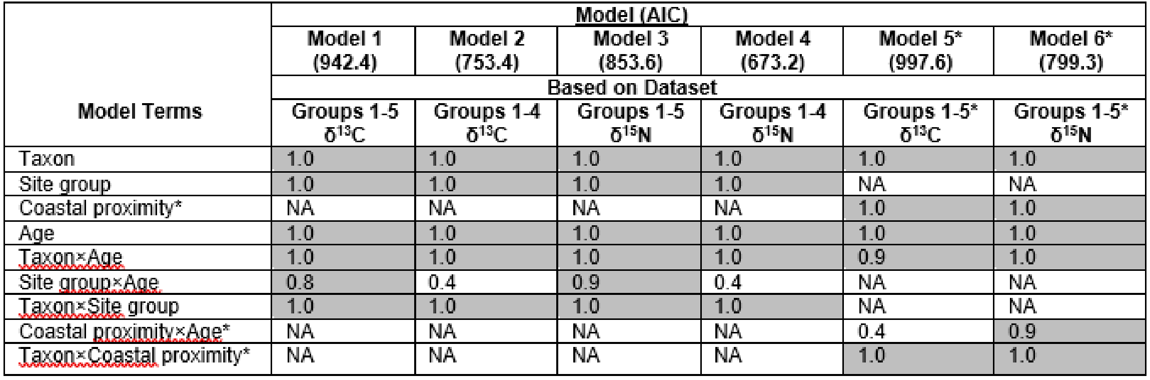
We follow the approach of Crowley and Godfrey (2013) to correct collagen δ^{13}C values for the Suess effect (recent depletion in $^{13}CO_2$ due to the burning of fossil fuel).

Specifically, we made modern and ancient collagen $\delta^{13}C$ values comparable by adding 1.5‰ to modern collagen $\delta^{13}C$ values. Previous work reports stable isotope data from both the calcite and organic fraction of elephant bird eggshell (see Dataset S1 "Element" column). We corrected $\delta^{13}C$ values for elephant bird eggshell calcite to make them comparable to ancient collagen $\delta^{13}C$ values by subtracting 8.1‰ from eggshell $\delta^{13}C$ values. We based this correction on the work of Clarke et al. (2006), which found that elephant bird eggshell calcite tends to be enriched in ^{13}C relative to the organic eggshell fraction by 10.6‰. Consumer collagen is enriched in ^{13}C relative to diet by about 3-5‰ (Crowley and Godfrey 2013; DeNiro and Epstein 1978), while the organic fraction of eggshell is enriched in ^{13}C relative to diet by about 1-2‰ (Johnson, et al. 1998; Tovondrafale, et al. 2014), which means that we must subtract 8.1‰ from eggshell calcite $\delta^{13}C$ values to make them comparable to collagen $\delta^{13}C$ values (10.6‰ [calcite to organic fraction] + 1.5‰ [organic fraction to diet] − 4‰ [diet to expected collagen]). Based on this reasoning, we also corrected $\delta^{13}C$ values for elephant bird eggshell organics to make them comparable to ancient collagen $\delta^{13}C$ values by adding 2.5‰ to eggshell organics $\delta^{13}C$ values (1.5‰ [organic fraction to diet] − 4‰ [diet to expected collagen]).

We used general linear models (GLMs, R package glmulti) to identify variables that influence herbivore stable isotope values (i.e. taxon, time, and location). Given relatively small site-specific sample sizes among taxa, we considered two approaches to grouping sites according to location. First, we grouped sites according to five ecogeographic zones (Fig. 2). These zones are defined by inland drainages or stretches of coastline that include clusters of sites. Second, we grouped sites according to whether they are inland or coastal (>10 km from coast is considered inland). Because samples from the far south (site group

5) were collected over a relatively large area, we ran analyses both including and excluding them from models/analysis. During analysis, we also excluded 1) unreliable data (see above), 2) *M. modestus*, *P. larvatus*, and *Ovis/Capra* specimens lacking species identification due to small sample sizes, and 3) four samples with stable isotope data from the relatively distant sites of Ankilibehandry and Beanka, which are considerably further north. This leaves 350 individuals with $\delta^{13}C$ measurements (including 283 with $\delta^{15}N$ data and 235 with known ages) for all site groups, and 239 individuals with $\delta^{13}C$ measurements (including 193 with $\delta^{15}N$ data and 190 with known ages) for site groups 1-4. Given that site groups 1-4 include only three sheep with $\delta^{13}C$ and $\delta^{15}N$ data and one elephant bird $\delta^{15}N$ datum, we did not consider these groups when fitting GLMs to the site group 1-4 dataset. Analysis of abundant elephant bird eggshell carbonate largely explains the mismatch in $\delta^{13}C$ to $\delta^{15}N$ measurements, and the remaining excess of $\delta^{13}C$ values can be explained by authors who have reported $\delta^{13}C$ and not $\delta^{15}N$ values. Table S2 shows the models that best explain variation in $\delta^{13}C$ and $\delta^{15}N$ data (in collagen space) following from different site groupings (groups 1-4 versus groups 1-5) as well as approaches to classifying location (site group versus coastal proximity), and Table S3 gives model outputs.

Table S2. Description of linear models discussed in text. See Table S3 for model outputs and main text for significant points of agreement among models that explain variation in $\delta^{13}C$ values or $\delta^{15}N$ values. Within each dataset and assigned spatial structure, glmulti considers all possible models and ranks them according an information criterion (AIC in our case, Lamberton 1934). The model-averaged importance of each term (e.g., “Taxon”) within each model (e.g., “Model 1”) reflects the support of the variable across all possible versions of the given model. These importance values range between 0.4 and 1.0 in our case and are given in corresponding cells. In our case, only terms with model-averaged importance greater than 0.4 contribute to best fit models.



Model Terms	Model (AIC)					
	Model 1 (942.4)	Model 2 (753.4)	Model 3 (853.6)	Model 4 (673.2)	Model 5* (997.6)	Model 6* (799.3)
	Based on Dataset					
	Groups 1-5 $\delta^{13}C$	Groups 1-4 $\delta^{13}C$	Groups 1-5 $\delta^{15}N$	Groups 1-4 $\delta^{15}N$	Groups 1-5* $\delta^{13}C$	Groups 1-5* $\delta^{15}N$
Taxon	1.0	1.0	1.0	1.0	1.0	1.0
Site group	1.0	1.0	1.0	1.0	NA	NA
Coastal proximity*	NA	NA	NA	NA	1.0	1.0
Age	1.0	1.0	1.0	1.0	1.0	1.0
Taxon×Age	1.0	1.0	1.0	1.0	0.9	1.0
Site group×Age	0.8	0.4	0.9	0.4	NA	NA
Taxon×Site group	1.0	1.0	1.0	1.0	NA	NA
Coastal proximity×Age*	NA	NA	NA	NA	0.4	0.9
Taxon×Coastal proximity*	NA	NA	NA	NA	1.0	1.0

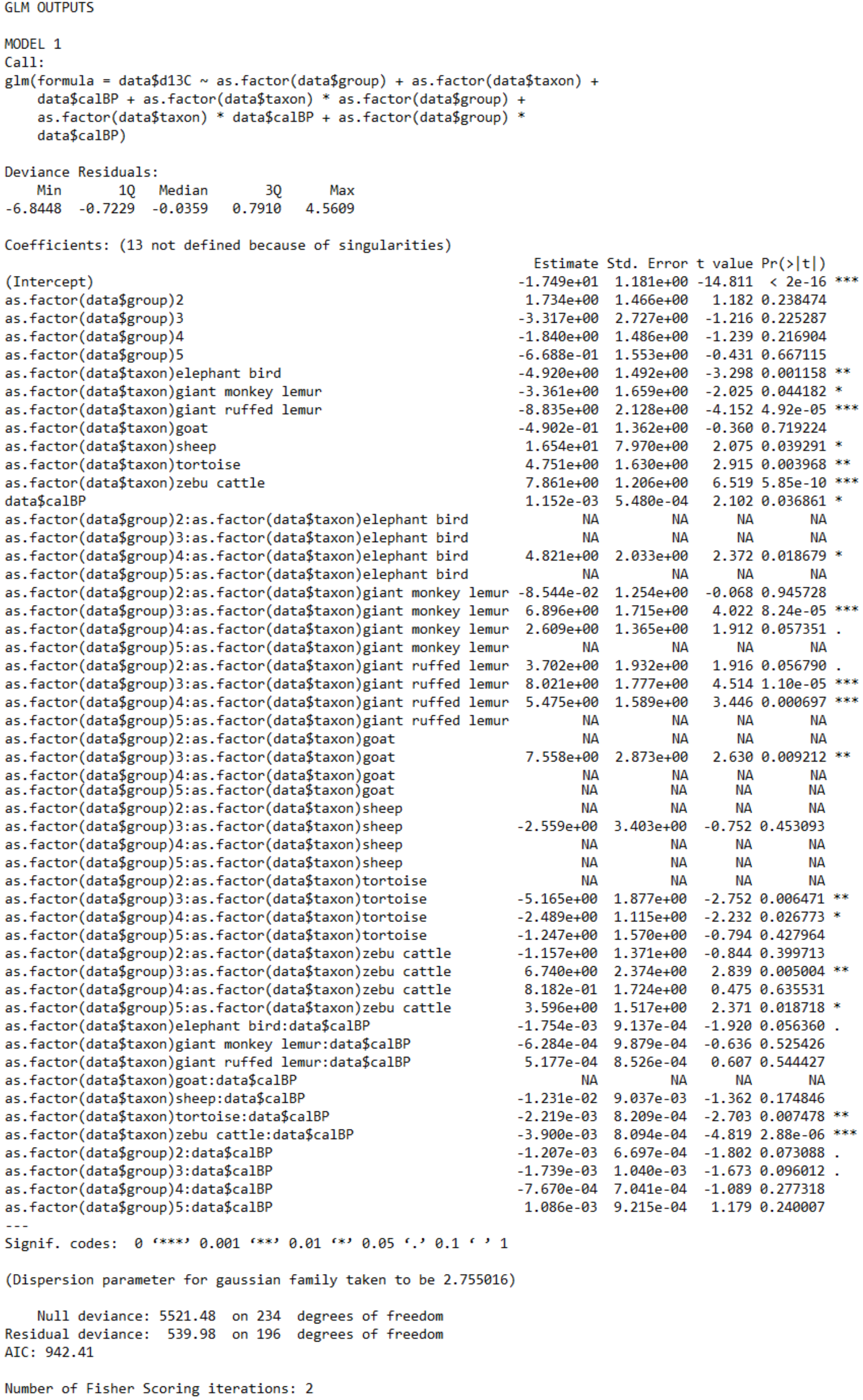
*Data grouped according to coastal versus inland

Taxon, age, site group, and interactions among all variables best explain variability in faunal $\delta^{13}C$ values when all five site groups are included in analysis (model 1, AIC=942.4, Table S3). When site group 5 is excluded from analysis, the interaction between age and site group is no longer part of the best fit model (model 2, AIC=753.4). Results are similar when we classify group 1-5 data according to coastal proximity (model 5, AIC=997.6). Points of agreement between models include that zebu have relatively high $\delta^{13}C$ values ($p<0.0001$) that increase through time ($p\leq0.03$) and that elephant birds have relatively low $\delta^{13}C$ values ($p\leq0.02$, Table S3). Model 5 suggests that coastal animals generally have relatively high $\delta^{13}C$ values ($p<0.0001$), yet all $\delta^{13}C$ models suggest that this difference is not consistent across taxa. Specifically, tortoises at both site groups 3 and 4, which are inland, tend to have lower $\delta^{13}C$ values than tortoises at site group 1, which is coastal ($p\leq0.03$, models 1 & 2), and model 5 similarly suggests that tortoises at coastal sites have higher $\delta^{13}C$ values than those from inland sites

($p=0.0003$). However, giant monkey lemurs, giant ruffed lemurs, goats, and zebu from inland site group 3 have relatively high $\delta^{13}C$ values ($p \leq 0.005$, models 1 & 2), and model 5 similarly suggests that these taxa from coastal sites have relatively low $\delta^{13}C$ values ($p \leq 0.002$). These taxon-specific spatial trends result in more similar $\delta^{13}C$ values among herbivores at coastal sites and more divergent $\delta^{13}C$ values among taxa at inland sites (Fig. 4, Fig. S6). For example, overlaps in the 95% ellipses between zebu and giant tortoises accounts for ~63% of giant tortoise isotopic niche space at coastal sites, yet the inland zebu and giant tortoise ellipses do not overlap.

Taxon, age, site group, and interactions among all three variables best explain variation in $\delta^{15}N$ data when site group 5 are included (model 3, AIC=853.6, Table S3). When site group 5 data are excluded, the interaction between age and site group no longer contributes to the best fit model (model 4, AIC=673.21), and results are similar when we classify group 1-5 data according to coastal proximity (model 6, AIC=799.3). The only points of agreement between models are that zebu $\delta^{15}N$ values tend to both decrease through time ($p<0.0001$, models 3, 4 & 6) and be relatively low at site group 3 ($p \leq 0.05$, models 3 & 4). The effect of coastal proximity on $\delta^{15}N$ values is insignificant ($p=0.29$, model 6).

Table S3. Outputs of general linear models that are described in Table S2 and analyzed in R 4.0.0. Each model includes features that are not shared by others, which suggests that certain results are artefacts of sample group choice.



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GLM OUTPUTS

MODEL 1
Call:
glm(formula = data$d13C ~ as.factor(data$group) + as.factor(data$taxon) + 
    data$calBP + as.factor(data$taxon) * as.factor(data$group) + 
    as.factor(data$taxon) * data$calBP + as.factor(data$group) * 
    data$calBP)

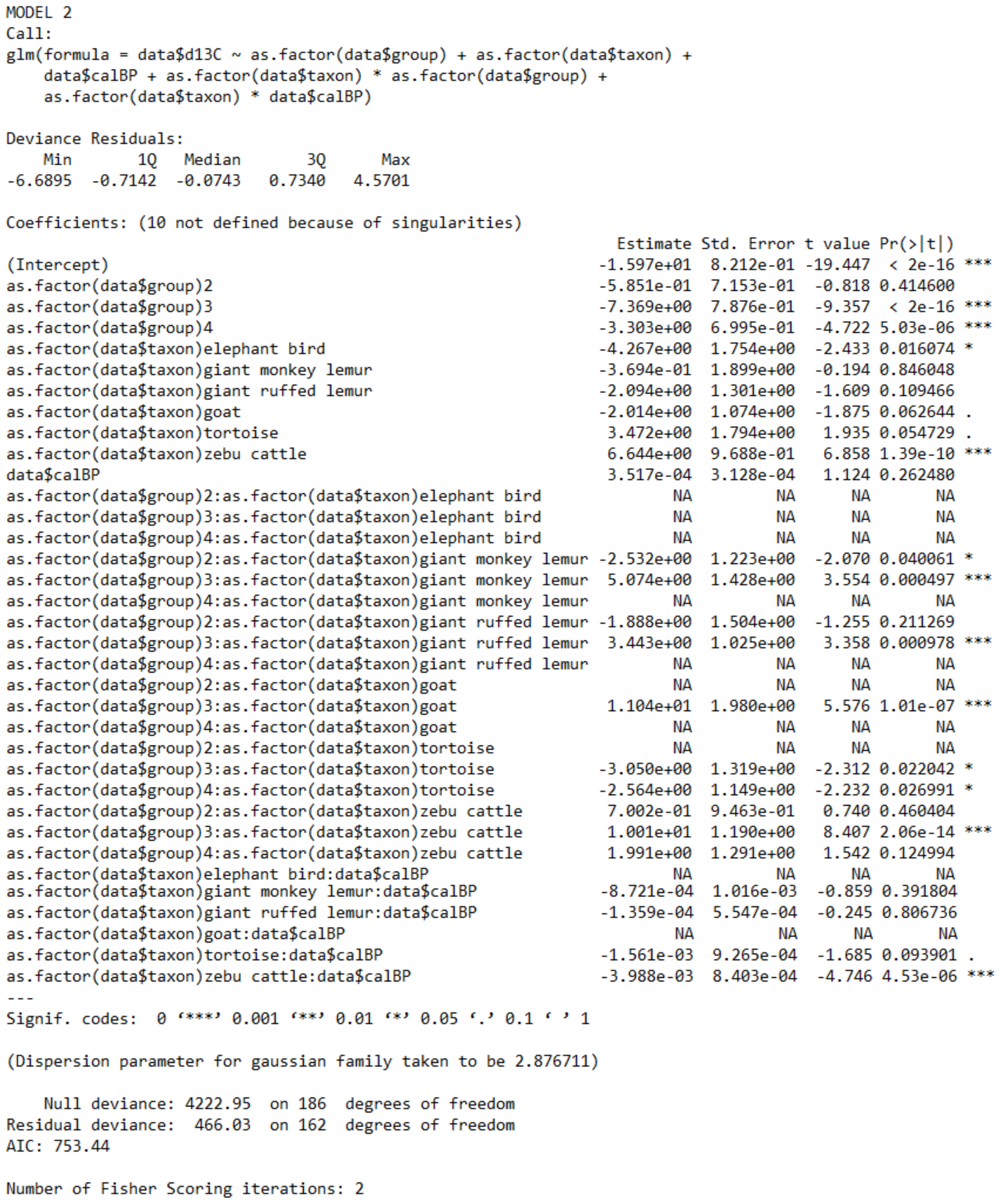
Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-6.8448  -0.7229  -0.0359   0.7910   4.5609  

Coefficients: (13 not defined because of singularities)
                                                                 Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                    -1.749e+01  1.181e+00 -14.811  < 2e-16 ***
as.factor(data$group)2                                          1.734e+00  1.466e+00   1.182 0.238474    
as.factor(data$group)3                                         -3.317e+00  2.727e+00  -1.216 0.225287    
as.factor(data$group)4                                         -1.840e+00  1.486e+00  -1.239 0.216904    
as.factor(data$group)5                                         -6.688e-01  1.553e+00  -0.431 0.667115    
as.factor(data$taxon)elephant bird                             -4.920e+00  1.492e+00  -3.298 0.001158 ** 
as.factor(data$taxon)giant monkey lemur                        -3.361e+00  1.659e+00  -2.025 0.044182 *  
as.factor(data$taxon)giant ruffed lemur                        -8.835e+00  2.128e+00  -4.152 4.92e-05 ***
as.factor(data$taxon)goat                                      -4.902e-01  1.362e+00  -0.360 0.719224    
as.factor(data$taxon)sheep                                      1.654e+01  7.970e+00   2.075 0.039291 *  
as.factor(data$taxon)tortoise                                   4.751e+00  1.630e+00   2.915 0.003968 ** 
as.factor(data$taxon)zebu cattle                                7.861e+00  1.206e+00   6.519 5.85e-10 ***
data$calBP                                                      1.152e-03  5.480e-04   2.102 0.036861 *  
as.factor(data$group)2:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)4:as.factor(data$taxon)elephant bird       4.821e+00  2.033e+00   2.372 0.018679 *  
as.factor(data$group)5:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)giant monkey lemur -8.544e-02  1.254e+00  -0.068 0.945728    
as.factor(data$group)3:as.factor(data$taxon)giant monkey lemur  6.896e+00  1.715e+00   4.022 8.24e-05 ***
as.factor(data$group)4:as.factor(data$taxon)giant monkey lemur  2.609e+00  1.365e+00   1.912 0.057351 .  
as.factor(data$group)5:as.factor(data$taxon)giant monkey lemur         NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)giant ruffed lemur  3.702e+00  1.932e+00   1.916 0.056790 .  
as.factor(data$group)3:as.factor(data$taxon)giant ruffed lemur  8.021e+00  1.777e+00   4.514 1.10e-05 ***
as.factor(data$group)4:as.factor(data$taxon)giant ruffed lemur  5.475e+00  1.589e+00   3.446 0.000697 ***
as.factor(data$group)5:as.factor(data$taxon)giant ruffed lemur         NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)goat                7.558e+00  2.873e+00   2.630 0.009212 ** 
as.factor(data$group)4:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)5:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)sheep              -2.559e+00  3.403e+00  -0.752 0.453093    
as.factor(data$group)4:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$group)5:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)tortoise                   NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)tortoise           -5.165e+00  1.877e+00  -2.752 0.006471 ** 
as.factor(data$group)4:as.factor(data$taxon)tortoise           -2.489e+00  1.115e+00  -2.232 0.026773 *  
as.factor(data$group)5:as.factor(data$taxon)tortoise           -1.247e+00  1.570e+00  -0.794 0.427964    
as.factor(data$group)2:as.factor(data$taxon)zebu cattle        -1.157e+00  1.371e+00  -0.844 0.399713    
as.factor(data$group)3:as.factor(data$taxon)zebu cattle         6.740e+00  2.374e+00   2.839 0.005004 ** 
as.factor(data$group)4:as.factor(data$taxon)zebu cattle         8.182e-01  1.724e+00   0.475 0.635531    
as.factor(data$group)5:as.factor(data$taxon)zebu cattle         3.596e+00  1.517e+00   2.371 0.018718 *  
as.factor(data$taxon)elephant bird:data$calBP                  -1.754e-03  9.137e-04  -1.920 0.056360 .  
as.factor(data$taxon)giant monkey lemur:data$calBP             -6.284e-04  9.879e-04  -0.636 0.525426    
as.factor(data$taxon)giant ruffed lemur:data$calBP              5.177e-04  8.526e-04   0.607 0.544427    
as.factor(data$taxon)goat:data$calBP                                   NA         NA      NA       NA    
as.factor(data$taxon)sheep:data$calBP                          -1.231e-02  9.037e-03  -1.362 0.174846    
as.factor(data$taxon)tortoise:data$calBP                       -2.219e-03  8.209e-04  -2.703 0.007478 ** 
as.factor(data$taxon)zebu cattle:data$calBP                    -3.900e-03  8.094e-04  -4.819 2.88e-06 ***
as.factor(data$group)2:data$calBP                              -1.207e-03  6.697e-04  -1.802 0.073088 .  
as.factor(data$group)3:data$calBP                              -1.739e-03  1.040e-03  -1.673 0.096012 .  
as.factor(data$group)4:data$calBP                              -7.670e-04  7.041e-04  -1.089 0.277318    
as.factor(data$group)5:data$calBP                               1.086e-03  9.215e-04   1.179 0.240007    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.755016)

    Null deviance: 5521.48  on 234  degrees of freedom
Residual deviance:  539.98  on 196  degrees of freedom
AIC: 942.41

Number of Fisher Scoring iterations: 2
```



```
MODEL 2
Call:
glm(formula = data$d13C ~ as.factor(data$group) + as.factor(data$taxon) +
    data$calBP + as.factor(data$taxon) * as.factor(data$group) +
    as.factor(data$taxon) * data$calBP)

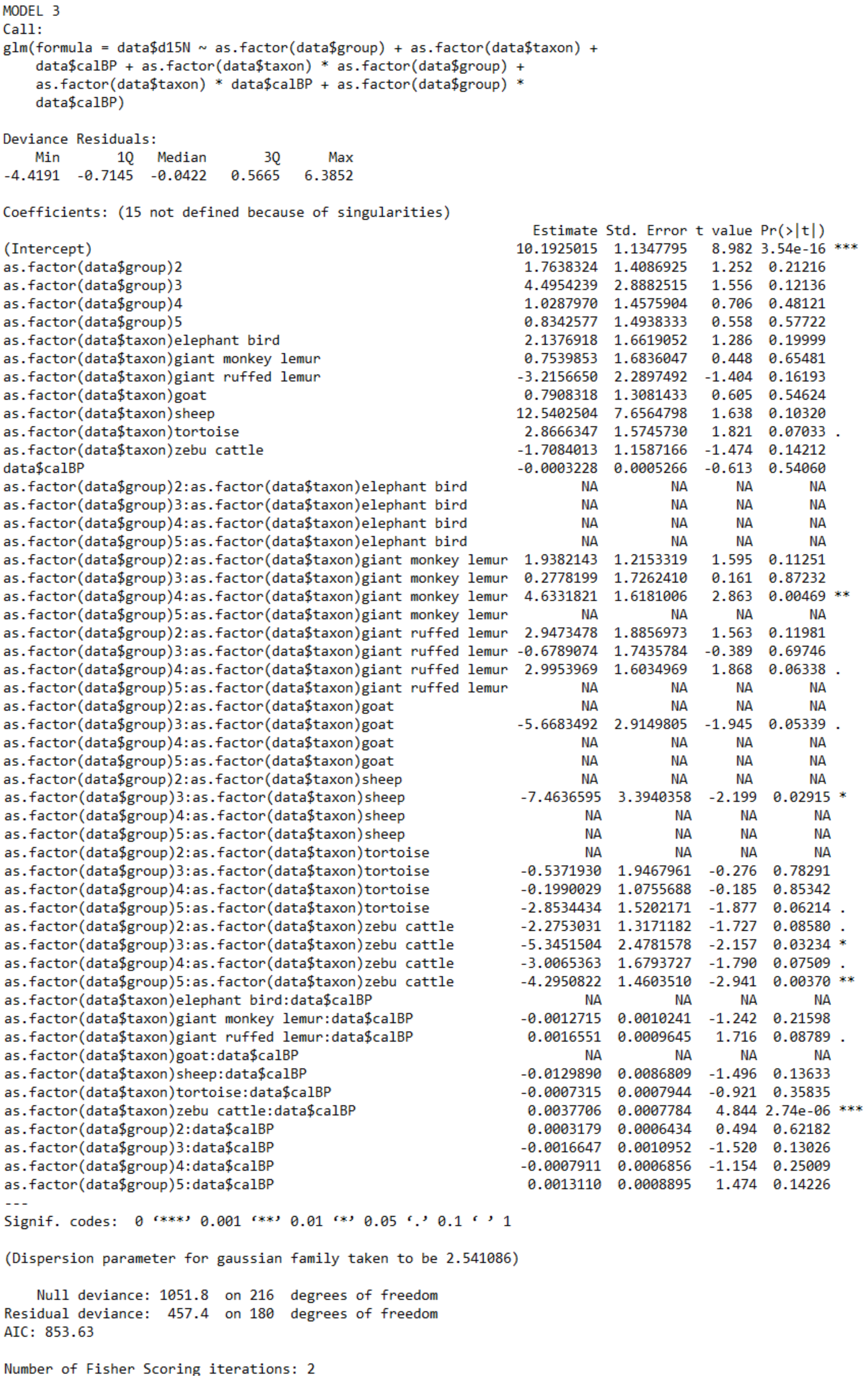
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-6.6895  -0.7142  -0.0743   0.7340   4.5701

Coefficients: (10 not defined because of singularities)
                                                              Estimate Std. Error t value Pr(>|t|)
(Intercept)                                                 -1.597e+01  8.212e-01 -19.447  < 2e-16 ***
as.factor(data$group)2                                      -5.851e-01  7.153e-01  -0.818 0.414600
as.factor(data$group)3                                      -7.369e+00  7.876e-01  -9.357  < 2e-16 ***
as.factor(data$group)4                                      -3.303e+00  6.995e-01  -4.722 5.03e-06 ***
as.factor(data$taxon)elephant bird                          -4.267e+00  1.754e+00  -2.433 0.016074 *
as.factor(data$taxon)giant monkey lemur                     -3.694e-01  1.899e+00  -0.194 0.846048
as.factor(data$taxon)giant ruffed lemur                     -2.094e+00  1.301e+00  -1.609 0.109466
as.factor(data$taxon)goat                                   -2.014e+00  1.074e+00  -1.875 0.062644 .
as.factor(data$taxon)tortoise                                3.472e+00  1.794e+00   1.935 0.054729 .
as.factor(data$taxon)zebu cattle                             6.644e+00  9.688e-01   6.858 1.39e-10 ***
data$calBP                                                   3.517e-04  3.128e-04   1.124 0.262480
as.factor(data$group)2:as.factor(data$taxon)elephant bird           NA         NA      NA       NA
as.factor(data$group)3:as.factor(data$taxon)elephant bird           NA         NA      NA       NA
as.factor(data$group)4:as.factor(data$taxon)elephant bird           NA         NA      NA       NA
as.factor(data$group)2:as.factor(data$taxon)giant monkey lemur -2.532e+00  1.223e+00  -2.070 0.040061 *
as.factor(data$group)3:as.factor(data$taxon)giant monkey lemur  5.074e+00  1.428e+00   3.554 0.000497 ***
as.factor(data$group)4:as.factor(data$taxon)giant monkey lemur         NA         NA      NA       NA
as.factor(data$group)2:as.factor(data$taxon)giant ruffed lemur -1.888e+00  1.504e+00  -1.255 0.211269
as.factor(data$group)3:as.factor(data$taxon)giant ruffed lemur  3.443e+00  1.025e+00   3.358 0.000978 ***
as.factor(data$group)4:as.factor(data$taxon)giant ruffed lemur         NA         NA      NA       NA
as.factor(data$group)2:as.factor(data$taxon)goat                    NA         NA      NA       NA
as.factor(data$group)3:as.factor(data$taxon)goat             1.104e+01  1.980e+00   5.576 1.01e-07 ***
as.factor(data$group)4:as.factor(data$taxon)goat                    NA         NA      NA       NA
as.factor(data$group)2:as.factor(data$taxon)tortoise                NA         NA      NA       NA
as.factor(data$group)3:as.factor(data$taxon)tortoise        -3.050e+00  1.319e+00  -2.312 0.022042 *
as.factor(data$group)4:as.factor(data$taxon)tortoise        -2.564e+00  1.149e+00  -2.232 0.026991 *
as.factor(data$group)2:as.factor(data$taxon)zebu cattle      7.002e-01  9.463e-01   0.740 0.460404
as.factor(data$group)3:as.factor(data$taxon)zebu cattle      1.001e+01  1.190e+00   8.407 2.06e-14 ***
as.factor(data$group)4:as.factor(data$taxon)zebu cattle      1.991e+00  1.291e+00   1.542 0.124994
as.factor(data$taxon)elephant bird:data$calBP                       NA         NA      NA       NA
as.factor(data$taxon)giant monkey lemur:data$calBP          -8.721e-04  1.016e-03  -0.859 0.391804
as.factor(data$taxon)giant ruffed lemur:data$calBP          -1.359e-04  5.547e-04  -0.245 0.806736
as.factor(data$taxon)goat:data$calBP                                NA         NA      NA       NA
as.factor(data$taxon)tortoise:data$calBP                    -1.561e-03  9.265e-04  -1.685 0.093901 .
as.factor(data$taxon)zebu cattle:data$calBP                 -3.988e-03  8.403e-04  -4.746 4.53e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.876711)

    Null deviance: 4222.95  on 186  degrees of freedom
Residual deviance:  466.03  on 162  degrees of freedom
AIC: 753.44

Number of Fisher Scoring iterations: 2
```



```
MODEL 3
Call:
glm(formula = data$d15N ~ as.factor(data$group) + as.factor(data$taxon) + 
    data$calBP + as.factor(data$taxon) * as.factor(data$group) + 
    as.factor(data$taxon) * data$calBP + as.factor(data$group) * 
    data$calBP)

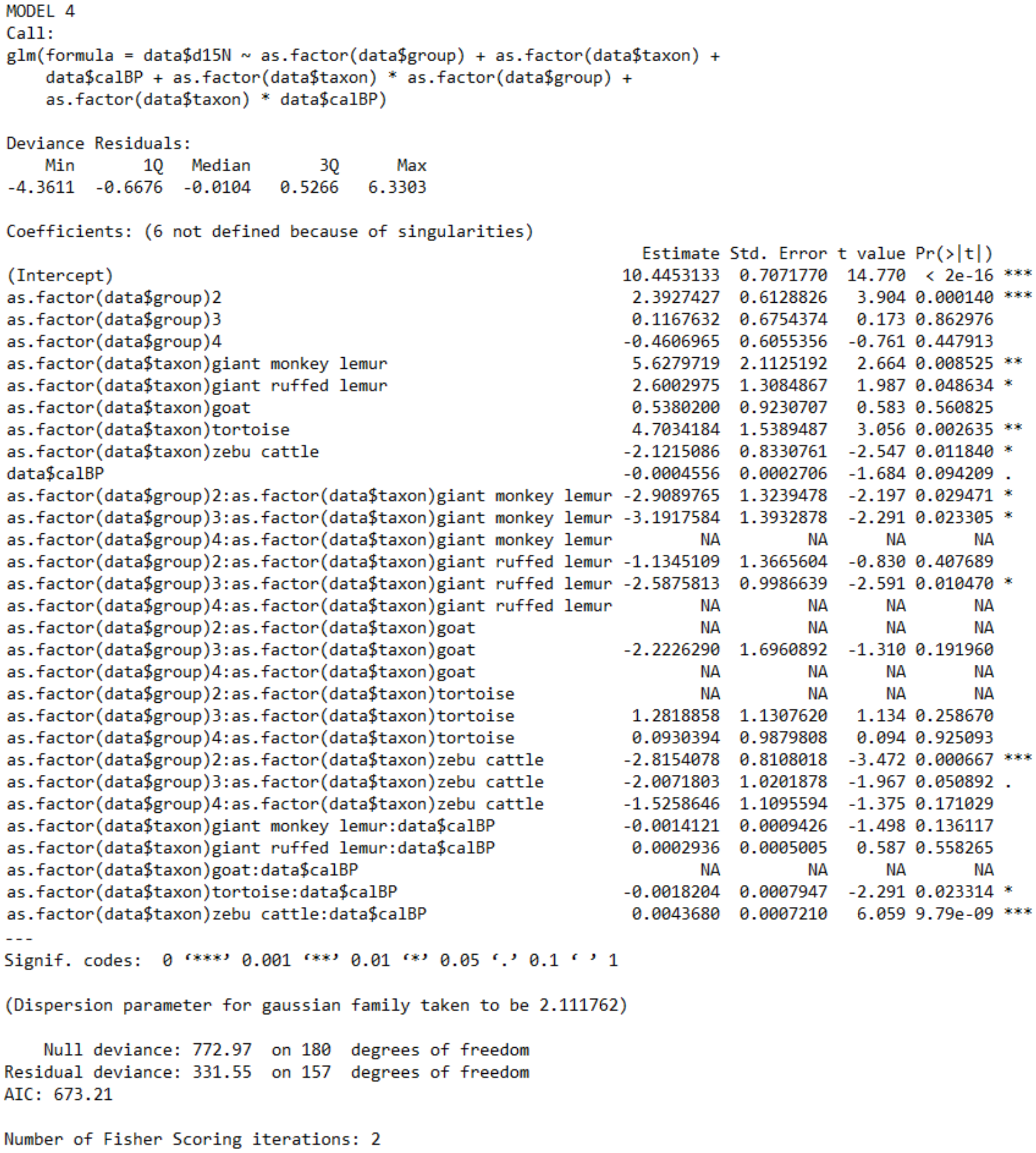
Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-4.4191  -0.7145  -0.0422   0.5665   6.3852  

Coefficients: (15 not defined because of singularities)
                                                                 Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                    10.1925015  1.1347795   8.982 3.54e-16 ***
as.factor(data$group)2                                          1.7638324  1.4086925   1.252  0.21216    
as.factor(data$group)3                                          4.4954239  2.8882515   1.556  0.12136    
as.factor(data$group)4                                          1.0287970  1.4575904   0.706  0.48121    
as.factor(data$group)5                                          0.8342577  1.4938333   0.558  0.57722    
as.factor(data$taxon)elephant bird                              2.1376918  1.6619052   1.286  0.19999    
as.factor(data$taxon)giant monkey lemur                         0.7539853  1.6836047   0.448  0.65481    
as.factor(data$taxon)giant ruffed lemur                        -3.2156650  2.2897492  -1.404  0.16193    
as.factor(data$taxon)goat                                       0.7908318  1.3081433   0.605  0.54624    
as.factor(data$taxon)sheep                                     12.5402504  7.6564798   1.638  0.10320    
as.factor(data$taxon)tortoise                                   2.8666347  1.5745730   1.821  0.07033 .  
as.factor(data$taxon)zebu cattle                               -1.7084013  1.1587166  -1.474  0.14212    
data$calBP                                                     -0.0003228  0.0005266  -0.613  0.54060    
as.factor(data$group)2:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)4:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)5:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)giant monkey lemur  1.9382143  1.2153319   1.595  0.11251    
as.factor(data$group)3:as.factor(data$taxon)giant monkey lemur  0.2778199  1.7262410   0.161  0.87232    
as.factor(data$group)4:as.factor(data$taxon)giant monkey lemur  4.6331821  1.6181006   2.863  0.00469 ** 
as.factor(data$group)5:as.factor(data$taxon)giant monkey lemur         NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)giant ruffed lemur  2.9473478  1.8856973   1.563  0.11981    
as.factor(data$group)3:as.factor(data$taxon)giant ruffed lemur -0.6789074  1.7435784  -0.389  0.69746    
as.factor(data$group)4:as.factor(data$taxon)giant ruffed lemur  2.9953969  1.6034969   1.868  0.06338 .  
as.factor(data$group)5:as.factor(data$taxon)giant ruffed lemur         NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)goat               -5.6683492  2.9149805  -1.945  0.05339 .  
as.factor(data$group)4:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)5:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)sheep              -7.4636595  3.3940358  -2.199  0.02915 *  
as.factor(data$group)4:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$group)5:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)tortoise                   NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)tortoise           -0.5371930  1.9467961  -0.276  0.78291    
as.factor(data$group)4:as.factor(data$taxon)tortoise           -0.1990029  1.0755688  -0.185  0.85342    
as.factor(data$group)5:as.factor(data$taxon)tortoise           -2.8534434  1.5202171  -1.877  0.06214 .  
as.factor(data$group)2:as.factor(data$taxon)zebu cattle        -2.2753031  1.3171182  -1.727  0.08580 .  
as.factor(data$group)3:as.factor(data$taxon)zebu cattle        -5.3451504  2.4781578  -2.157  0.03234 *  
as.factor(data$group)4:as.factor(data$taxon)zebu cattle        -3.0065363  1.6793727  -1.790  0.07509 .  
as.factor(data$group)5:as.factor(data$taxon)zebu cattle        -4.2950822  1.4603510  -2.941  0.00370 ** 
as.factor(data$taxon)elephant bird:data$calBP                          NA         NA      NA       NA    
as.factor(data$taxon)giant monkey lemur:data$calBP             -0.0012715  0.0010241  -1.242  0.21598    
as.factor(data$taxon)giant ruffed lemur:data$calBP              0.0016551  0.0009645   1.716  0.08789 .  
as.factor(data$taxon)goat:data$calBP                                   NA         NA      NA       NA    
as.factor(data$taxon)sheep:data$calBP                          -0.0129890  0.0086809  -1.496  0.13633    
as.factor(data$taxon)tortoise:data$calBP                       -0.0007315  0.0007944  -0.921  0.35835    
as.factor(data$taxon)zebu cattle:data$calBP                     0.0037706  0.0007784   4.844 2.74e-06 ***
as.factor(data$group)2:data$calBP                               0.0003179  0.0006434   0.494  0.62182    
as.factor(data$group)3:data$calBP                              -0.0016647  0.0010952  -1.520  0.13026    
as.factor(data$group)4:data$calBP                              -0.0007911  0.0006856  -1.154  0.25009    
as.factor(data$group)5:data$calBP                               0.0013110  0.0008895   1.474  0.14226    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.541086)

    Null deviance: 1051.8  on 216  degrees of freedom
Residual deviance:  457.4  on 180  degrees of freedom
AIC: 853.63

Number of Fisher Scoring iterations: 2
```



```
MODEL 4
Call:
glm(formula = data$d15N ~ as.factor(data$group) + as.factor(data$taxon) + 
    data$calBP + as.factor(data$taxon) * as.factor(data$group) + 
    as.factor(data$taxon) * data$calBP)

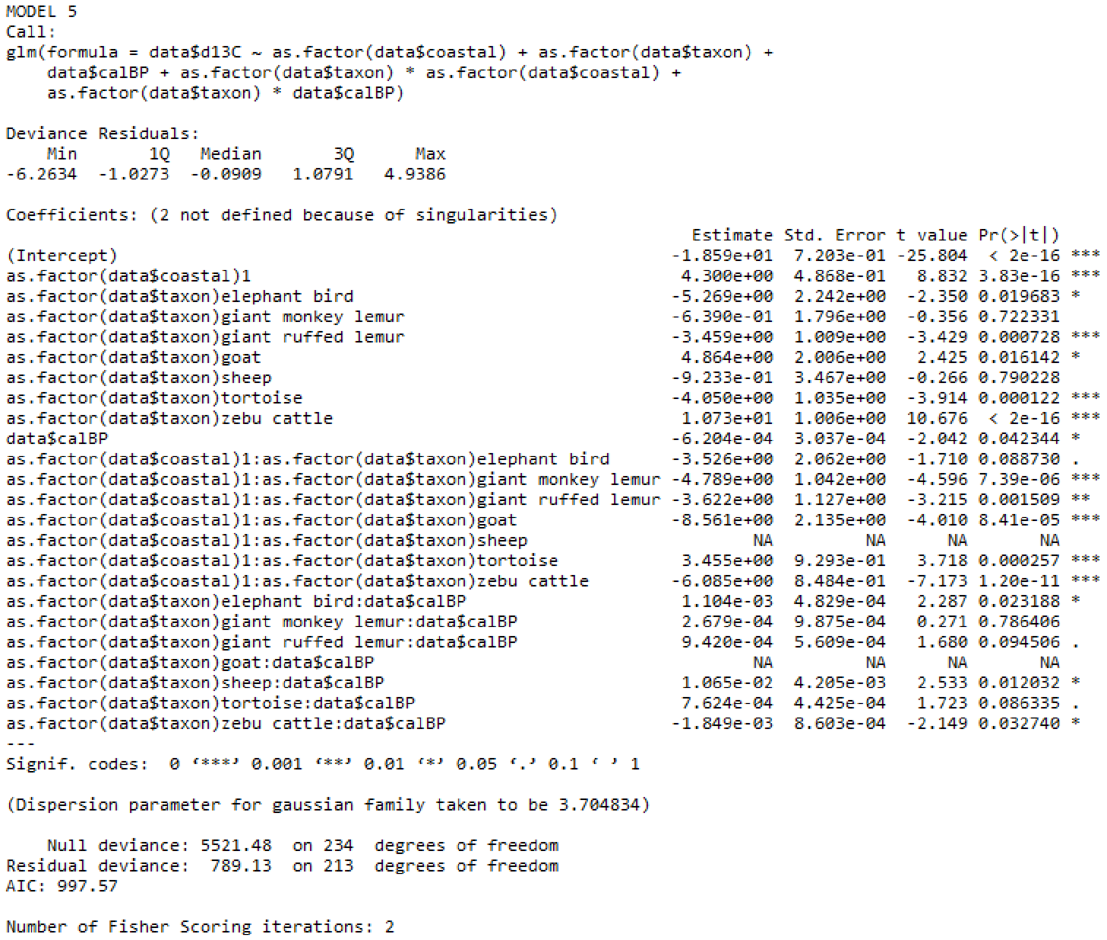
Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-4.3611  -0.6676  -0.0104   0.5266   6.3303  

Coefficients: (6 not defined because of singularities)
                                                                 Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                    10.4453133  0.7071770  14.770  < 2e-16 ***
as.factor(data$group)2                                          2.3927427  0.6128826   3.904 0.000140 ***
as.factor(data$group)3                                          0.1167632  0.6754374   0.173 0.862976    
as.factor(data$group)4                                         -0.4606965  0.6055356  -0.761 0.447913    
as.factor(data$taxon)giant monkey lemur                         5.6279719  2.1125192   2.664 0.008525 ** 
as.factor(data$taxon)giant ruffed lemur                         2.6002975  1.3084867   1.987 0.048634 *  
as.factor(data$taxon)goat                                       0.5380200  0.9230707   0.583 0.560825    
as.factor(data$taxon)tortoise                                   4.7034184  1.5389487   3.056 0.002635 ** 
as.factor(data$taxon)zebu cattle                               -2.1215086  0.8330761  -2.547 0.011840 *  
data$calBP                                                     -0.0004556  0.0002706  -1.684 0.094209 .  
as.factor(data$group)2:as.factor(data$taxon)giant monkey lemur -2.9089765  1.3239478  -2.197 0.029471 *  
as.factor(data$group)3:as.factor(data$taxon)giant monkey lemur -3.1917584  1.3932878  -2.291 0.023305 *  
as.factor(data$group)4:as.factor(data$taxon)giant monkey lemur         NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)giant ruffed lemur -1.1345109  1.3665604  -0.830 0.407689    
as.factor(data$group)3:as.factor(data$taxon)giant ruffed lemur -2.5875813  0.9986639  -2.591 0.010470 *  
as.factor(data$group)4:as.factor(data$taxon)giant ruffed lemur         NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)goat               -2.2226290  1.6960892  -1.310 0.191960    
as.factor(data$group)4:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$group)2:as.factor(data$taxon)tortoise                   NA         NA      NA       NA    
as.factor(data$group)3:as.factor(data$taxon)tortoise            1.2818858  1.1307620   1.134 0.258670    
as.factor(data$group)4:as.factor(data$taxon)tortoise            0.0930394  0.9879808   0.094 0.925093    
as.factor(data$group)2:as.factor(data$taxon)zebu cattle        -2.8154078  0.8108018  -3.472 0.000667 ***
as.factor(data$group)3:as.factor(data$taxon)zebu cattle        -2.0071803  1.0201878  -1.967 0.050892 .  
as.factor(data$group)4:as.factor(data$taxon)zebu cattle        -1.5258646  1.1095594  -1.375 0.171029    
as.factor(data$taxon)giant monkey lemur:data$calBP             -0.0014121  0.0009426  -1.498 0.136117    
as.factor(data$taxon)giant ruffed lemur:data$calBP              0.0002936  0.0005005   0.587 0.558265    
as.factor(data$taxon)goat:data$calBP                                   NA         NA      NA       NA    
as.factor(data$taxon)tortoise:data$calBP                       -0.0018204  0.0007947  -2.291 0.023314 *  
as.factor(data$taxon)zebu cattle:data$calBP                     0.0043680  0.0007210   6.059 9.79e-09 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.111762)

    Null deviance: 772.97  on 180  degrees of freedom
Residual deviance: 331.55  on 157  degrees of freedom
AIC: 673.21

Number of Fisher Scoring iterations: 2
```



```
MODEL 5
Call:
glm(formula = data$d13C ~ as.factor(data$coastal) + as.factor(data$taxon) + 
    data$calBP + as.factor(data$taxon) * as.factor(data$coastal) + 
    as.factor(data$taxon) * data$calBP)

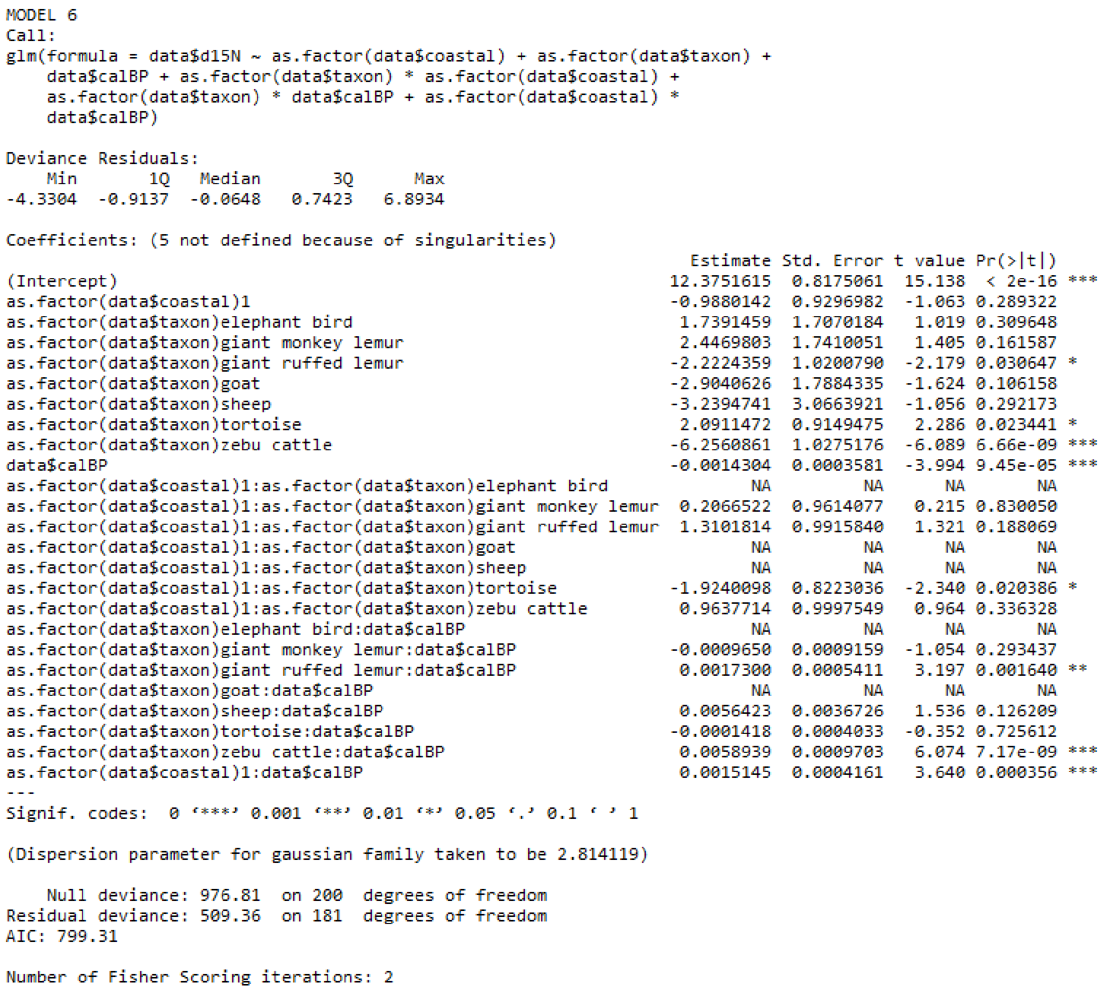
Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-6.2634  -1.0273  -0.0909   1.0791   4.9386  

Coefficients: (2 not defined because of singularities)
                                                              Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                 -1.859e+01  7.203e-01 -25.804  < 2e-16 ***
as.factor(data$coastal)1                                     4.300e+00  4.868e-01   8.832 3.83e-16 ***
as.factor(data$taxon)elephant bird                          -5.269e+00  2.242e+00  -2.350 0.019683 *  
as.factor(data$taxon)giant monkey lemur                     -6.390e-01  1.796e+00  -0.356 0.722331    
as.factor(data$taxon)giant ruffed lemur                     -3.459e+00  1.009e+00  -3.429 0.000728 ***
as.factor(data$taxon)goat                                    4.864e+00  2.006e+00   2.425 0.016142 *  
as.factor(data$taxon)sheep                                  -9.233e-01  3.467e+00  -0.266 0.790228    
as.factor(data$taxon)tortoise                               -4.050e+00  1.035e+00  -3.914 0.000122 ***
as.factor(data$taxon)zebu cattle                             1.073e+01  1.006e+00  10.676  < 2e-16 ***
data$calBP                                                  -6.204e-04  3.037e-04  -2.042 0.042344 *  
as.factor(data$coastal)1:as.factor(data$taxon)elephant bird -3.526e+00  2.062e+00  -1.710 0.088730 .  
as.factor(data$coastal)1:as.factor(data$taxon)giant monkey lemur -4.789e+00  1.042e+00  -4.596 7.39e-06 ***
as.factor(data$coastal)1:as.factor(data$taxon)giant ruffed lemur -3.622e+00  1.127e+00  -3.215 0.001509 ** 
as.factor(data$coastal)1:as.factor(data$taxon)goat          -8.561e+00  2.135e+00  -4.010 8.41e-05 ***
as.factor(data$coastal)1:as.factor(data$taxon)sheep                 NA         NA      NA       NA    
as.factor(data$coastal)1:as.factor(data$taxon)tortoise       3.455e+00  9.293e-01   3.718 0.000257 ***
as.factor(data$coastal)1:as.factor(data$taxon)zebu cattle   -6.085e+00  8.484e-01  -7.173 1.20e-11 ***
as.factor(data$taxon)elephant bird:data$calBP                1.104e-03  4.829e-04   2.287 0.023188 *  
as.factor(data$taxon)giant monkey lemur:data$calBP           2.679e-04  9.875e-04   0.271 0.786406    
as.factor(data$taxon)giant ruffed lemur:data$calBP           9.420e-04  5.609e-04   1.680 0.094506 .  
as.factor(data$taxon)goat:data$calBP                                NA         NA      NA       NA    
as.factor(data$taxon)sheep:data$calBP                        1.065e-02  4.205e-03   2.533 0.012032 *  
as.factor(data$taxon)tortoise:data$calBP                     7.624e-04  4.425e-04   1.723 0.086335 .  
as.factor(data$taxon)zebu cattle:data$calBP                 -1.849e-03  8.603e-04  -2.149 0.032740 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 3.704834)

    Null deviance: 5521.48  on 234  degrees of freedom
Residual deviance:  789.13  on 213  degrees of freedom
AIC: 997.57

Number of Fisher Scoring iterations: 2
```



```
MODEL 6
Call:
glm(formula = data$d15N ~ as.factor(data$coastal) + as.factor(data$taxon) + 
    data$calBP + as.factor(data$taxon) * as.factor(data$coastal) + 
    as.factor(data$taxon) * data$calBP + as.factor(data$coastal) * 
    data$calBP)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-4.3304  -0.9137  -0.0648   0.7423   6.8934  

Coefficients: (5 not defined because of singularities)
                                                                   Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                      12.3751615  0.8175061  15.138  < 2e-16 ***
as.factor(data$coastal)1                                         -0.9880142  0.9296982  -1.063 0.289322    
as.factor(data$taxon)elephant bird                                1.7391459  1.7070184   1.019 0.309648    
as.factor(data$taxon)giant monkey lemur                           2.4469803  1.7410051   1.405 0.161587    
as.factor(data$taxon)giant ruffed lemur                          -2.2224359  1.0200790  -2.179 0.030647 *  
as.factor(data$taxon)goat                                        -2.9040626  1.7884335  -1.624 0.106158    
as.factor(data$taxon)sheep                                       -3.2394741  3.0663921  -1.056 0.292173    
as.factor(data$taxon)tortoise                                     2.0911472  0.9149475   2.286 0.023441 *  
as.factor(data$taxon)zebu cattle                                 -6.2560861  1.0275176  -6.089 6.66e-09 ***
data$calBP                                                       -0.0014304  0.0003581  -3.994 9.45e-05 ***
as.factor(data$coastal)1:as.factor(data$taxon)elephant bird              NA         NA      NA       NA    
as.factor(data$coastal)1:as.factor(data$taxon)giant monkey lemur  0.2066522  0.9614077   0.215 0.830050    
as.factor(data$coastal)1:as.factor(data$taxon)giant ruffed lemur  1.3101814  0.9915840   1.321 0.188069    
as.factor(data$coastal)1:as.factor(data$taxon)goat                       NA         NA      NA       NA    
as.factor(data$coastal)1:as.factor(data$taxon)sheep                      NA         NA      NA       NA    
as.factor(data$coastal)1:as.factor(data$taxon)tortoise           -1.9240098  0.8223036  -2.340 0.020386 *  
as.factor(data$coastal)1:as.factor(data$taxon)zebu cattle         0.9637714  0.9997549   0.964 0.336328    
as.factor(data$taxon)elephant bird:data$calBP                            NA         NA      NA       NA    
as.factor(data$taxon)giant monkey lemur:data$calBP               -0.0009650  0.0009159  -1.054 0.293437    
as.factor(data$taxon)giant ruffed lemur:data$calBP                0.0017300  0.0005411   3.197 0.001640 ** 
as.factor(data$taxon)goat:data$calBP                                     NA         NA      NA       NA    
as.factor(data$taxon)sheep:data$calBP                             0.0056423  0.0036726   1.536 0.126209    
as.factor(data$taxon)tortoise:data$calBP                         -0.0001418  0.0004033  -0.352 0.725612    
as.factor(data$taxon)zebu cattle:data$calBP                       0.0058939  0.0009703   6.074 7.17e-09 ***
as.factor(data$coastal)1:data$calBP                               0.0015145  0.0004161   3.640 0.000356 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.814119)

    Null deviance: 976.81  on 200  degrees of freedom
Residual deviance: 509.36  on 181  degrees of freedom
AIC: 799.31

Number of Fisher Scoring iterations: 2
```

We further explored site group-specific temporal changes in $\delta^{13}C$ and $\delta^{15}N$ values for specific taxa with enough data (multiple within site-group sample sizes of ≥5 and temporal spreads of approximately ≥1,000 years) using Spearmann correlation coefficients (Fig. S5). These highlight patterns similar to the GLMs. Limited site group-specific sample sizes for *A. majori*, elephant birds, sheep, and goats do not permit confident identification of changes in stable isotope values through time. Also, small sample sizes and temporal spreads for hippos and other taxa from inland sites prevent the meaningful identification of changes through time at site groups 3 and 4. For example, inland site group 3 (Mangoky Drainage) has a reasonably large number of ^{14}C-dated hippos (n=12) and *P. insignis* (n=41), yet the taxon-specific age midspreads for these samples are limited to just 287 and 165 years, respectively.

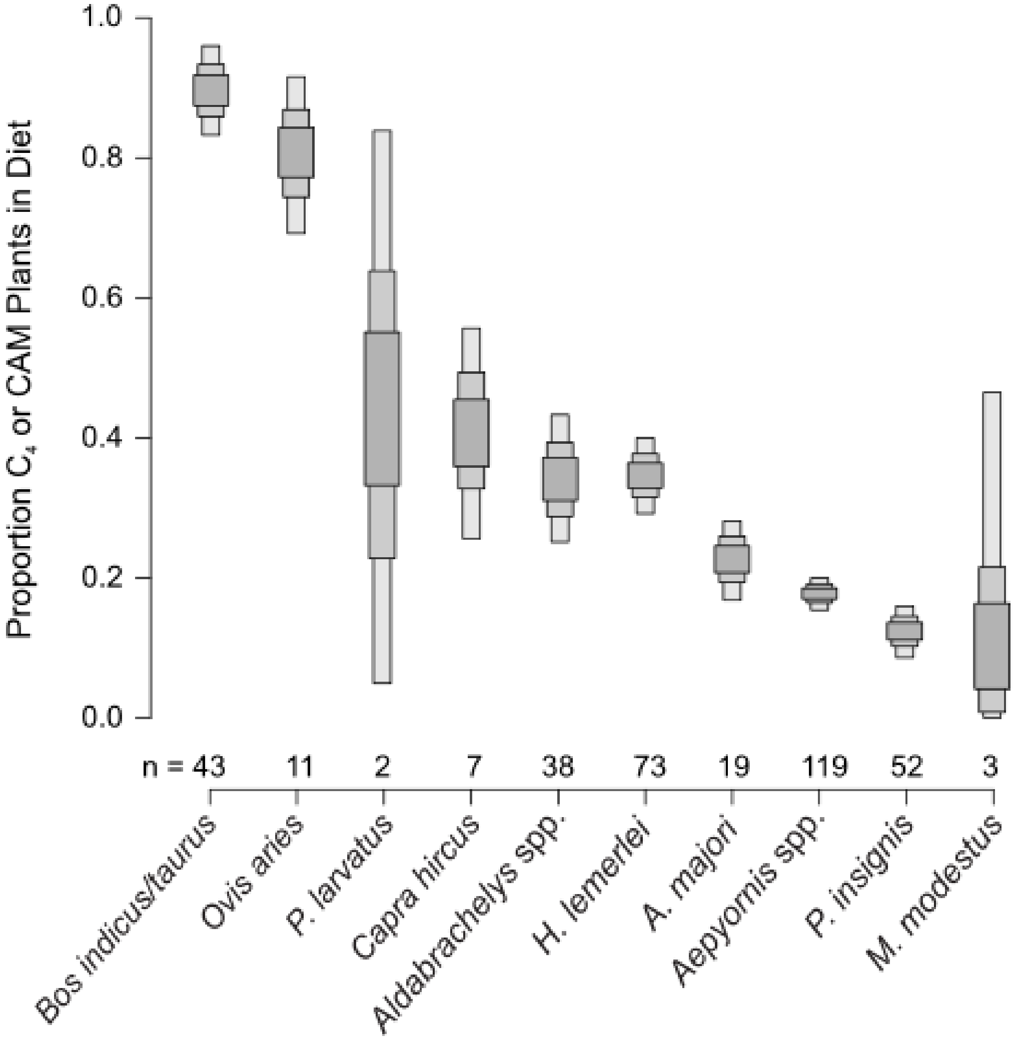


Figure S4. Proportions of C_4 + CAM plant material in the diet of introduced and endemic herbivores, with estimates shown as shaded boxes that span 25%, 75%, and 95% of the estimates made from 30,000 iterations of a mixing model based on $\delta^{13}C$ values in SIAR. These plant types (primarily grasses and succulents) contributed primarily to the diet of zebu cattle and other introduced herbivores. Note that unspecified *Ovis/Capra* data (n=2) are not included in this plot.

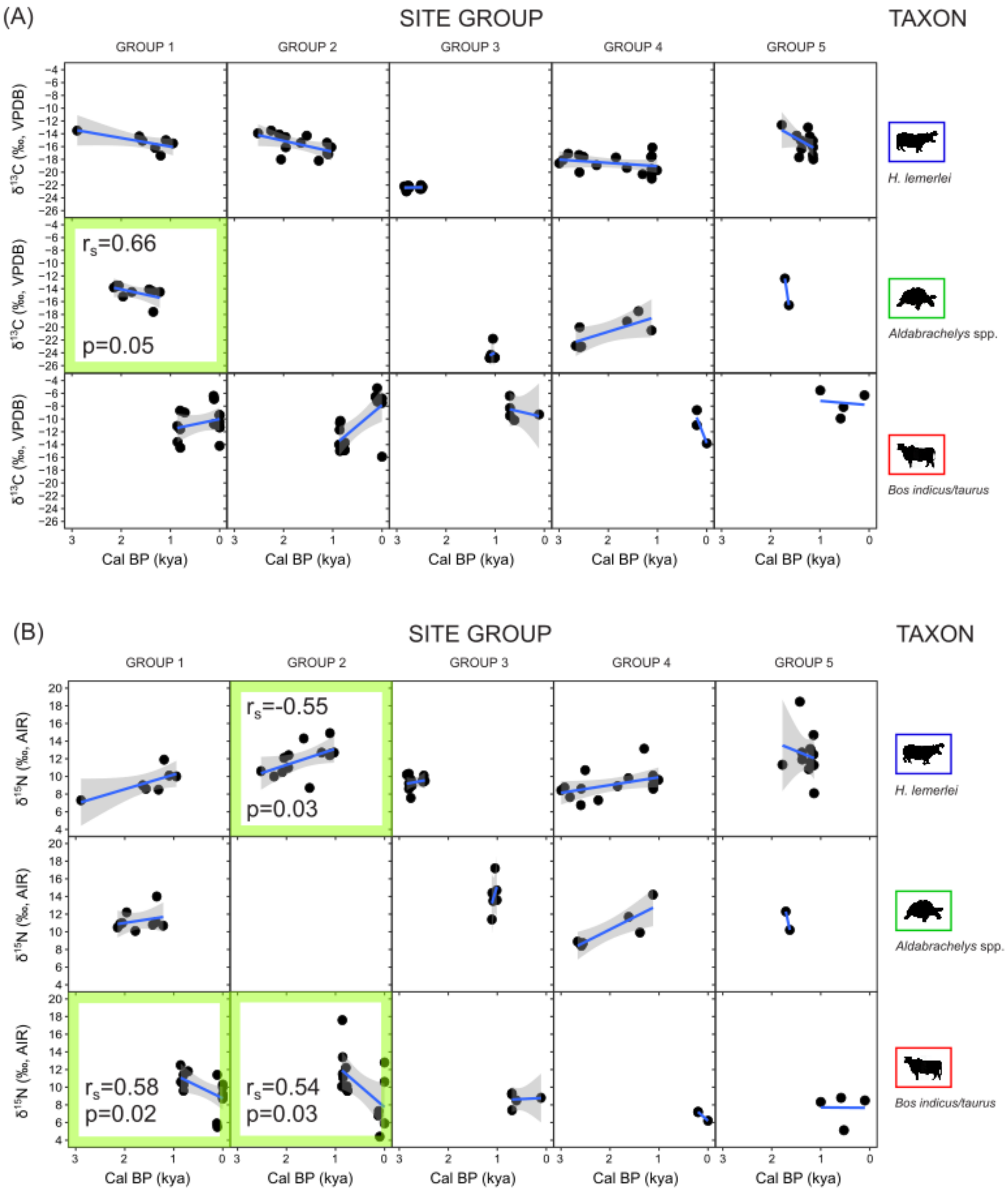
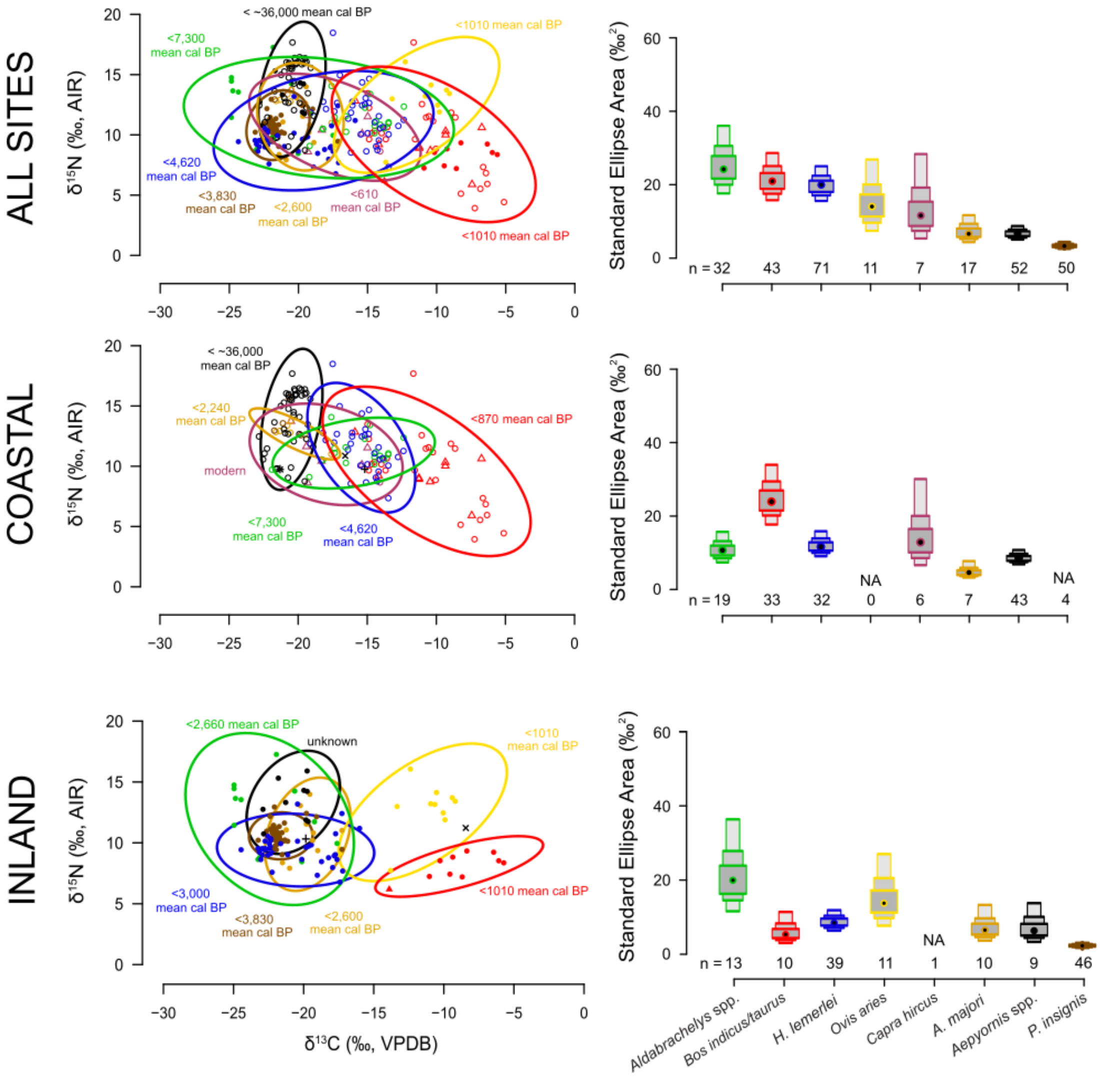

(A)
SITE GROUP
TAXON
GROUP 1
GROUP 2
GROUP 3
GROUP 4
GROUP 5
δ13C (‰, VPDB)
rs=0.66
p=0.05
H. lemerlei
Aldabrachelys spp.
Bos indicus/taurus
Cal BP (kya)
(B)
SITE GROUP
TAXON
GROUP 1
GROUP 2
GROUP 3
GROUP 4
GROUP 5
δ15N (‰, AIR)
rs=-0.55
p=0.03
rs=0.58
p=0.02
rs=0.54
p=0.03
H. lemerlei
Aldabrachelys spp.
Bos indicus/taurus
Cal BP (kya)

Figure S5 (previous page). Monotonic temporal trends in $\delta^{13}C$ values (A) and $\delta^{15}N$ values (B) according to both site group (Fig. 2) and taxon (n = 133 individuals of known age with $\delta^{13}C$ and $\delta^{15}N$ data: 65 *Hippopotamus lemerlei*, 25 *Aldabrachelys* spp., and 43 *Bos indicus/taurus*). Data in each frame are fitted with lines and 95% confidence bands; Spearman correlation coefficients and associated p values are given only for datasets that include significant monotonic change through time (highlighted in green). Note that only taxa with relatively large sample sizes and temporal spreads are shown. Higher spatial and temporal resolution comes at the cost of diminished sample sizes.

We also used Stable Isotope Bayesian Ellipses in R (SIBER) to visually inspect collagen space consumer $\delta^{13}C$ and $\delta^{15}N$ data and to extract isotopic standard ellipse area metrics that are unbiased with respect to sample size (Table S4, Jackson, et al. 2011). Given that the GLMs indicate some spatial structure associated with herbivore $\delta^{13}C$ values within the region, we plotted both a regional overview of data (Fig. 4) and coastal and inland data separately (Fig. S6). The shape and size of the standard ellipses are based on the covariance matrix of the $\delta^{13}C$ and $\delta^{15}N$ data, and mean $\delta^{13}C$ and $\delta^{15}N$ values define the absolute locations of ellipses. To generate posterior estimates for the covariance matrix, SIBER uses Markov chain Monte Carlo simulations that start with uninformed priors for mean $\delta^{13}C$ and $\delta^{15}N$ values and the covariance matrix. We used the Shapiro-Wilk test to check for normality of $\delta^{13}C$ and $\delta^{15}N$ values within taxonomic and taxonomic × coastal proximity groups before analysis with SIBER. When both inland and coastal data are included, only *P. insignis* $\delta^{13}C$ and $\delta^{15}N$ values failed this test with W-statistics <0.9 (0.70, and 0.85, respectively, with $p<0.001$ for both). In the inland dataset, *P. insignis* $\delta^{13}C$ and *Aepyornis* spp. $\delta^{13}C$ values failed this test with W-statistics less than 0.85 (0.64 and 0.79, respectively with $p\leq0.02$ for both). However, these distributions have relatively narrow ranges, and we chose not to transform them. For this analysis, we excluded *M. modestus* and *P. larvatus* due to small sample sizes, as well as the four samples from Ankilibehandry and Beanka, which are further north and relatively distant from all other sites (Fig. 2). Uneven sampling through space and time influences observed variation in stable isotope data from different herbivores and can complicate inferences of resource overlap. However, we confirmed that number of sampled sites and timespan account for only a small proportion of the variation in standard ellipse area metrics associated with regional data (Table S4).

Table S4. SIBER estimates of the standard ellipse area (SEA) and SEA corrected for sample size (SEAc) for each taxonomic group when consider an overview of data from the region and coastal and inland data separately. Each group includes samples drawn from a different number of sites and timespan, yet these variables account for little of the variation in overview SEAc values (adjusted r^2=0.24). This remains true when we ignore the *Aepyornis* spp. data (adjusted r^2=0.05), which may be justified given that the large *Aepyornis* spp. time midspread (*) is approximate and based on associations with ^{14}C-dated gastropods (Tovondrafale, et al. 2014). As in the main manuscript text, temporal midspread is here defined as the period spanning 50% of the mean calibrated dates. Note that the temporal midspread of inland *Aepyornis* spp. is unknown given that only one individual with δ^{13}C and δ^{15}N data is ^{14}C-dated.

Taxa	n	SEA (‰^{2})	SEAc (‰^{2})	# of Sites	Temporal Midspread (yrs.)
All Sites					
Aepyornis spp.	52	6.7	6.8	3	36,000*
Aldabrachelys spp.	32	25.3	26.1	8	1,010
Archaeolemur majori	17	7.3	7.8	4	880
Hippopotamus lemerlei	71	19.8	20.1	9	1,600
Pachylemur insignis	50	3.4	3.5	4	460
Bos indicus/taurus	43	21.2	21.7	15	710
Ovis aries	11	14.4	16.0	2	200
Capra hircus	7	12.7	15.3	4	0
Coastal					
Aepyornis spp.	43	6.7	6.8	1	36,000*
Aldabrachelys spp.	19	8.6	9.1	6	710
Archaeolemur majori	7	2.2	2.6	1	330
Hippopotamus lemerlei	32	9.8	10.1	6	880
Pachylemur insignis	4	NA	NA	2	780
Bos indicus/taurus	33	22.3	23.0	9	800
Ovis aries	0	NA	NA	NA	NA
Capra hircus	6	11.8	14.8	3	0
Inland					
Aepyornis spp.	9	7.0	8.0	2	unknown
Aldabrachelys spp.	13	21.2	23.1	2	1,500
Archaeolemur majori	10	7.1	7.9	3	1,110
Hippopotamus lemerlei	39	8.7	8.9	3	1,660
Pachylemur insignis	46	2.3	2.3	2	420
Bos indicus/taurus	10	5.5	6.2	6	600
Ovis aries	11	14.4	16.0	2	200
Capra hircus	1	NA	NA	1	NA



ALL SITES
COASTAL
INLAND
δ15N (‰, AIR)
δ13C (‰, VPDB)
Standard Ellipse Area (‰²)
< ~36,000 mean cal BP
<7,300 mean cal BP
<1010 mean cal BP
<4,620 mean cal BP
<3,830 mean cal BP
<2,600 mean cal BP
<610 mean cal BP
<2,240 mean cal BP
<870 mean cal BP
modern
<2,660 mean cal BP
unknown
<3,000 mean cal BP
n = 32 43 71 11 7 17 52 50
n = 19 33 32 0 6 7 43 4
NA
n = 13 10 39 11 1 10 9 46
Aldabrachelys spp.
Bos indicus/taurus
H. lemerlei
Ovis aries
Capra hircus
A. majori
Aepyornis spp.
P. insignis

Figure S6 (previous page). Taxon-specific stable isotope values in bone collagen space (left), with bolded ellipses that outline approximately 95% of the data from each group. All data from site groups 1-5 are plotted both according to coastal (n=144) vs. inland (n=139) and together in an overview (n=283). Modern individuals of *Ovis*, *Capra* and *Bos* are marked as triangles. Stable carbon isotope data from *Aepyornis* spp. eggshell organics are corrected so that they are comparable to bone collagen values (SI "Data Analysis –Stable Isotopes"). Only one *Aepyornis* spp. individual on this figure is represented by bone collagen data (UCIAMS 224190, $\delta^{13}C=-22.7‰$, $\delta^{15}N=10.7‰$). Mean calibrated date ranges next to ellipses specify the age range for each group. Note that the sample size of some groups with n<5 does not permit the creation of ellipses (Jackson, et al. 2011). This is true for coastal *Ovis* and *Pachylemur*, inland *Capra*, and all *Mullerornis modestus* and *Potamochoerus larvatus*. Note that a single coastal *Mullerornis modestus* (✱) plots in the bolded ellipse of *Aepyornis* spp. and both a coastal *P. larvatus* (+) and indistinguishable *Ovis/Capra* (×) plot in the bolded ellipse of *Capra hircus*. Additionally, an inland *P. larvatus* (+) plots in the bolded ellipse of *Hippopotamus lemerlei*, and an unspecified *Ovis/Capra* (×) plots in the bolded ellipse of *Ovis aries*. Sample size corrected standard ellipse areas (SEAc, containing approximately 40% of the data from each group, right) give relative estimates for the similarity of stable isotope values between individuals of the same taxon. SEAc estimates for each taxonomic group (right, with taxon-specific sample sizes marked along x-axis) appear as modes (points) surrounded by shaded boxes that span 50%, 75%, and 95% of the estimates (from dark to light).

We used the Markov chain Monte Carlo simulation algorithm in Stable Isotope Analysis in R (SIAR) version 4.2 to infer the proportional contribution of C_3 versus C_4 or CAM plants to herbivore diet. We used both previously published and new plant $\delta^{13}C$ data from SW Madagascar (Dataset S3) to establish mixing model endmembers. Note that we do not use $\delta^{15}N$ data in our mixing model with C_3 and C_4 + CAM plants for multiple reasons: 1) Previously-published differences in mean $\delta^{15}N$ values of C_3, C_4, and CAM plants in the region are small (<1‰) and insignificant (Kruskal-Wallis H(2)=4.8, p=0.09, Dataset S3); and 2) An analysis that depends on both $\delta^{15}N$ and $\delta^{13}C$ data forces us to ignore published data for 81 eggshell and bone samples that only have $\delta^{13}C$ data. Moreover, given that ecosystem $\delta^{15}N$ values are sensitive to moisture availability (Austin and Vitousek 1998; Handley, et al. 1999), which varies significantly across space and time in SW Madagascar (Crowley, et al. 2017; Hixon, et al. 2018), modern plant $\delta^{15}N$ values may be inappropriate to compare with $\delta^{15}N$ values from ancient animals that lived in relatively arid habitat. In our mixing model, we corrected plant $\delta^{13}C$ by +4±1‰ to account for the expected difference in $\delta^{13}C$ between bone collagen and plants (DeNiro and Epstein 1978; Kelly 2000) , as well as by +1.5‰ to account for the Suess effect (Crowley and Godfrey 2013; Tans, et al. 1979). Estimates of the absolute proportion of C_3 versus C_4 or CAM plants in herbivore diet (Fig. S4) should be treated with caution, because $\delta^{13}C$ value of at least the C_3 plant endmember could have changed as a function of past aridity (Crowley, McGoogan, et al. 2012; Swap, et al. 2004). If we unintentionally use lower than actual $\delta^{13}C$ values for the C_3 plant endmember, then the mixing model would inflate estimates of the proportion of C_4 or CAM plants in herbivore diet.

III. CH. 3: Ecological consequences of a millennium of dogs on Madagascar[2]

A. Abstract

Introduced predators currently threaten endemic animals on Madagascar through predation, facilitation of human-led hunts, competition, and disease transmission, but the antiquity and past consequences of these introductions are poorly known. We use directly radiocarbon dated bones of introduced dogs (*Canis familiaris*) to test whether dogs could have aided human-led hunts of the island's extinct megafauna. We compare carbon and nitrogen isotope data from the bone collagen of dogs and endemic 'fosa' (*Cryptoprocta* spp.) in central and southwestern Madagascar to test for competition between introduced and endemic predators. The distinct isotopic niches of dogs and fosa suggest that any past antagonistic relationship between these predators did not follow from predation or competition for shared prey. Radiocarbon dates confirm that dogs have been present on Madagascar for over a millennium and suggest that they at least briefly co-occurred with the island's extinct megafauna, which included giant lemurs, elephant birds, and pygmy hippopotamuses. Today, dogs share a mutualism with pastoralists who also occasionally hunt endemic vertebrates, and similar behavior is reflected in deposits at several Malagasy mixed paleontological and archaeological sites that contain dog and livestock bones along with butchered bones of extinct megafauna and extant lemurs. Dogs on Madagascar have had a wide range of diets during the past millennium, but relatively high stable carbon isotope values suggest few individuals relied primarily on forest bushmeat. Our newly generated data suggest that dogs were part of a suite of animal

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[2] This chapter is accepted for publication in *Frontiers in Ecology and Evolution*.

introductions beginning more than a millennium ago that coincided with widespread landscape transformation and megafaunal extinction.

B. Introduction

Madagascar is a biodiversity hotspot that has repeatedly faced a variety of biological invasions over the past millennium (Hixon, et al. accepted; Kolby 2014; Middleton 1999). A debate regarding when humans first arrived on Madagascar is ongoing, with some researchers favoring recent arrival 1,600-1,000 years ago based on cultural considerations (Anderson, et al. 2018) and other researchers favoring early human arrival 10,000-4,000 years ago based on rare stone tools and cutmarks on ancient elephant bird bone (Dewar, et al. 2013; Hansford, et al. 2018). Endemic vertebrates >10 kg declined by ~950 years ago (Crowley 2010), and over half of the island's surface is currently dedicated to pastoralism involving introduced zebu cattle (World Bank Anonymous 2003). Hunting, deforestation, and regional aridification help explain aspects of past extinctions (Anderson, et al. 2018; Burney, et al. 2004; Crowley, et al. 2017; Faina, et al. in press; Godfrey and Douglass in press; Godfrey, et al. 2019; Hixon, et al. 2018; Virah-Sawmy, et al. 2010); interactions with introduced species (e.g., livestock, rodents, and predators) may have exacerbated these stressors (Dewar 1997; Hixon, et al. accepted). Globally, changes in human land use (i.e., the spread of pastoralism and commensal species) generally coincide with past environmental transformations (Stephens, et al. 2019) that contribute to biotic homogenization (McKinney 1997; McKinney and Lockwood 1999). As part of this transformation, introduced predators can disrupt island ecosystems by facilitating human hunting, creating novel predation pressure, and competing with other predators (e.g., competition between dingoes and red foxes in Australia; Cupples, et al. 2011), yet we know very little about the antiquity of introduced predators on Madagascar.

We use radiocarbon (^{14}C) and stable isotope (δ^{13}C and δ^{15}N) data from bone collagen to test the following hypotheses: 1) introduced dogs (*Canis familiaris*) preyed on lemurs; and 2) dogs competed with the island's largest endemic carnivorans (*Cryptoprocta* spp., the fosa). Limited chronological overlap (as inferred from directly ^{14}C-dated dog and lemur bones) would reduce the potential for humans to hunt extinct lemurs with dogs, and lack of isotopic niche overlap among dogs and *Cryptoprocta* spp. would diminish the potential for direct forms of competition. However, lack of dietary overlap would not necessarily exclude the possibility that dogs interacted aggressively with *Cryptoprocta* spp. or helped people hunt prey that *Cryptoprocta* spp. also hunted. This work expands our understanding of both past megafaunal extinction and modern functional diversity of predators on Madagascar.

Madagascar's endemic family of carnivorans (Eupleridae) includes ten extant species that range in size from the ~550 g broad-striped vontsira (*Galidictis fasciata*) to the ~8.5 kg fosa (C*ryptoprocta ferox*, Wampole, et al. 2021). The so-called "cave" fosa (*Cryptoprocta spelea*, thought to be extinct) was likely double the size of *C. ferox* (Goodman, et al. 2004) and may still exist in remote parts of northern Madagascar (Nomenjanahary, et al. in press). All members of Eupleridae are currently threatened, and the IUCN red list currently includes *C. ferox* as vulnerable due to rapid population decline (Hawkins and Racey 2008). Introduced mammalian predators include domestic dogs, domestic cats (*Felis* spp.), and the small Indian civet (*Viverricula indica*, Fig. 1), yet only relatively large predators (dogs and *Cryptoprocta* spp.) are reasonably well represented in Madagascar's subfossil (partially fossilized) record (Crowley 2010;

Rakotozafy and Goodman 2005). It is not known when people introduced dogs to the island (Fig. 2, Crowley 2010; Douglass, et al. 2019), and traces of predation by dogs on subfossil bones (e.g., gnaw marks) are understudied and possibly difficult to identify (Brockman, et al. 2008). A rare set of cave rock drawings in western Madagascar may depict a hunting scene that includes people, dogs, an extinct sloth lemur, and symbols that have parallels from around the Indian Ocean, but the age of these drawings is uncertain (Burney, et al. 2020). Madagascar's modern dogs are descended from African dogs that people brought to the island (Ardalan, et al. 2015), which is consistent with the Bantu origin of the most common Malagasy word for dog (amboa, Blench 2008).

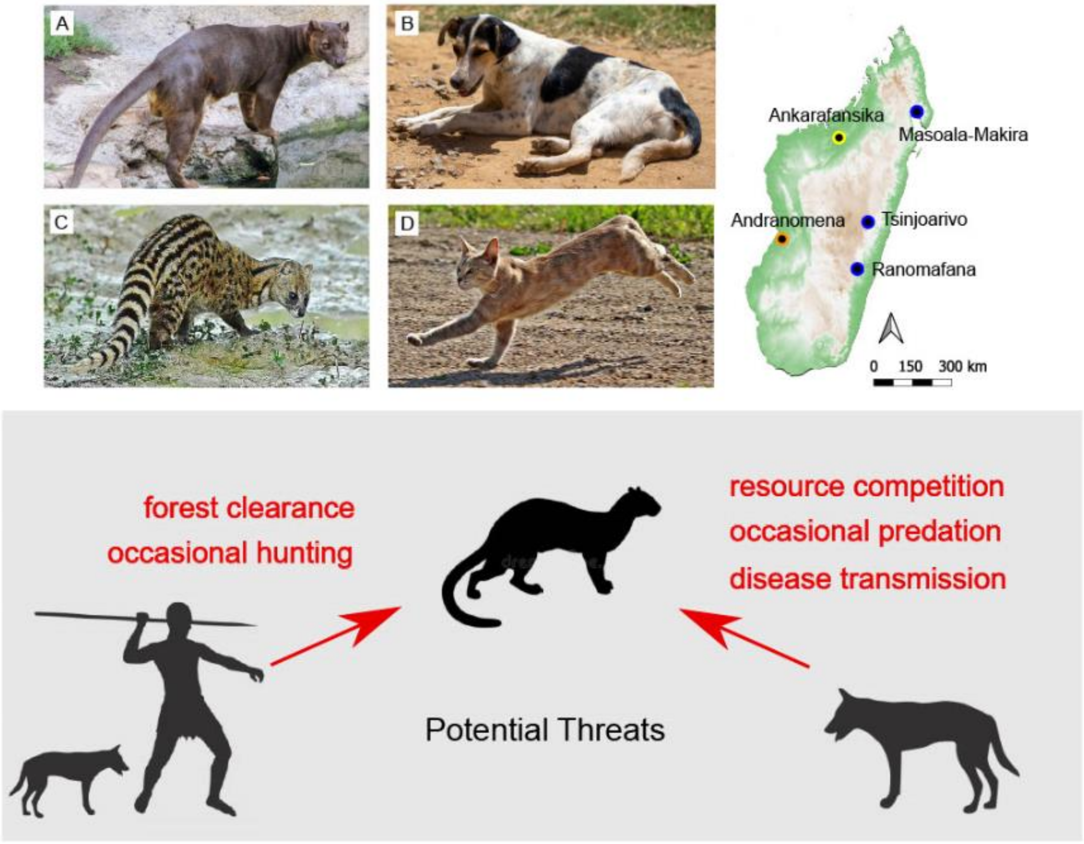


Figure 1. Endemic fosa (A, *Cryptoprocta ferox*) may interact with introduced dogs (B, *Canis familiaris*), Indian civets (C, *Viverricula indica*), and cats (D, *Felis* sp.). National parks discussed in the text where antagonistic interactions between introduced and endemic predators have been observed are shown in the map at right. The ecoregion for each park is denoted using colors (orange = succulent woodland, yellow = dry deciduous

forest, blue = central highlands and humid forest). Human and introduced predator threats to *C. ferox* are summarized in shaded area below.

The diet of dogs on Madagascar is poorly characterized. Modern and historic surveys suggest dogs rely heavily on plant and animal scraps in human-derived food waste (Decary 1939; Kshirsagar, et al. 2020). Yet dogs are also known to stalk lemurs (Brockman, et al. 2008) and help humans hunt a variety of bushmeat (Dataset S2, Decary 1939; Garcia and Goodman 2003; Gardner and Davies 2014). Dogs in SW and NW Madagascar currently subsist largely on food scraps, and people often feed their hunting dogs the innards of bushmeat (Godfrey, et al. submitted, Kate Thompson & Cortni Borgerson, pers. comm.). Dogs are popular protection animals for people around Ranomafana National Park, in central Madagascar (Kshirsagar, et al. 2020). However, dogs can also transmit rabies and represent a general nuisance toe people while they scavenge (Rajeev, et al. 2019). Some dog owners have reported that their dogs harass and kill *C. ferox* around Ranomafana (Kshirsagar, et al. 2020; Valenta, et al. 2016). Data from live traps and camera traps suggest that *C. ferox* avoids dogs in several national parks (Fig. 1), which may follow from a combination of aggressive interactions and disease transmission (Barcala 2009; Dollar, et al. 2007; Farris, et al. 2015; Gerber, et al. 2012; S. Merson, et al. 2019; Pomerantz, et al. 2016; Rasambainarivo, et al. 2017). For example, *C. ferox* is typically cathemeral, yet individuals around Ankarafantsika (in the NW) and Masoala–Makira (in the East) tend to be primarily nocturnal, where dogs are active during the dawn and day (Farris, et al. 2015; S. Merson, et al. 2019). Additionally, following the euthanasia of dogs at Ankarafantsika, *C. ferox* captures increased (Barcala 2009), which suggests that interactions involving dogs affect both *C. ferox* abundance and activity patterns.

Madagascar's modern dogs have at least some dietary overlap with *C. ferox* that creates potential for exploitation competition (Farris, et al. 2017; S. Merson, et al. 2019). Data from modern kill sites and *C. ferox* scat from multiple ecoregions in Madagascar indicate that they are opportunistic predators with the potential for heavy reliance on lemurs (Dataset S3, Dollar, et al. 2007; Goodman, et al. 1997; Hawkins and Racey 2008; Rasoloarison, et al. 1995; Wright, et al. 1997). Modern *C. ferox* and dogs are both known to consume sifakas (e.g., *Propithecus verreauxi*), tenrecs, rodents, birds (e.g., chicken and coua), frogs, snakes, and scraps of bushpigs and zebu cattle (Fig. 2, Brockman, et al. 2008; Decary 1939; Gardner and Davies 2014; Goodman, et al. 1997; Hawkins and Racey 2008; Rasoloarison, et al. 1995; Valenta, et al. 2016). There is no published evidence for omnivory by *C. ferox* beyond possible occasional fruit consumption as a source of water during the dry season (Hawkins and Racey 2008). Dogs raid bird and reptile nests and can engage in devastating amounts of surplus killing. Though they are typically more inefficient hunters than wild canids (Butler, et al. 2004; Serpell and Barrett 2017), their impacts can still be considerable. For example, a single stray dog killed hundreds of North Island brown kiwis (*Apteryx mantelli*, >50% of the local population) in New Zealand within a couple of months (Taborsky 1988). The dramatic impact that dogs can have on their prey may diminish prey for *C. ferox*.

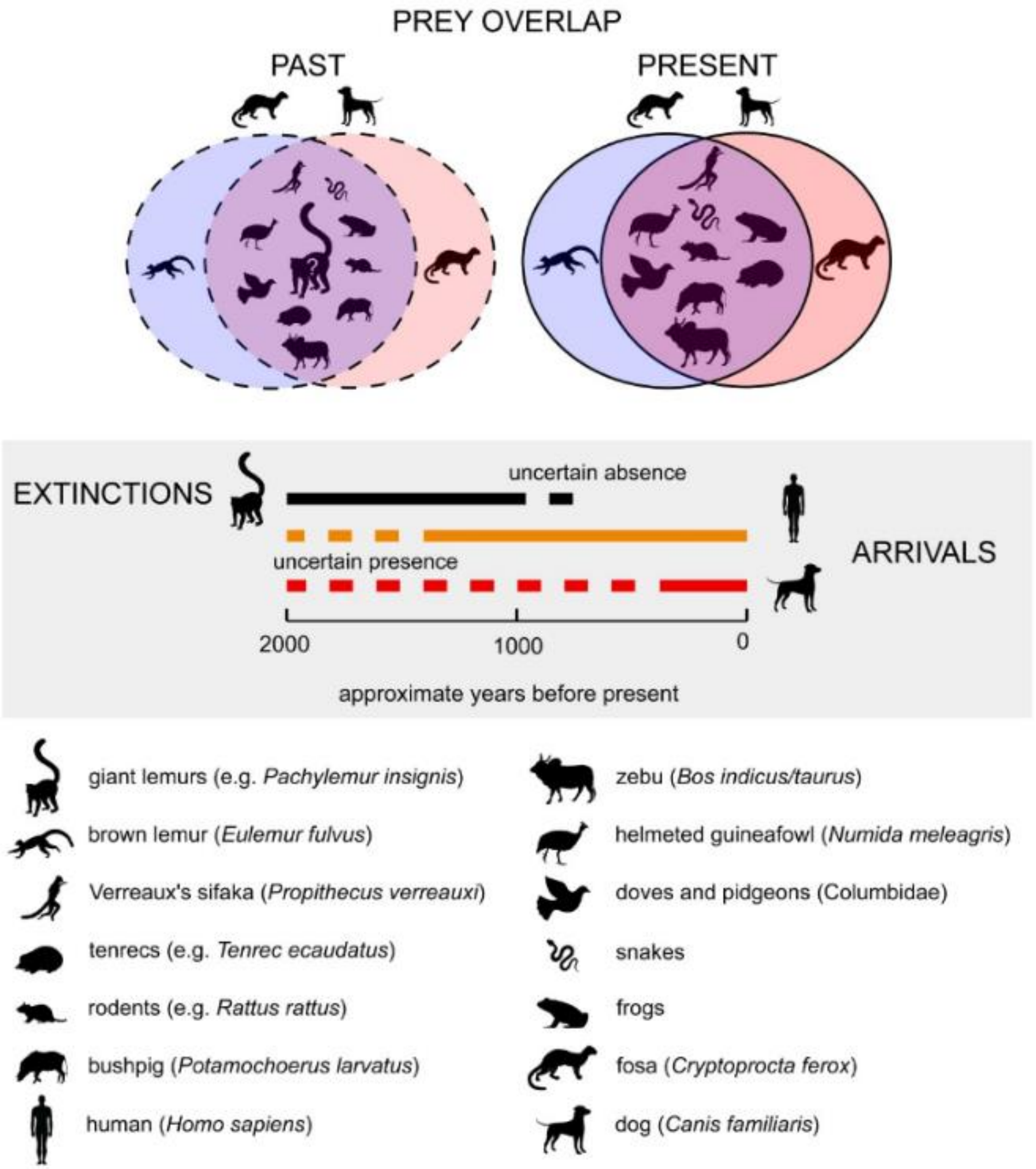


Figure 2. Overlaps in dog and *C. ferox* diet (top) and chronology of extinctions and arrivals as understood before the present study (center, shaded, with uncertain occurrence prior to this publication marked with dashed lines). The spread of dogs (red bar) to Madagascar before European contact (~500 BP) has been poorly documented, and it is unknown whether they overlapped chronologically with extinct megafauna such as giant lemurs (black bar). Dogs and *C. ferox* currently scavenge and prey on many of the same animals (see inexhaustive list at bottom), but the antiquity of this dietary overlap is unknown (dashed lines). Before the present study, it was unknown whether past dogs preyed on extinct giant lemurs, yet there are abundant traces of human and mammalian carnivoran predation on extinct giant lemurs. Note that examples of exclusively dog or *C. ferox* prey are token and do not represent the diversity of predator-specific diets (see Datasets S2 and S3).

Exclusion competition between dogs and *C. ferox* follows from the potential for aggressive encounters and occurs regardless of impacts on prey populations. Dogs are avid chasers that contribute to habitat fragmentation by inducing fear and avoidance in a wide range of animals (Lenth, et al. 2008; Ritchie, et al. 2014; Young, et al. 2011). Dogs associated with human hunters increase the potential for exclusion competition with native predators throughout Madagascar. Some evidence of the past association of dogs with human hunters (Burney, et al. 2020) suggests that there may be a history of exclusion competition between dogs and *Cryptoprocta* spp.

Radiocarbon and stable isotope data from bone collagen can give a long-term perspective on predator interactions and clarify past and ongoing processes that influence endemic biodiversity. Based on the potential association of dog bones with extinct megafauna from paleontological sites (Douglass, et al. 2019), we expect some chronological overlap among these animals. We also expect some overlap in dog and *Cryptoprocta* spp. isotope values. Animals with similar diets that forage in similar habitats have tissues with similar $\delta^{13}C$ and $\delta^{15}N$ values (Crawford, et al. 2008). Carbon isotope values predominantly reflect the plants at the base of the food web (Farquhar, et al. 1989). Plants that use the C_3 photosynthetic pathway (primarily trees, shrubs, and herbs) tend to be depleted in ^{13}C by over 10‰ relative to plants that use the C_4 pathway (primarily grasses) or the CAM pathway (primarily succulents). Data from sympatric C_3, C_4, and CAM plants from SW Madagascar reflect this difference, with combined CAM and C_4 plant tissue ($\delta^{13}C$ $\mu\pm\sigma = -12.8\pm1.6$‰) enriched in ^{13}C by ~15‰ relative to C_3 plant tissue ($\mu\pm\sigma = -27.2\pm2.3$‰, Hixon et al., submitted). To a lesser extent, plant $\delta^{13}C$ values also depend on variables such as canopy cover, moisture availability, salinity, and soil microbe respiration (reviewed in Farquhar, et al. 1989). These patterns are passed on to herbivores and higher order consumers over time. If both dogs and *Cryptoprocta* spp. consumed forest-dwelling herbivores (such as most of the island's extinct megaherbivores), then we would expect overlap in collagen δ^{13}C values among these groups (Godfrey and Crowley 2016). Alternatively, if dogs regularly consumed scraps of human introduced grazers (e.g., zebu cattle and ovicaprids), then we would expect dogs to have relatively high collagen δ^{13}C values and minimal overlap with *Cryptoprocta* spp.

We also expect overlap in collagen δ^{15}N values among co-occurring dogs and *Cryptoprocta* spp. Consumer tissues tend to be enriched in ^{15}N relative to diet such that each increase in trophic level corresponds to a 3-5‰ increase in collagen δ^{15}N values (Cleland 2001; Hyodo, et al. 2010; McCutchan, et al. 2003). As secondary consumers, dogs and *Cryptoprocta* spp. should have comparable δ^{15}N values, though omnivory or the preferential consumption of certain prey tissue (e.g., intestines) may reduce dog δ^{15}N values relative to *Cryptoprocta* spp. δ^{15}N values (Reid and Koch 2017). Soil nitrogen cycling also strongly influences ecosystem δ^{15}N values and is sensitive to moisture availability (Austin and Vitousek 1998), so both plant and consumer δ^{15}N values vary considerably among ecoregions in Madagascar (Crowley, et al. 2011). Specifically, values are highest in the xerophytic spiny thicket in SW Madagascar and lowest in the humid forests in the east and north. There can also be pronounced differences among microhabitats in the same region (Crowley, McGoogan, et al. 2012; Crowley, et al. 2014; Heck, et al. 2016). Plants and animals living on saline coastal soils that are influenced by marine-derived nitrates may also have higher δ^{15}N values than those that live inland (Heaton 1987; Hixon, et al. accepted; Mosher, et al. 2020; Sparks and Crowley 2018). Thus, only in comparable environments can consumer δ^{15}N values be interpreted primarily in terms of diet.

C. Methods

Specimen and Site Selection

Sampled dog bones come from 13 sites spread throughout Madagascar (Fig. 3, Dataset S1 & S4). We sampled all available bones from existing collections (n = 16 subfossils + 3 modern dog bones). Most specimens (n = 12) are housed at the University of Antananarivo; others are curated at the National Museum of Natural History, Paris as well as Yale University, the University of Massachusetts, Amherst, and the University of California at Santa Barbara (Dataset S1). These bones were collected from both archaeological sites (Rezoky, Andranosoa, and Lakato'ni Gavin) and paleontological sites (e.g., Andolonomby and Tsirave) that span four of Madagascar's five major ecoregions but are concentrated in the spiny thicket and succulent woodland of the southwest (Fig. 3). We also analyzed two subfossil *C. ferox* bones from Taolambiby that are currently housed at the Australian National University (ANU). To augment these datasets, we compiled previously published data from five dogs (includes two modern bones, Crowley 2010; Douglass, et al. 2019), nine subfossil *C. ferox* (Anderson, et al. 2018; Crowley 2010; Crowley and Godfrey 2013; Crowley, et al. 2017), and three subfossil *C. spelea* (Crowley 2010). Note that all subfossil *Cryptoprocta* spp. come from paleontological sites and that all but one of the previously published predators (a subfossil *C. ferox*, OxA 27174) have both $\delta^{13}C$ and $\delta^{15}N$ data.

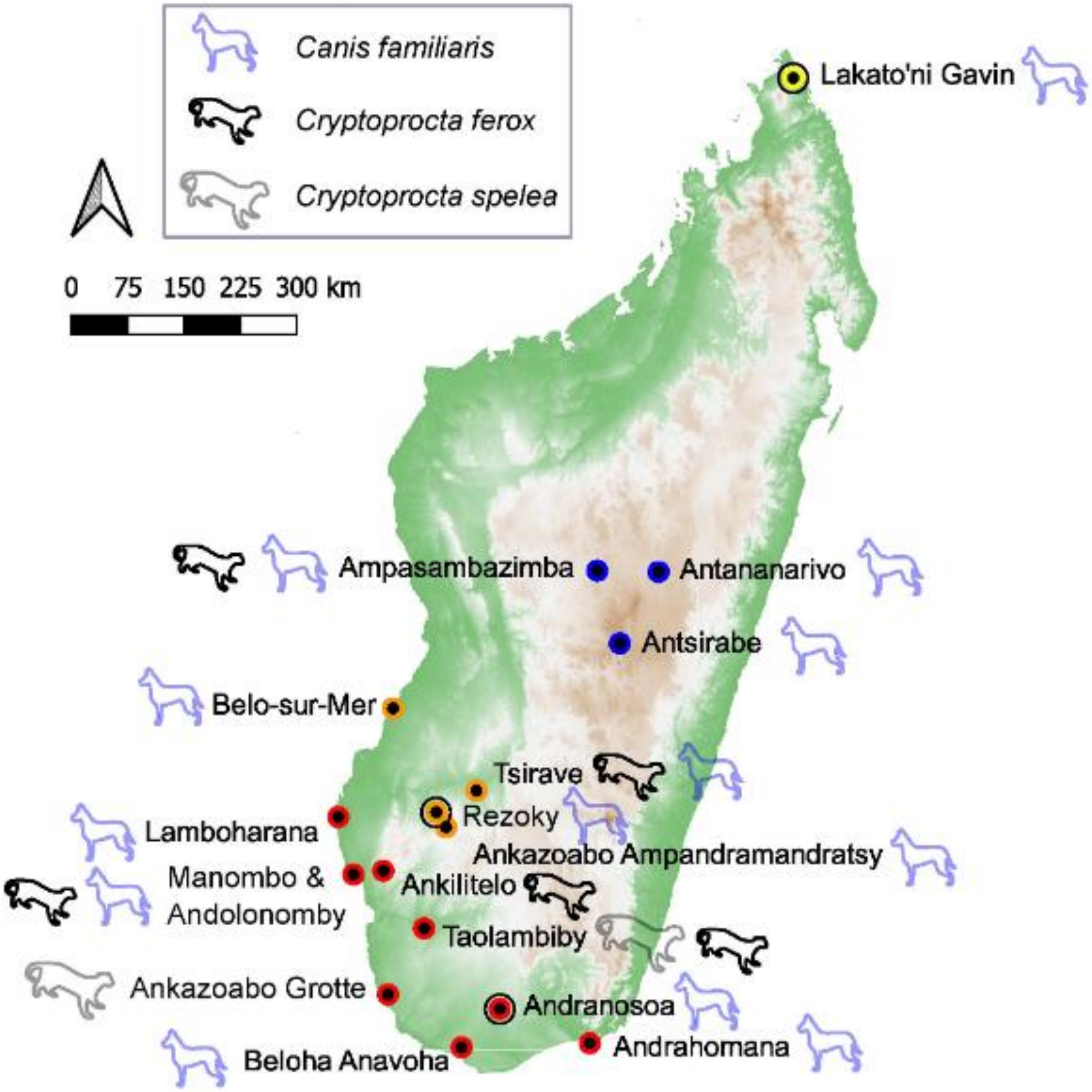


Figure 3. Collection sites of dog and *Cryptoprocta* spp. bones considered in this study, with archaeological sites (Lakoto'ni Gavin, Rezoky, and Andranosa) circled and sites colored according to ecoregion (red = spiny thicket, orange = succulent woodland, blue = central highlands, yellow = dry deciduous forest).

To compare an estimated time of dog introduction with hunting and extinction chronologies (see section "2.3 Data Analysis" below), we also compiled previously published ^{14}C data from butchered bone of multiple endemic taxa from SW Madagascar (extinct giant lemurs, an extant lemur consumed by *C. ferox* [*P. verreauxi*], elephant birds, and pygmy hippo, Dataset S1) and three species of giant lemurs with relatively large sample sizes ($n \geq 20$ each, *Pachylemur insignis*, *Archaeolemur majori,* and *Palaeopropithecus ingens*, all from SW Madagascar, Dataset S1). We focus on the arid SW, because each ecoregion has its own chronology of species introductions and extinctions, and most existing ^{14}C datasets come from this ecoregion (Crowley 2010; Douglass, et al. 2019). We focus on comparing dog and *Cryptoprocta* spp. data with those from extinct giant lemurs, because 1) there is widespread evidence that at least *Cryptoprocta* spp. and humans preyed on these animals (Godfrey, et al. submitted; Meador, et al. 2019), and 2) these taxa have robust ^{14}C chronologies that suggest they disappeared as approximately coeval with other megafauna such as pygmy hippos and giant tortoises (Crowley 2010; Hixon, et al. accepted). To help infer past dog and *C. ferox* diet, we compiled published lists of prey species from across the island (Datasets S2 & S3). We make stable isotope comparisons involving prey taxa within the arid SW (Dataset S1), and we also focus on subfossil bone, because few of our sampled specimens are modern, and some extant and introduced taxa likely shifted their diet and habitat use in response to the recent expansion of grasslands on the island (Crowley and Samonds 2013). The previously published literature includes 298 potential prey individuals with stable isotope data from the SW, and we include unpublished records from 11 individuals in our dataset (analyzed previously by B.E.C. using approach from Sparks & Crowley, 2018). We further expanded this dataset by sampling bones from an additional 13 potential prey individuals from Taolambiby and Lamboharana/Lamboara in SW Madagascar, which brings the potential prey total to 311 individuals. During analyses, we excluded 21 previously-published data from specimens that: 1) lack explicit reference to bone collagen purification protocols or 2) include signs of contamination (i.e., atomic C:N > 3.5, Brock, et al. 2010).

^{14}C and Stable Isotope Analyses

Pretreatment of the 31 subfossil and three modern specimens took place in the Human Paleoecology and Isotope Geochemistry Laboratory at Pennsylvania State University (PSU). Prior to demineralization, bones sampled from museum collections suspected of using ink labels and conservants/consolidants such as polyvinyl acetate must go through solvent rinses to remove exogenous carbon with distinct ^{14}C content and δ^{13}C values (France, et al. 2011). We sonicated museum specimens in sequential washes of methanol (MeOH), acetone, dichloromethane (DCM), and nanopure water. Samples were sonicated in 20 mL of each fluid for 20 minutes. For the three modern bone samples, we removed lipids using 3× sonication in 2:1 DCM:MeOH followed by 3× rinsing in nanopure water (modified from Guiry, et al. 2016).

All bones were mechanically cleaned, demineralized in 0.5 N hydrochloric acid (HCl) under refrigeration, and gelatinized in 0.01 N HCl at 60°C. Collagen from the bone of subfossil individuals was purified through ultrafiltration (14 samples, Beaumont, et al. 2010; Fernandes, et al. 2021) or purification with XAD resin (17 samples, Dataset S1, Lohse, et al. 2014; Stafford, et al. 1988; Stafford, et al. 1991). When collagen is relatively intact and yields are high, ultrafiltration can purify a sample by mechanically removing the smaller (<30 kDa) fraction, which includes degraded collagen and exogenous contaminants (Higham, et al. 2006). When collagen is stained or degraded, the relatively less polar contaminants (humates, in particular) can be separated chromatographically by passing the hydrolyzed sample through a column filled with XAD resin (Stafford, et al. 1988).

Stable isotope data were obtained at the Yale Analytical and Stable Isotope Center, the University of Cincinnati’s Stable Isotope Laboratory, and the University of

New Mexico’s Center for Stable Isotopes (Dataset S1). Secondary standards from each lab were used to correct data using two-point normalization, and the mean accuracy of $\delta^{13}C$ and $\delta^{15}N$ measurements across runs was ≤0.3‰. Standard quality assurance data indicate that the mean precision of $\delta^{13}C$ and $\delta^{15}N$ measurements across runs was ≤0.3‰ and ≤0.2‰, respectively.

We confirmed sample quality and collagen preservation using percent collagen yield, atomic C:N, $\delta^{13}C$ values, and $\delta^{15}N$ values prior to AMS ^{14}C measurement (Beaumont, et al. 2010; DeNiro 1985; D. Kennett, et al. 2017; Van Klinken 1999). Residual contaminants can have distinct C:N and stable isotope values, and this was the case for one sample (a dog from Rezoky, sample ID “615,” which was not dated and not further considered; see Dataset S1). We graphitized collagen from the remaining 30 subfossil specimens at PSU and submitted graphite for ^{14}C analysis at the Pennsylvania State University AMS facility and UC Irvine’s W.M. Keck Carbon Cycle AMS (Dataset S1).

Data Analysis

We calibrated radiocarbon dates in OxCal 4.4 using the Southern Hemisphere calibration curve SHCal20 (Hogg, et al. 2020), or the post-bomb atmospheric SH3 curve (Hua, et al. 2013) for three dogs that yielded $>^{14}C$ modern ages (Dataset S1). We used both classical frequentist and Bayesian statistical approaches to event estimation to compare estimated times of dog introduction and lemur extinctions (Bradshaw, et al. 2012; Buck and Bard 2007).

Our Bayesian approach starts with the assumption that dateable material was deposited uniformly during the past several thousand years. This assumption is conservative and underestimates the true degree of temporal overlap between introduced and extinct taxa. Extinctions actually involve a period of declining population (and decreasing rate of deposition), while introductions tend to involve a period of expanding population (and increasing rate of deposition). Both approaches produce confidence/credible intervals for extinction and introduction events. Note that, in the case of an extinction event, the Bayesian credible interval represents the posterior probability that a species is extinct at a certain time given that it was not sampled, while the extinction confidence interval produced through the classical approach reflects the probability that a species was not sampled at a certain time because it was no longer present. We used the package "rcarbon" in R to create summed probability distributions for calibrated dates from extinct and extant fauna, and each distribution was normalized such that it integrates to one (Crema and Bevan 2020). Note that all confidence/credible intervals for event estimation are sensitive to outliers (such as rare late occurrence data), and numerous historical accounts suggest that relict populations of extinct species may have survived until recent centuries (Burney and Ramilisonina 1998; Flacourt 1995; Godfrey 1986; Nomenjanahary, et al. in press).

We follow the approach of Crowley and Godfrey (2013) to correct collagen $\delta^{13}C$ values for the Suess effect (recent enrichment of atmospheric CO_2 in ^{13}C due to the burning of fossil fuel). Specifically, we made modern and subfossil collagen $\delta^{13}C$ values comparable by adding 0.004‰ to modern data for each year that passed from 1860 to 1965 AD and 0.02‰ for each year that passed from 1965 to the time of death (if known) or sample collection (2019 most recently).

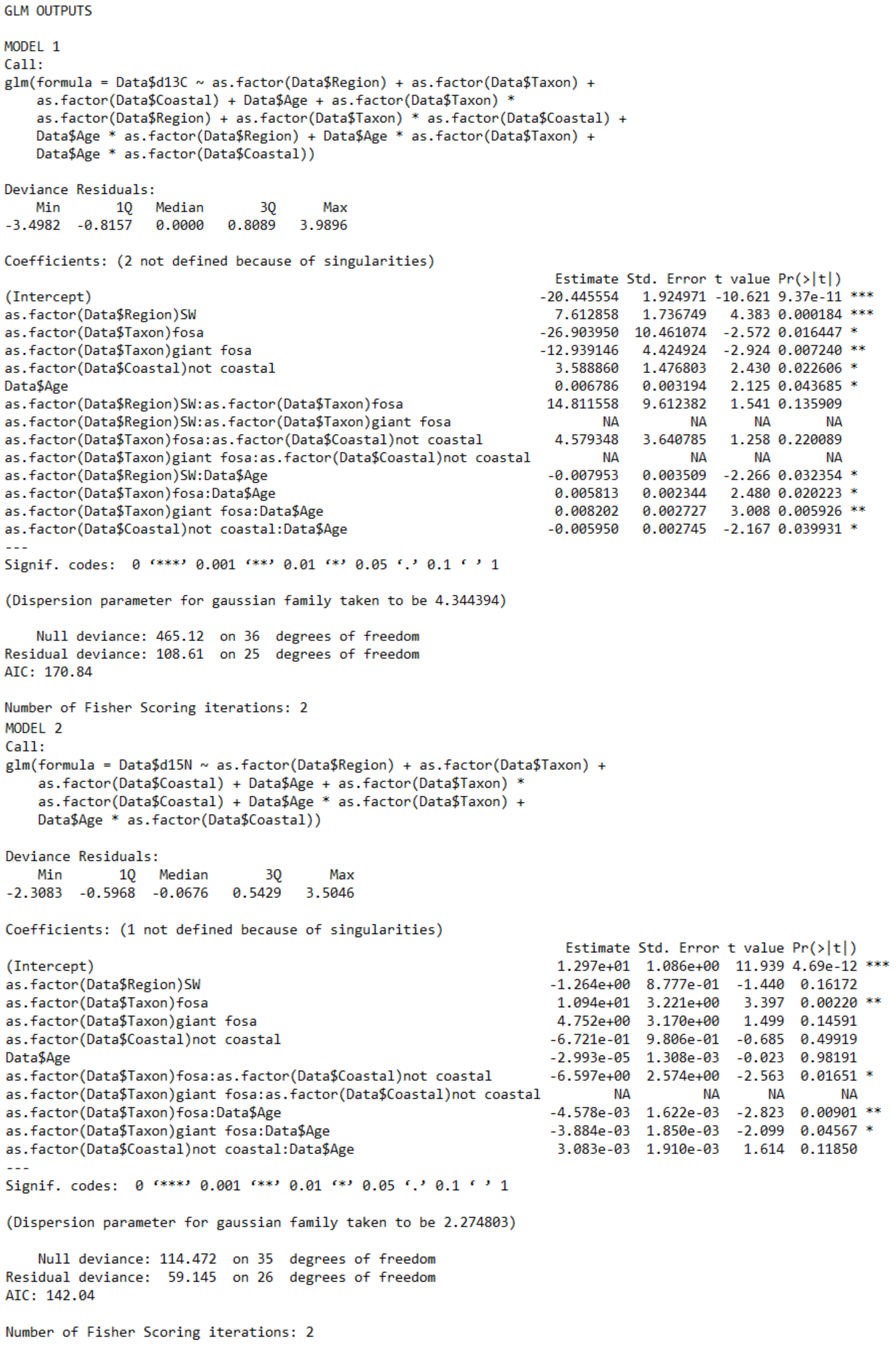
We used general linear models (GLMs, R package "glmulti," Calcagno and de Mazancourt 2010) with corrected data to identify which variables drive variation in predator $\delta^{13}C$ and $\delta^{15}N$ values (i.e. taxon, time, and location, Tables 1-2). Sites with data from both dogs and *Cryptoprocta* spp. (Fig. 3, Andolonomby, Tsirave, and Ampasambazimba) are ideal for stable isotope comparisons. For example, Tsirave dog and *C. ferox* δ^{15}N values are comparable (dog $n = 4$, $\bar{x} = 10.6$‰, *C. ferox* $n = 3$, $\bar{x} = 11.5$‰), yet Tsirave dog δ^{13}C values ($n = 4$, $\bar{x} = -9.4$‰) tend to be ~10‰ higher than *C. ferox* δ^{13}C values from this site ($n = 3$, $\bar{x} = -19.6$‰). Unfortunately, most sites include data from less than five specimens. Given limited site-specific sample sizes, we classified site location of dogs, *C. ferox,* and *C. spelea* according to coastal proximity and ecoregion. We defined coastal sites as those ≤10 km from the coast and inland sites as those >10 km from the coast.

We simplified ecoregion data into two groups: SW Madagascar (including the spiny thicket and succulent woodland), and North-Central Madagascar (including the dry deciduous forest and central highlands). We combined data from the spiny thicket and succulent woodland ecoregions because they have similar climate and are both dominated by relatively xerophytic vegetation. Plants and animals from these two ecoregions have similar δ^{13}C and δ^{15}N values, and are isotopically distinct from those of the relatively mesic central highlands and humid forest (Crowley, et al. 2011). For similar reasons, we combine the single dog from the dry deciduous forest (PSUAMS 7663 from Lakato'ni Gavin in the far north) with the group from the central highlands. Note that only in our GLMs do we consider the limited stable isotope dataset for predators from North-Central Madagascar ($n = 5$). The rest of our analyses are focused exclusively on the SW.

Table 1. Description of linear models discussed in text. See Table 2 for model outputs. Within each dataset, glmulti considers all possible models and ranks them according to an information criterion (AIC in our case, Lamberton 1934). The model-averaged importance of each term (e.g., “Taxon”) within each model (e.g., “Model 1”) reflects the support of the variable across all possible versions of the given model. These importance values range between 0.2 and 1.0 in our case and are given in corresponding cells. In our case, only terms with model-averaged importance of about 0.4 or greater contribute to best fit models (which include the only the shaded terms).

Model Terms	**Model 1** **Predator $\delta^{13}C$** **(AIC = 170.84)**	**Model 2** **Predator $\delta^{15}N$** **(AIC = 142.04)**
Taxon	1.0	1.0
Region	1.0	0.6
Coastal proximity	0.8	1.0
Age	0.9	0.8
Taxon×Age	0.7	0.6
Region×Age	0.6	0.2
Coastal proximity×Age	0.6	0.4
Region×Coastal Proximity	0.4	0.2
Region×Taxon	0.5	0.2
Coastal proximity×Taxon	0.4	0.8

Table 2. Outputs of general linear models that are described in Table 1 and analyzed in R 4.0.0.



```
GLM OUTPUTS

MODEL 1
Call:
glm(formula = Data$d13C ~ as.factor(Data$Region) + as.factor(Data$Taxon) + 
    as.factor(Data$Coastal) + Data$Age + as.factor(Data$Taxon) * 
    as.factor(Data$Region) + as.factor(Data$Taxon) * as.factor(Data$Coastal) + 
    Data$Age * as.factor(Data$Region) + Data$Age * as.factor(Data$Taxon) + 
    Data$Age * as.factor(Data$Coastal))

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-3.4982  -0.8157   0.0000   0.8089   3.9896  

Coefficients: (2 not defined because of singularities)
                                                                     Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                        -20.445554   1.924971 -10.621 9.37e-11 ***
as.factor(Data$Region)SW                                             7.612858   1.736749   4.383 0.000184 ***
as.factor(Data$Taxon)fosa                                          -26.903950  10.461074  -2.572 0.016447 *  
as.factor(Data$Taxon)giant fosa                                    -12.939146   4.424924  -2.924 0.007240 ** 
as.factor(Data$Coastal)not coastal                                   3.588860   1.476803   2.430 0.022606 *  
Data$Age                                                             0.006786   0.003194   2.125 0.043685 *  
as.factor(Data$Region)SW:as.factor(Data$Taxon)fosa                  14.811558   9.612382   1.541 0.135909    
as.factor(Data$Region)SW:as.factor(Data$Taxon)giant fosa                   NA         NA      NA       NA    
as.factor(Data$Taxon)fosa:as.factor(Data$Coastal)not coastal         4.579348   3.640785   1.258 0.220089    
as.factor(Data$Taxon)giant fosa:as.factor(Data$Coastal)not coastal         NA         NA      NA       NA    
as.factor(Data$Region)SW:Data$Age                                   -0.007953   0.003509  -2.266 0.032354 *  
as.factor(Data$Taxon)fosa:Data$Age                                   0.005813   0.002344   2.480 0.020223 *  
as.factor(Data$Taxon)giant fosa:Data$Age                             0.008202   0.002727   3.008 0.005926 ** 
as.factor(Data$Coastal)not coastal:Data$Age                         -0.005950   0.002745  -2.167 0.039931 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 4.344394)

    Null deviance: 465.12  on 36  degrees of freedom
Residual deviance: 108.61  on 25  degrees of freedom
AIC: 170.84

Number of Fisher Scoring iterations: 2
MODEL 2
Call:
glm(formula = Data$d15N ~ as.factor(Data$Region) + as.factor(Data$Taxon) + 
    as.factor(Data$Coastal) + Data$Age + as.factor(Data$Taxon) * 
    as.factor(Data$Coastal) + Data$Age * as.factor(Data$Taxon) + 
    Data$Age * as.factor(Data$Coastal))

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-2.3083  -0.5968  -0.0676   0.5429   3.5046  

Coefficients: (1 not defined because of singularities)
                                                                     Estimate Std. Error t value Pr(>|t|)    
(Intercept)                                                         1.297e+01  1.086e+00  11.939 4.69e-12 ***
as.factor(Data$Region)SW                                           -1.264e+00  8.777e-01  -1.440  0.16172    
as.factor(Data$Taxon)fosa                                           1.094e+01  3.221e+00   3.397  0.00220 ** 
as.factor(Data$Taxon)giant fosa                                     4.752e+00  3.170e+00   1.499  0.14591    
as.factor(Data$Coastal)not coastal                                 -6.721e-01  9.806e-01  -0.685  0.49919    
Data$Age                                                           -2.993e-05  1.308e-03  -0.023  0.98191    
as.factor(Data$Taxon)fosa:as.factor(Data$Coastal)not coastal       -6.597e+00  2.574e+00  -2.563  0.01651 *  
as.factor(Data$Taxon)giant fosa:as.factor(Data$Coastal)not coastal         NA         NA      NA       NA    
as.factor(Data$Taxon)fosa:Data$Age                                 -4.578e-03  1.622e-03  -2.823  0.00901 ** 
as.factor(Data$Taxon)giant fosa:Data$Age                           -3.884e-03  1.850e-03  -2.099  0.04567 *  
as.factor(Data$Coastal)not coastal:Data$Age                         3.083e-03  1.910e-03   1.614  0.11850    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.274803)

    Null deviance: 114.472  on 35  degrees of freedom
Residual deviance:  59.145  on 26  degrees of freedom
AIC: 142.04

Number of Fisher Scoring iterations: 2
```

We also compared $\delta^{13}C$ and $\delta^{15}N$ values for dogs from archaeological and paleontological sites in inland SW Madagascar using t-tests. Sample sizes in these comparisons are small (archaeological n = 5, paleontological n = 6), but neither $\delta^{13}C$ nor $\delta^{15}N$ values within these groups violate the t-test assumptions of normality (Shapiro-Wilk $p \geq 0.06$) or equal variance (Brown-Forsythe $p \geq 0.23$).

Uneven sampling of individuals through space and time influences the observed variance in stable isotope values for dogs and *Cryptoprocta* spp. We used Stable Isotope Bayesian Ellipses in R (SIBER) to visually inspect the breadth of $\delta^{13}C$ and $\delta^{15}N$ data from SW Madagascar (combining spiny thicket and succulent woodland) and also compare isotopic overlap between predator genera in a way that is unbiased by sample size (Jackson, et al. 2011). We consider both standard ellipse areas (SEAs, which contain ~40% of the data from each group) and ellipses that include 95% of the data from each group. Because our sample of *C. spelea* includes fewer than the recommended five specimens, we combined data from *C. spelea* and *C. ferox*. We feel this is reasonable because, within SW Madagascar, the two species have indistinguishable $\delta^{15}N$ values (Fig. 6, *C. spelea* n = 3, m = 14.0‰; *C. ferox* $\delta^{15}N$ value: n = 9, m = 13.9‰, Mann-Whitney U = 12.00; p = 0.85), and $\delta^{13}C$ values (*C. spelea* n = 3, m = −19.3‰; *C. ferox* n = 10, m = −18.6‰, Mann-Whitney U = 8.50, p = 0.31). Note that the similar stable isotope values of *C. spelea* and *C. ferox* do not exclude the possibility that these species preyed on different taxa that were isotopically similar. Before analysis with SIBER, we used Shapiro-Wilk tests to confirm that *Cryptoprocta* spp. and dog $\delta^{13}C$ and $\delta^{15}N$ values from SW Madagascar are normally distributed ($p \geq 0.67$).

Lastly, we plotted stable isotope data from predators and potential prey from SW Madagascar on the same graph to visually assess the potential for different patterns of predation. In this graph, we shifted predator $\delta^{13}C$ and $\delta^{15}N$ values by −0.5‰ and −3‰, respectively, to account for estimated offsets in stable isotope values between trophic levels (McCutchan, et al. 2003), and we grouped prey species at different taxonomic levels (family and above). Large, species-specific lemur datasets are grouped according to family due to relatively similar isotopic niche spaces occupied by different species. We use higher level classification for other prey types (e.g., all birds grouped in Aves) due to limited sample sizes.

D. Results

Chronological Data

Directly ^{14}C-dated bones suggest a brief period of overlap between dogs and extinct giant lemurs in SW Madagascar and that dogs could have been present at kill sites during times that humans butchered extinct megafauna and an extant lemur (*Propithecus verreauxi*). Limited sample sizes prevent us from meaningfully considering differences in introduction and extinction timing in different ecoregions. However, our results suggest that dogs were widespread on Madagascar by ~900 calibrated years before present (cal BP, Fig. 4). The oldest ^{14}C-dated dog comes from the far northern archaeological site of Lakato'ni Gavin (Fig. 3, PSUAMS 7663, 1035 ± 15 ^{14}C BP, 960-810 cal BP) and is roughly contemporaneous with a dog from the archaeological site of Andranosoa in the far south (PSUAMS 7623, 1010 ± 15 ^{14}C BP, 930-800 cal BP). The calibrated 95% age ranges of these two individuals overlap with those of five subfossil butchered extant lemurs (*Propithecus verreauxi*) from Taolambiby and with the three youngest ^{14}C-dated extinct giant ruffed lemurs (*Pachylemur insignis*) from Tsirave (Fig. 5). The youngest dated *P. insignis* from Tsirave (UCIAMS 167930, 940 ± 20 ^{14}C BP, 900-740 cal BP) postdates the two earliest dogs by less than a century, and predates the oldest dog from Tsirave by ca. 80 years (CAMS 142889, 860 ± 30 ^{14}C BP, 790-670 cal BP).

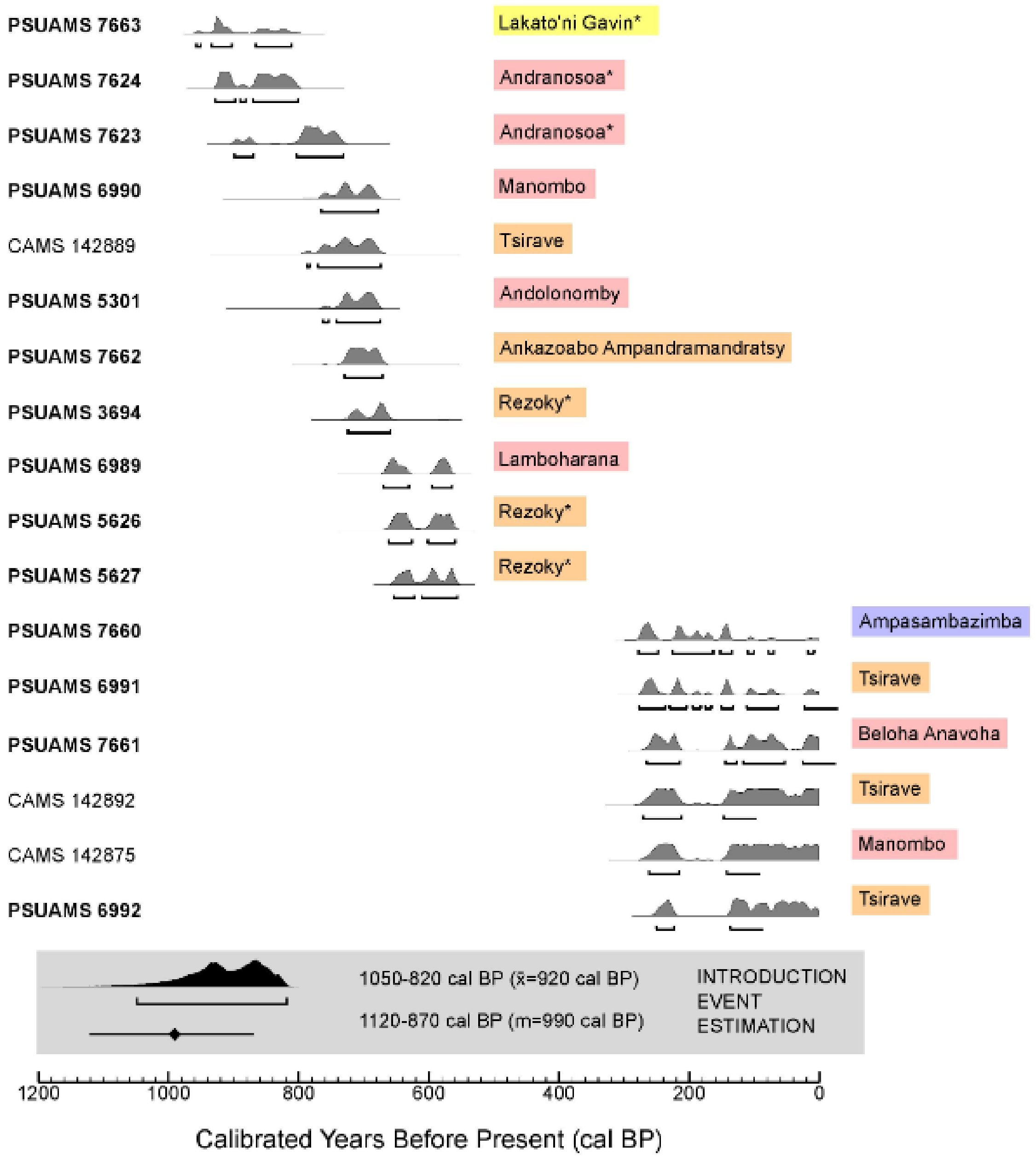


Figure 4. Dog collagen ^{14}C dates calibrated in OxCal 4.4 with SHCal 20 (Hogg, et al. 2020). Previously unpublished dates are bolded, sites are colored according to ecoregion (red = spiny thicket, orange = succulent woodland, blue = central highlands, yellow = dry deciduous forest), and archaeological sites are marked with asterisks. Shaded box includes results from two approaches to introduction event estimation: The bracket under the Bayesian posterior probability distribution spans 95.5% of the distribution, and the

diamond and associated line marks the median and 95% confidence interval estimate from the classical frequentist approach.

Conservative estimates for SW Madagascar suggest the introduction of dogs (approximately 1,000 years ago) roughly coincided with the population collapse and possible extinction of *Palaeopropithecus ingens*, *Archaeolemur majori*, and *P. insignis* (between about 1100 and 700 cal BP; Fig. 5). The classical 95% confidence interval for dog introduction (1120-870 cal BP) also overlaps with the calibrated 95% age ranges for all 26 of the dated butchered bones in Fig. 5. These include bones of extant *P. verreauxi* (n = 15), as well as extinct giant lemurs (*P. insignis* [n = 7] and *A. majori* [n = 1]), elephant birds (*Aepyornis maximus* [n = 1] and *Mullerornis modestus* [n =1]), and a pygmy hippo (*Hippopotamus* sp. [n = 1]).

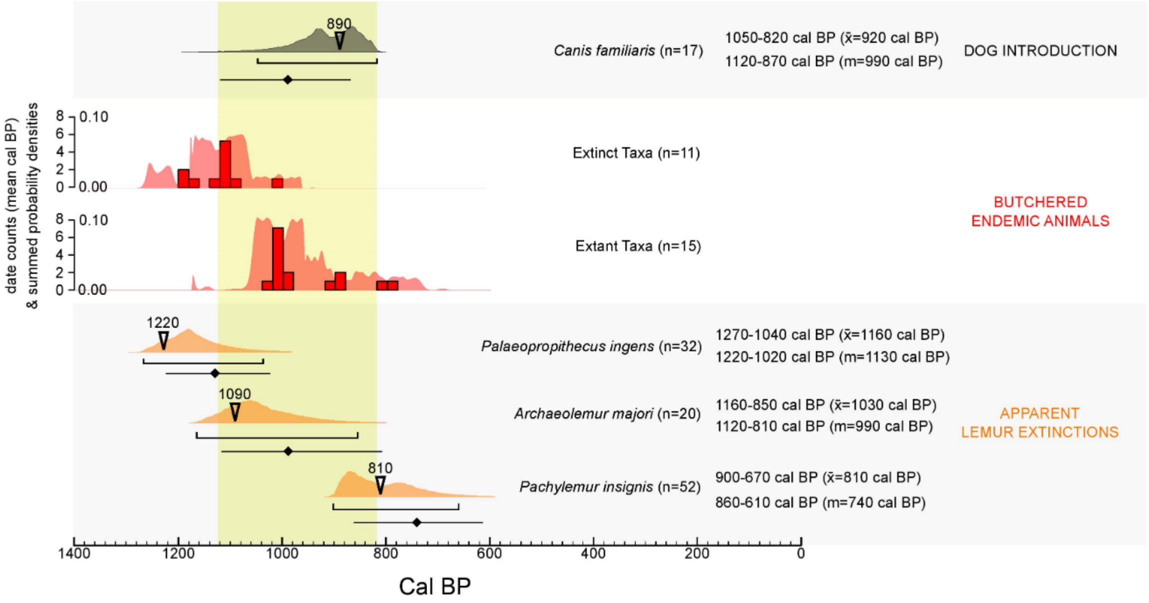


Figure 5. Dog introduction event estimate compared to dates from butchered endemic animal bone and giant lemur extinction event estimation. Numbered arrowheads mark the mean calibrated date from the oldest recognized dog and youngest recognized giant lemur belonging to each taxon. See Fig. 4 for explanation of confidence intervals for event estimation. Note that extinction confidence intervals consider only data from purified collagen. Dates from butchered animal bone are binned in 20-year intervals (saturated color) and are also displayed through summed probability distribution overlays (unsaturated color). Butchered extinct taxa represented in the histogram include

Pachylemur insignis, *Archaeolemur majori*, *Hippopotamus* sp., *Aepyornis maximus*, and *Mullerornis modestus*. All of these taxa disappear from the subfossil record by ~800 cal BP (Crowley 2010). Butchered extant taxa in the histogram include only *P. verreauxi*.

Stable Isotope Data

Predator collagen $\delta^{13}C$ and $\delta^{15}N$ values suggest dietary flexibility for dogs and some limited dietary overlap between *Cryptoprocta* spp. and dogs (Fig. 6, Table 3). All included predictor variables (i.e., taxon, ecoregion, coastal proximity, and time) contribute to the best fit GLMs (Table 1) that explain variation in predator $\delta^{13}C$ values (Model 1, n = 37, AIC = 170.84) and $\delta^{15}N$ values (Model 2, n = 36, AIC = 142.04). Model 1 suggests that both *C. spelea* and *C. ferox* had low $\delta^{13}C$ values relative to dogs (Table 2, p = 0.007 and p = 0.02, respectively). It also suggests that predator $\delta^{13}C$ values in general tend to be relatively high in SW Madagascar (p = 0.0002) and that they also tend to be higher at coastal sites (p = 0.02). Overall, predator $\delta^{13}C$ values may have decreased through time (Model 1 p = 0.04, Fig. 7), primarily among the three *C. spelea* (p = 0.006). However, the model also suggests that combined predator $\delta^{13}C$ increased through time both in SW Madagascar (p = 0.03) and at inland sites island-wide (p = 0.04). Model 2 suggests that *C. ferox* have high $\delta^{15}N$ values relative to dogs (Table 2, p = 0.002) and that *C. ferox* from coastal sites tend to have higher $\delta^{15}N$ values than those from inland sites (p = 0.02). It also suggests that both *C. spelea* and *C. ferox* $\delta^{15}N$ values increased through time (p = 0.05 and p = 0.009, respectively, Fig. 7).

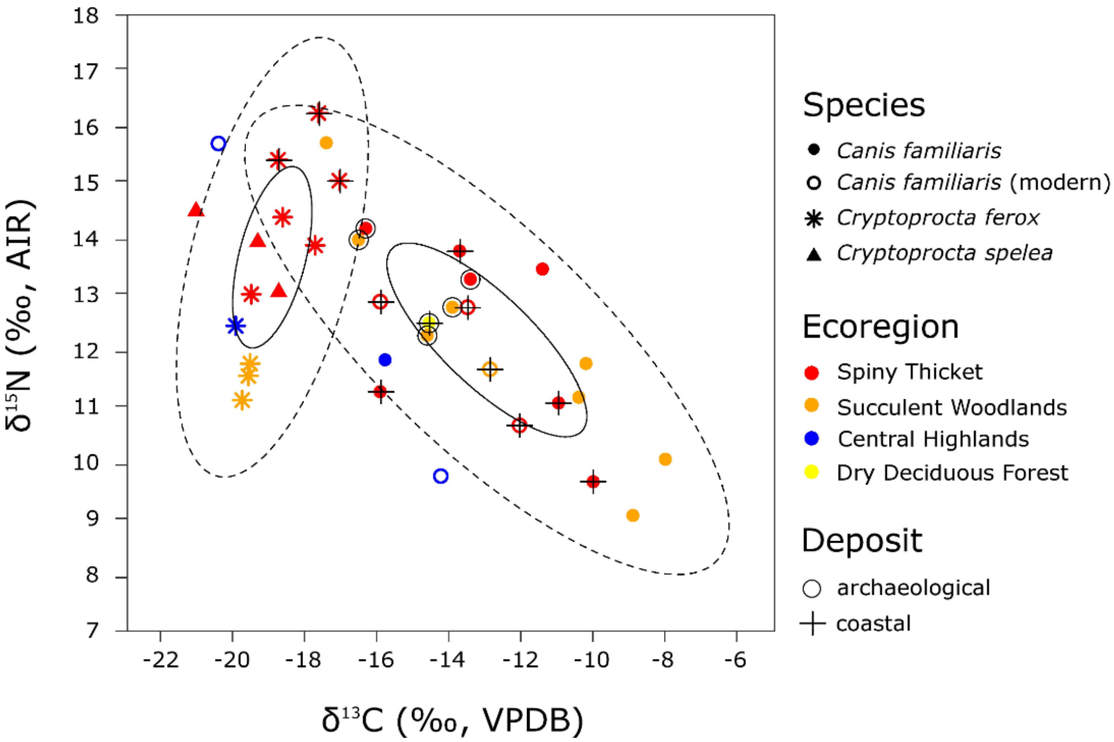


Figure 6. Stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil), with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type (n=36). For each genus, ellipses outline approximately 95% of the data (dashed) and 40% of the data (solid) from only the SW ecoregions (spiny thicket and succulent woodlands, *Canis* n=19, *Cryptoprocta* n=12). Island-wide, average calibrated dates for *C. spelea* specimens (n=3) range from 3280 to 1760 cal BP, those for *C. ferox* (n=10) range from 2900 to 1010 cal BP, and those for *C. familiaris* (n=23) span from 890 cal BP to the present. The six modern dogs have δ^{13}C values that are corrected for the Suess Effect (following Crowley and Godfrey 2013) so that they are comparable with subfossil collagen values.

Table 3. Descriptive statistics for island-wide *Canis familiaris* and *Cryptoprocta* spp. δ^{13}C, δ^{15}N, and age data. Note that the range within each group includes both spatial and temporal variability (Figs. 6 & 7), and the δ^{13}C values for the six modern dogs were corrected for the Suess Effect (following Crowley and Godfrey 2013) so that they are comparable with subfossil collagen values.

	Taxon	n	x̄	SD	range	[min,max]
δ^{13}C (‰, VPDB)						
	Canis familiaris	23	−13.5	3.0	12.4	[−20.4,−8.0]
	Cryptoprocta spp.	14	−18.9	1.1	4.0	[−21.0,−17.0]
δ^{15}N (‰, AIR)						
	Canis familiaris	23	12.3	1.8	6.6	[9.1,15.7]
	Cryptoprocta spp.	13	13.6	1.6	5.1	[11.2,16.3]
Age (mean cal BP)						
	Canis familiaris	23	NA	NA	959	[890, −69]
	Cryptoprocta spp.	14	NA	NA	2280	[3280,1000]

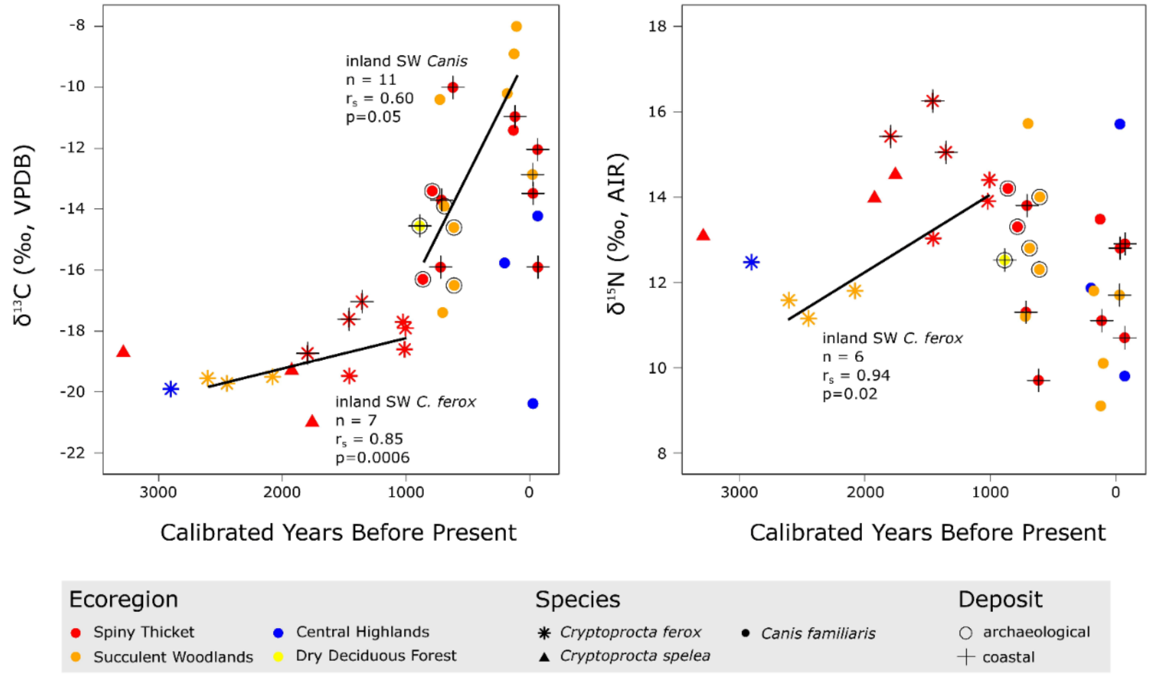


Figure 7. Temporal trends in stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil), with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type (δ^{13}C n=37, δ^{15}N n=36). The six modern dogs have δ^{13}C values that are corrected for the Suess Effect (following Crowley and Godfrey 2013) so that they are comparable with subfossil collagen values. Trend lines illustrate the only significant temporal trends when controlling for region and coastal proximity: In inland SW Madagascar (including both spiny thicket and succulent woodlands), dog and *C. ferox* δ^{13}C values and *C. ferox* δ^{15}N values significantly increased through time, yet these trends could be explained by uneven sampling across archaeological versus paleontological deposits in the case of dogs or by uneven sampling between the spiny thicket and succulent woodlands in the case of *C. ferox*.

Standard ellipse areas (SEAs which encompass 40% of a group's data) are nearly twice as large for dogs (9.6‰^{2}) as they are for *Cryptoprocta* spp. in SW Madagascar (5.2‰^{2}; Fig. 6). While the SEAs do not overlap, ellipses that contain ~95% of the data from each group do overlap (Fig. 6). The area of overlap between the 95% ellipses accounts for ~34% of the isotopic niche space of *Cryptoprocta* spp. but only ~16% of the isotopic niche space of dogs. Samples of dog and *Cryptoprocta* spp. bones integrate different amounts of time and space, but these variables alone cannot explain the relatively large isotopic niche space occupied by dogs. Specifically, the range of dates for

Cryptoprocta spp. is about twice as great as that for dogs (Fig. 7). Also, although dogs from SW Madagascar come from a greater number of sites than *Cryptoprocta* spp. (n = 8 vs. n = 4), these sites represent similar geographical spread and include both inland and coastal sites (Fig. 3).

Dogs generally tend to have higher δ^{13}C values and lower δ^{15}N values than *Cryptoprocta* spp., but dogs from inland archaeological sites in SW Madagascar (Rezoky & Andranosoa) tend to have δ^{13}C and δ^{15}N values that are relatively comparable with those of *Cryptoprocta* spp. (Figs. 6-7). Specifically, the mean (±1 SD) δ^{13}C value for dogs from inland archaeological sites in SW Madagascar ($n = 5$, $\bar{x} = -14.9 \pm 1.4$‰) is significantly lower than the mean value for dogs from inland paleontological sites in this region ($n = 6$, $\bar{x} = -11.1 \pm 3.3$‰, $t(9) = 2.42$, $p = 0.04$). However, limited sample sizes and limited contemporary samples from archaeological and paleontological sites may confound this comparison, since dog δ^{13}C values across inland SW sites significantly increased during the past millennium ($n = 11$, $r_{\text{Spearman}} = 0.60$, $p = 0.05$, Fig. 7). Additionally, the mean δ^{15}N value for dog collagen from archaeological sites in this region ($n = 5$, $\bar{x} = 13.3 \pm 0.8$‰) is apparently, yet insignificantly, higher than the mean value for dogs from inland paleontological sites ($n = 6$, $\bar{x} = 11.9 \pm 2.4$‰, $t(9)=1.26$, $p=0.24$).

E. Discussion

Brief overlap in directly-dated introduced dogs and extinct megafauna means that we cannot reject the hypothesis that humans hunted giant lemurs and possibly other megafauna with dogs at least ~1,000 years ago. Dogs have had diverse diets that are largely distinct from *Cryptoprocta* spp. diets and include only minor inputs from forest-dwelling species, which is inconsistent with the hypothesis that dogs competed with

Cryptoprocta spp. (Figs. 6 and 8). Nevertheless, given their highly generalized diets, dogs may very well have contributed to interference competition with endemic predators.

The introduction of dogs coincided with expanding human presence on Madagascar, which included the significant growth and movement of Malagasy populations (Pierron, et al. 2017), the rise of the island's earliest urban center (Radimilahy 1998), and the expansion of trade along the west coast of the island (Boivin, et al. 2013; Dewar and Wright 1993). Early trade connections between East Africa and Madagascar (as attested by the exchange of ceramics and other resources) help explain the primarily African ancestry of Madagascar's dogs (Ardalan, et al. 2015). However, given that the earliest directly ^{14}C-dated dog (from Lakato'ni Gavin) slightly preceded the appearance of SE Asian rice and cotton in the region (Crowther, et al. 2016), the potential for multiple past dog introductions (associated with the movement of crops from SE Asia or with the movement of other domesticated animals from E Africa) should be considered through analysis of ancient DNA, if possible.

Early introduced dogs could have aided past human-led hunts of extant lemurs like *P. verreauxi* and megafauna that went extinct within the past millennium (Crowley 2010; Hixon, et al. accepted), but isotope data suggest that these kills did not form the bulk of dog diet (Fig. 8). Most extinct megafauna browsed woody C_3 vegetation (Crowley, et al. Accepted; Crowley and Samonds 2013; Godfrey and Crowley 2016; Hixon, et al. accepted). A modern dog from Antsirabe does have an exceptionally low δ^{13}C value (−20.4‰) and relatively high δ^{15}N value (15.7‰), which may indicate that it relied heavily on forest bushmeat. However, the wide range of dog δ^{13}C values likely reflects a continuum of reliance on agropastoralist-supplied foods (based on C_4 or CAM plants), which is also observed in modern free-roaming dogs (Valenta, et al. 2016).

Consumption of scraps from butchered grazing livestock (e.g., zebu cattle) could have contributed to relatively high dog $\delta^{13}C$ values (Fig. 8), particularly at archaeological sites that include bones of dogs as well as livestock (Hixon, et al. accepted; Rasamuel 1984; Vérin and Battistini 1971). However, rather counterintuitively, dogs from inland archaeological sites in the arid SW tend to have lower $\delta^{13}C$ values than those from inland paleontological sites where they were less likely to be associated with pastoralists. The relatively low $\delta^{13}C$ values of dogs from archaeological sites could be explained by reliance on provisioned scraps from crops or ovicaprids that browsed on a wide range of vegetation (Hixon, et al. accepted) or from endemic, forest-dwelling game hunted by humans in forests dominated by C_3 plants (Fig. 8, Decary 1939). Archaeological bone deposits in SW Madagascar tend to be highly fragmentary and may include traces of scavenging (Douglass, et al. 2018; Vérin and Battistini 1971). There are abundant marks of mammalian carnivoran predation and scavenging on the bones of extinct giant lemurs at paleontological sites (Meador, et al. 2019, also at Taolambiby, Clark, pers. comm.), and the possibility that both *Cryptoprocta* spp. and dogs contributed to these patterns of gnaw marks on relatively recent bones cannot be excluded.

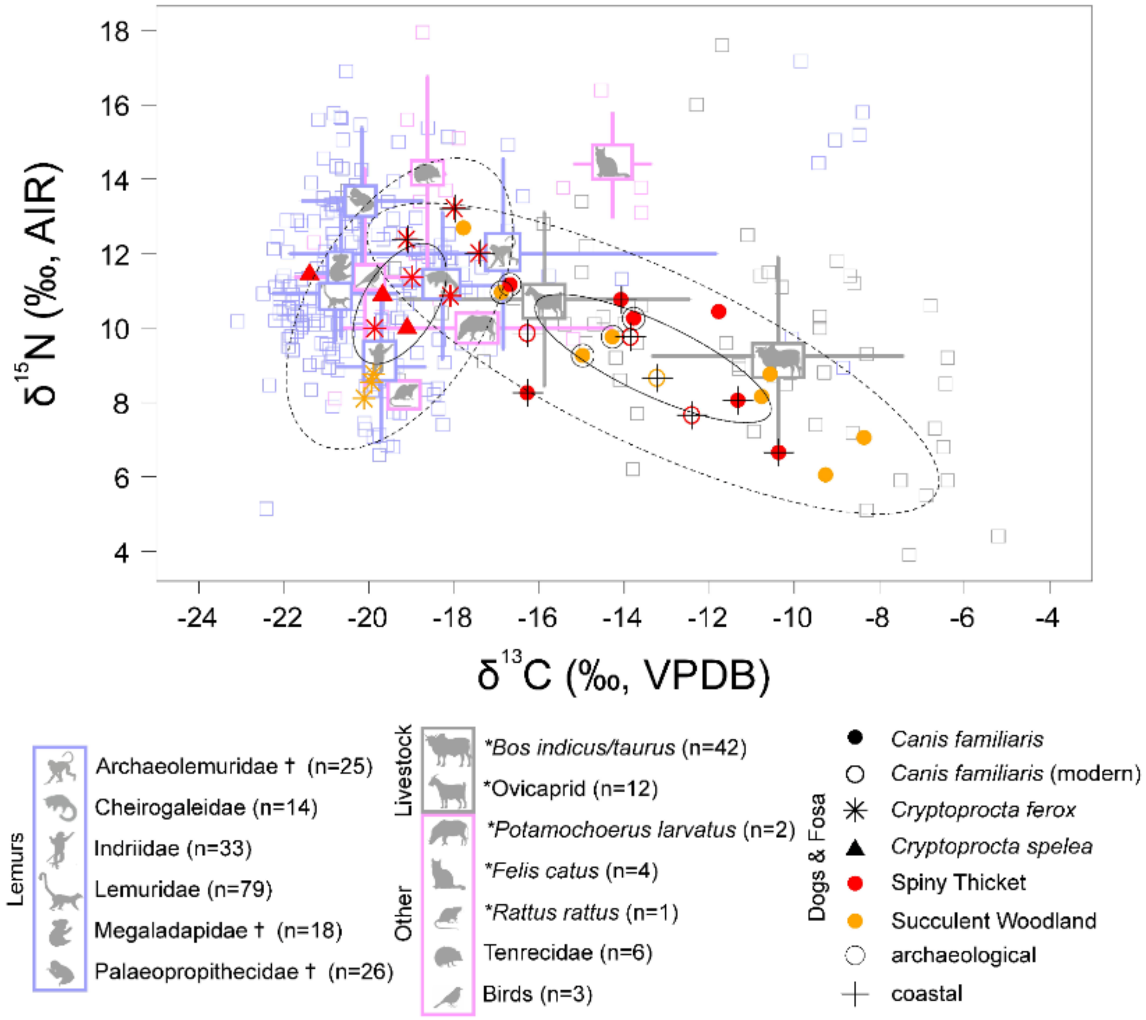


Figure 8. Stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil) collected in SW Madagascar, with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type (n=36, see Fig. 5 explanation of ellipses fitted to dog and *Cryptoprocta* spp. data). Stable isotope data from the bone collagen of lemurs, livestock, and other animals collected in SW Madagascar are plotted for reference, with icons marking means and lines marking standard deviations in $\delta^{13}C$ and $\delta^{15}N$ values. Note that extinct families of giant lemurs are marked with (†), introduced taxa are marked with (*), and modern individuals (including six modern dogs) have $\delta^{13}C$ values that are corrected for the Suess Effect (following Crowley and Godfrey 2013) so that they are comparable with subfossil collagen values. Also note that dog and *Cryptoprocta* spp. $\delta^{13}C$ and $\delta^{15}N$ values are shifted by −0.5‰ and −3‰, respectively, to account for estimated offsets in stable isotope values between trophic levels (McCutchan, et al. 2003). Thus, the dog and *Cryptoprocta* spp. points approximate the isotopic composition of their diet.

Past exploitation competition between dogs and *Cryptoprocta* spp. seems unlikely given that isotope data suggest ancient *Cryptoprocta* spp. consumed mostly forest dwelling animals (e.g., lemurs), while dogs have relied more heavily on prey from relatively open habitats (e.g., scraps from the food of agropastoral communities). Dogs may be replacing endemic predators around human communities today (Farris, et al. 2016), but the distinct diets of dogs and *Cryptoprocta* spp. suggest that dogs are not fulfilling the ecological role of *Cryptoprocta* spp. In particular, the distinct isotopic niches of dogs and *Cryptoprocta* spp. suggest that any past antagonistic relationship between these predators did not follow from predation or competition for shared prey. Instead, dogs could have antagonized *Cryptoprocta* spp. through exclusion competition by chasing shared prey, creating a landscape of fear, and thus contributing to habitat fragmentation (Laundré, et al. 2010). The directly ^{14}C-dated subfossil record for *C. spelea* is sparse (n=3), yet recent accounts of what may be *C. spelea* still living in the far north of Madagascar (Nomenjanahary, et al. in press) suggest that there may be a history of interaction between dogs and *C. spelea*. Dogs may occasionally prey on *C. ferox* (Valenta, et al. 2016), yet comparable δ^{15}N values for dogs and *C. ferox* suggest that dogs have not routinely consumed endemic predators, such as *C. ferox*, or other introduced predators, such as cats, during the past millennium (Fig. 8). The observation that dogs rarely prey on cats is consistent with the modern observation that both exotic predators are often simultaneously abundant (Farris, et al. 2014).

Although there was limited dietary overlap between *C. ferox* and dogs ~1,000 years ago, this may have expanded during the past millennium as *C. ferox* came into more frequent contact with human modified landscapes that tend to have higher plant and animal δ^{13}C values. Palynological and geochemical records from much of Madagascar document the expansion of grasslands favored by livestock and dogs during the past millennium (Burney 1987; Burns, et al. 2016; Crowley and Samonds 2013; Domic, et al. submitted; Virah-Sawmy, et al. 2016). Future stable isotope work with modern and subfossil *C. ferox* individuals that span the past millennium can test this possibility. *C. ferox* continues to hunt in shrinking forest fragments but may partly exploit the expanding anthropogenic niche, as documented in other taxa such as vervet monkeys (*Chlorocebus pygerythrus*) on mainland Africa (e.g., Loudon, et al. 2014). *Cryptoprocta ferox* is known to navigate deforested areas (Wyza, et al. 2020), and there are numerous recent accounts of *C. ferox* raiding poultry and controlling introduced rat populations (S. D. Merson, et al. 2019).

Ongoing efforts try to control dog populations, yet dogs are only part of the picture. A growing body of directly ^{14}C-dated specimens of introduced animals suggests that dogs became established on Madagascar at approximately the same time as introduced herbivores (zebu, sheep, and goats, Hixon et al., submitted) and at possibly the same time as cats (Sauther, et al. 2020). Genetic data from Madagascar's modern cats indicate that their ancestors colonized the island from the Arabian Sea region within the past millennium (Sauther, et al. 2020). Similar to dogs, cats are a successful invasive predator on numerous islands (Medina, et al. 2011; Nogales, et al. 2013). However, unlike dogs, cats may be a closer functional replacement for *Cryptoprocta* spp. since they also climb trees. Cats successfully prey on a large variety of endemic species on Madagascar (Brockman, et al. 2008; Merson 2017) and are difficult for endemic predators to avoid (Gerber, et al. 2012). Existing δ^{13}C data from four cats in SW Madagascar (Fig. 8) could suggest that they consumed different prey than *Cryptoprocta* spp., but the available sample size is quite small. Though cats are well-represented in archaeological deposits of ~1,000 years ago on the island of Mayotte (~330 km NW of Madagascar), subfossil felid remains are unfortunately very scarce in Madagascar’s paleontological and archaeological deposits (Chanudet 1975; Petit 1933). The analysis of additional cat remains would better clarify when cats arrived on Madagascar and how their diets compared to those of other predators.

Madagascar’s ecosystems continue to face new species introductions (e.g., Asian toads; Kolby 2014) and shifts in land use (e.g., cash cropping; Réau 2002) that threaten endemic biodiversity. The suite of past animal introductions that included dogs and livestock coincided with a pulse of megafaunal extinction and constituted an early turning point in Malagasy socio-ecological history. This situation is analogous to the colonization of Remote Oceania by people with a “transported landscape” that included dogs, pigs, rats, and chickens (Anderson 2009). During the brief co-occurrence of dogs, introduced livestock, and endemic megafauna on Madagascar, pastoralists both relied on their livestock and opportunistically hunted endemic animals (Rasamuel 1984; Vérin and Battistini 1971). Introduced animals compounded negative impacts of humans on endemic fauna. Livestock provided a reliable food supply for growing human populations (Pierron, et al. 2017), and we have shown here that dogs could have aided human-led hunts and contributed to habitat fragmentation during the past millennium. However, forest-dwelling endemic animals contributed relatively little to dog diet. The colonization of Madagascar by pastoralists and introduced predators likely had dramatic environmental consequences and formed what can be considered the first step in the biotic homogenization of the island.

IV. CH. 4: Drought coincided with, but does not explain, Late Holocene megafauna extinctions in SW Madagascar[3]

A. *Abstract*

Aridification is a major concern for agropastoralists in southern Madagascar, and past changes in moisture availability may have contributed to transformations of local ecosystems, which involved extinction of endemic megafauna during the past millennium. The mechanisms and geographic extent of aridification in SW Madagascar during the past 2000 years, however, are poorly known, as are the responses of endemic animals and economically important livestock to climate drying. We inferred climate change during the last ~1600 years around Lake Ranobe, SW Madagascar based on the oxygen isotope ($\delta^{18}O$) analysis of monospecific freshwater ostracods (*Bradleystrandesia* cf. *fuscata*) and elemental analyses of bulk and acidified sediment. We also characterized associated changes in habitat and diet of introduced and extinct endemic megaherbivores by using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses with directly ^{14}C-dated bones collected near the lake (n=63). The driest period of the past 1600 years (inferred from high sediment Ca/Zr values, scarce ostracods, and low sedimentation rate) coincided with the Medieval Climate Anomaly (~1000-700 cal BP), consistent with multi-millennial paleoclimate records from the Mascarene Islands and Indonesia. Extinct pygmy hippos and multiple giant lemur species (*Paleopropithecus ingens*, *Archaeolemur majori*, and *Megaladapis* spp.) disappeared from the vicinity of Lake Ranobe during this dry interval, but simultaneous appearance of introduced cattle (*Bos indicus/taurus*), peaks in charcoal, and other evidence of human activity confound inference of drought-driven

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[3] This chapter is in review for publication in *Climate*.

extirpations. Possible human settlement along the south shore of Lake Ranobe ~600 years ago occurred during one of the wettest intervals of the past millennium and may have coincided with an inland expansion of agropastoralists. Unlike the endemic megafauna, cattle may have been sensitive to drought, as their relatively low collagen $\delta^{15}N$ values during dry intervals of the past millennium suggest they survived by strategically exploiting patches of wet habitat. Positive correlations between aridity records derived from the Lake Ranobe sediment core and higher collagen $\delta^{13}C$ values in bones of pygmy hippos and cattle suggest the animals tracked vegetation changes by consuming more xerophytic C4 and CAM plants during dry times. Although megafaunal extirpations coincided with drought in SW Madagascar, coupled data from bone and lake sediments do not support the hypothesis that extinct megafauna populations collapsed solely due to drought.

B. Introduction

Water scarcity has left subsistence farmers and pastoralists in the grip of famine in southern Madagascar (Bhalla 2019), and climate change simulations suggest that the region will experience more periods of severe drought during the next century (Tadross, et al. 2008). Paired records of past climate change and biotic responses to such fluctuations can inform management plans designed to ensure human and ecosystem health. Ancient dunes and the diversity of endemic succulents attest to a long history of water scarcity in SW Madagascar, yet biotic responses to regional climate change during the ~2000-year human history on the island are poorly known. We provide historical context for the current drought by inferring changes in past water availability using geochemical measures (ostracod $\delta^{18}O$ and $\delta^{13}C$, sediment $\delta^{15}N$ and $\delta^{13}C$, %$CaCO_3$, heavy element abundance, magnetic susceptibility, and charcoal) from a ^{14}C-dated sediment core collected from Lake Ranobe (a shallow coastal pond) and by characterizing the responses of local endemic and introduced animals to past climate changes through analysis of purified bone collagen (^{14}C, δ^{13}C, and δ^{15}N).

Although perennial bodies of water exist in some artesian springs and pans in SW Madagascar (Vallet-Coulomb, et al. 2006), most surface fresh water in the area is ephemeral. The aridity of the region reflects an orographic rain shadow in the west and absence of the Intertropical Convergence Zone during the austral summer (Wells 2003). Oscillations in sea surface temperatures also affect Madagascar's climate through the Indian Ocean Dipole (IOD). Positive IOD states occur when westerly winds weaken and easterly winds sometimes form, which brings cold water to the surface in the eastern Indian Ocean and enables warm water and wet air masses to concentrate in the west, around Madagascar (Saji and Yamagata 2003). During the last deglaciation, SW Madagascar may have been wetter and warmer than present, with relatively dry periods associated with cooler sea surface temperatures and northward retreat of the tropical rain belt (Scroxton, et al. 2019). A paleohydrological record from Lac Ihotry (in the coastal plains ~100 km north of Ranobe) revealed a drying trend during the Late Holocene that involved a decline in the water table and salinization of coastal pans and wetlands (Vallet-Coulomb, et al. 2006). That record probably reflects, in part, a drop in relative sea level and coastal water tables (René Battistini 1971; Camoin, et al. 2004). However, a speleothem from Rodrigues Island recorded at least four megadroughts over the past 2000 years that likely also affected southern Madagascar (Li, et al. 2020), and a speleothem from SW Madagascar recorded a prolonged drought ~1000 years ago (Faina, et al. in press).

Lake Ranobe is a shallow (<3 m deep) closed basin ~20 meters above sea level, and its geochemistry was sensitive to regional aridification during the Late Holocene. The $\delta^{18}O$ values of subfossil ostracod shells (*Bradleystrandesia* cf. *fuscata*), supported by complementary lines of elemental data, serve as a proxy for the past ratio of evaporation to precipitation (E/P) around the lake. Whereas both temperature and the $\delta^{18}O$ value of lake water determine the $\delta^{18}O$ values in ostracod shell calcite, water temperature likely had little influence on shifts in our ostracod $\delta^{18}O$ record, because: 1) seasonal differences in temperature of freshwater bodies in the tropics are small; 2) ostracods may survive over multiple seasons, thereby integrating minor intra-annual differences in lake water $\delta^{18}O$; and 3) individual measurements of ostracod $\delta^{18}O$ were run on multiple individuals, thus integrating changes in lake water $\delta^{18}O$ over both seasons and years (Curtis, et al. 1996). Lake water $\delta^{18}O$ values were thus the primary influence on ostracod $\delta^{18}O$ values, and we assume that ostracods fractionate oxygen at T-dependent equilibrium with lake water. Lake water $\delta^{18}O$, in turn, is sensitive to integrated rainfall $\delta^{18}O$ and intensity of evaporation. Although average rainfall $\delta^{18}O$ values can differ by as much as 8‰ between wet and dry months in the central highlands of Madagascar (Antananarivo, IAEA GNIP Database), the arid SW part of the country receives rainfall almost entirely during a single wet season. Because the vapor pressure of $H_2{}^{16}O$ is greater than that of $H_2{}^{18}O$, evaporation causes preferential loss of $H_2{}^{16}O$ from the lake, with consequent ^{18}O enrichment in lake water and associated ostracod carbonates (Lloyd 1966). High E/P thus results in higher $\delta^{18}O$ values in ostracod shells, and, in extreme cases, promotes authigenic carbonate precipitation, which leads to higher $CaCO_3$ concentration and Ca/Zr ratios in lake sediment (Haberzettl, et al. 2007; Kylander, et al. 2011). Low E/P leads to lower $\delta^{18}O$ values in ostracod shells, and higher rainfall may be associated with greater erosion, higher magnetic susceptibility of the sediment, and greater abundance of mobile elements such as K (Aufgebauer, et al. 2012; Kylander, et al. 2011; Piva, et al. 2008).

Aridification favors drought-tolerant animals by limiting access to surface water and certain types of forage for less xeric-adapted animals. *Drought-sensitive* species move to areas that host a narrow range of suitable habitat and forage, whereas *drought-tolerant* species can exploit whatever habitat is most abundant, regardless of dryness (Fig. 1). Differential responses of herbivores to aridification can be tracked by considering how aspects of their niche vary across regional conditions. The long-term drought tolerance of recently-extinct endemic megafauna such as pygmy hippos (*Hippopotamus* spp.) and giant tortoises (*Aldabrachelys* spp.), as well as economically important, introduced zebu cattle (*Bos indicus/taurus*) are poorly known. Modern zebu herds browse in a wide range of habitats yet migrate seasonally to track freshwater resources and succulent fodder (Feldt and Schlecht 2016). Endemic megafauna may have been drought-tolerant given that they persisted through relatively severe Pleistocene climate fluctuations (Burney 1996; Godfrey, et al. 2019), but they nevertheless went extinct after the spread of pastoralism and concomitant forest clearance occurring ~1000 BP (Godfrey, et al. 2019; Hixon, et al. accepted). Still, some extinct taxa (e.g., pygmy hippos) may have been more sensitive to drought than others, and it remains unclear whether Late Holocene aridification promoted or hampered the spread of pastoralism at the expense of endemic fauna.

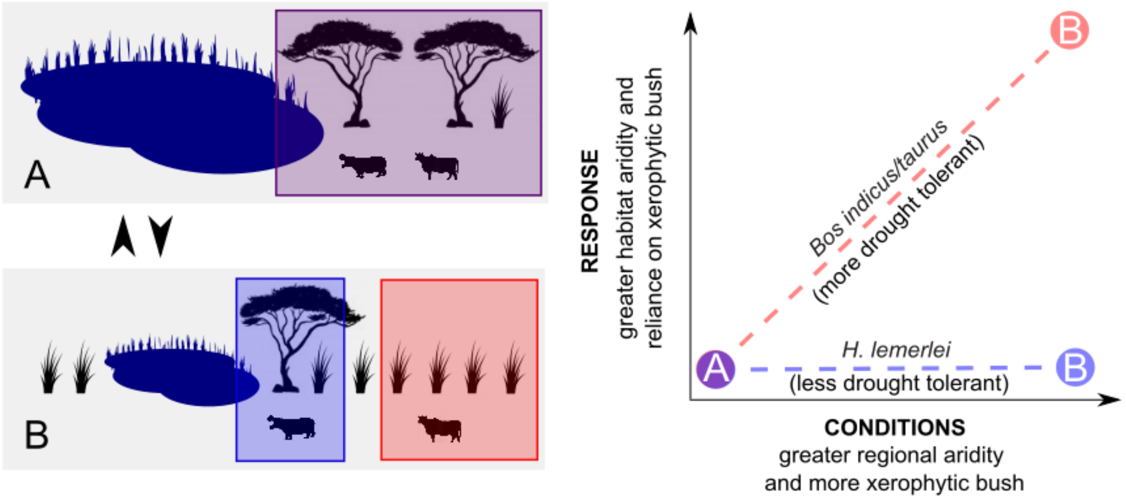


Figure 1. Hypothetical divergent responses of herbivores to drought and associated vegetation change. During mesic conditions (A), zebu (*Bos indicus/taurus*) and pygmy hippos (*H. lemerlei*) exploit abundant wet habitat and consume relatively few xerophytic plants. During dry conditions (B), zebu exploit relatively abundant arid habit and have a greater reliance on xerophytic bush, while hippos continue to exploit relatively scarce mesic habitat and forage. In this case, the flexibility of zebu makes them relatively drought-tolerant. Paleoclimatological and palynological data can characterize regional conditions and stable isotope data from herbivore bone proteins can characterize the responses of different species to changing climate. This simplified scenario does not consider other potentially important variables that may have affected fauna, such as human-mediated deforestation and the impacts of exotic megaherbivores on vegetation.

We used ^{14}C and stable isotope data from herbivore bone collagen to test the hypothesis that introduced zebu are drought-tolerant relative to extinct endemic herbivores. Extirpations that coincided with past droughts can indicate drought sensitivity. Bone ^{14}C datasets provide robust estimates of the timing of extirpation and introduction, and they complement estimates of large-herbivore biomass inferred from fecal fungus (*Sporormiella* spp.) spore counts (Burney, et al. 2003). Stable isotope (δ^{13}C and δ^{15}N) data from herbivore bones reflect aspects of both diet and habitat and can track long-term changes in aridity to different extents. The photosynthetic pathway used by plants exerts the strongest influence on δ^{13}C values in plant tissues and herbivore collagen (Crowley and Samonds 2013; Farquhar, et al. 1989). Plants that use the C$_3$ photosynthetic pathway (primarily trees, shrubs, and herbs) tend to be depleted in ^{13}C (i.e., have more negative $\delta^{13}C$ values) relative to plants that use the C_4 (primarily tropical grasses) or CAM pathway (primarily succulents). Local environmental conditions influence plant and animal $\delta^{15}N$ values such that plants and animals in relatively arid landscapes have higher $\delta^{15}N$ values (Crowley, et al. 2017; Crowley, et al. 2011). For example, in Madagascar's Beza Mahafaly Special Reserve, which lies in the spiny thicket ~100 km SE of Lake Ranobe (Fig. 2), mouse lemurs (*Microcebus griseorufus*) that live in the lush riparian forest have bulk tissue $\delta^{15}N$ values that are ~2‰ lower than those that live in the surrounding xerophytic thicket (Crowley, et al. 2011).

We identify drought-tolerant taxa as those that exploited dry habitat (with relatively high $\delta^{15}N$ values) and consumed xerophytic forage (with relatively high $\delta^{13}C$ values) when the region was relatively dry (Fig 1.). An example of such an animal from mainland Africa is the rock hyrax (*Procavia capensis*), which lives in colonies that inhabit a restricted geographic area and continuously produce middens composed of urine and feces. These middens have stable isotope values that faithfully track regional climate (Chase, et al. 2010). Drought-sensitive taxa here are identified as ones that move to stay within their preferred habitat, and maintain relatively constant $\delta^{15}N$ and $\delta^{13}C$ values, even during times of regional aridification.

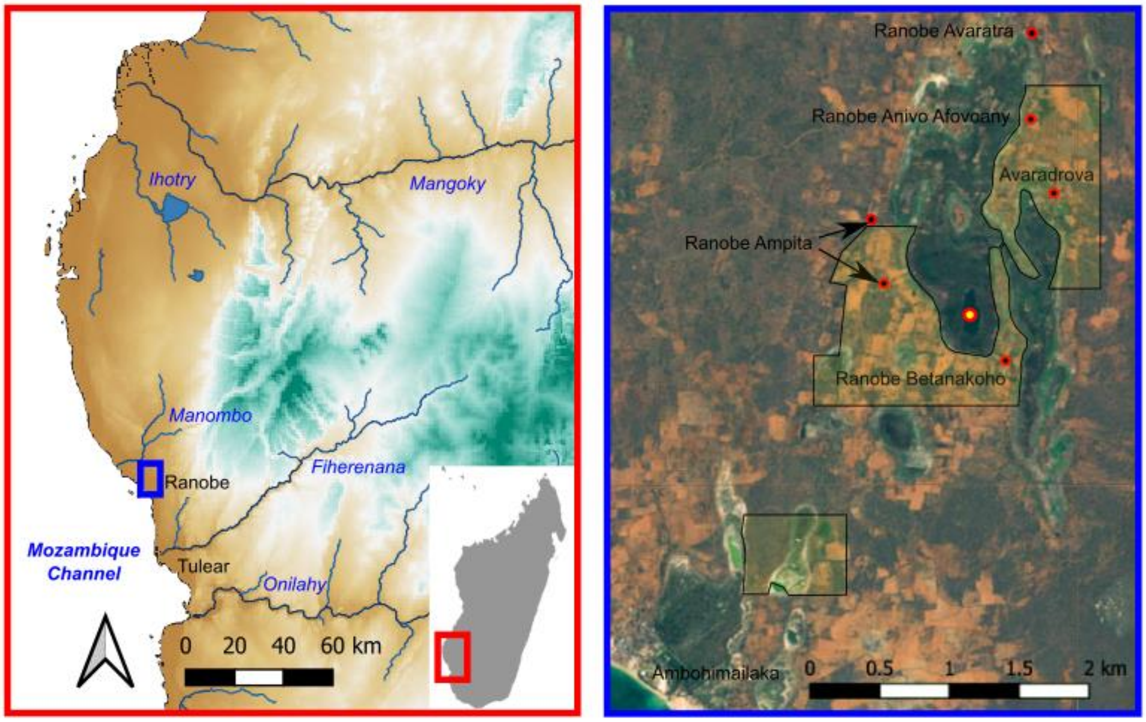


Figure 2. Regional map of southwestern Madagascar showing the location of Lake Ranobe relative to other bodies of water, the regional capital (Tulear), and other sites discussed in the text. The Lake Ranobe inset at right (Sentinel 2 imagery) includes the sediment coring site marked with a red and yellow circle, and the archaeological survey areas around the water body marked as yellow areas. Modern towns and hamlets are labelled, and hamlets around Lake Ranobe are marked with red and black circles. The vegetation around Lake Ranobe is currently a mosaic of cultivation (light brown and green) and dry spiny forest thicket (grey brown).

Regional Setting

Lake Ranobe is located in the coastal plains of Quaternary alluvium that extend north of Tulear (personal observation). There are a number of other small lakes in the region, such as those in the vicinity of Ambohimailaka, as well as some relatively larger pans such as Lac Ihotry (Fig. 2). The lake is bounded by dunes between the Manombo and Fiherenana drainages, which host a suite of cultivated crops (e.g., sugarcane, sweet potato, cassava, and beans) and fragments of endemic spiny forest that include members of the families Didiereaceae and Euphorbiaceae. The lake possesses rooted emergent (e.g. Cyperaceae, Typhaceae) and floating-leaved plants (Nymphaceae) and receives groundwater inputs that flow through sediments dominated by quartz sand, which extend over a catchment of ~150 km^2 (calculated from SRTM DEM). During September 2017, Lake Ranobe was smaller (~0.5 km^2) but somewhat deeper (z_{max} = 2.47 m) than nearby coastal pans in the region such as Ihotry and Namonte (1-2 m deep), which local informants considered typical. The monsoonal climate around Tulear is characterized by monthly average air temperatures that range between 25˚C and 30˚C and annual precipitation (~400 mm) that falls primarily during austral summer (November-March, Dewar and Richard 2007). Lake Ranobe lies ~3.5 km inland from the coastal village of Ambohimailaka, which is near a series of shallow ponds (Andolonomby/Ambolisatra) that have been mined for megafauna bones since the 19th century (Burney 1993; Chanudet 1975; G Grandidier 1905; Virah-Sawmy, et al. 2016). The archaeology around Lake Ranobe is poorly described, yet pygmy hippo bones from Andolonomby/Ambolisatra show evidence of human modification (MacPhee and Burney 1991) and road construction uncovered recent (<200 BP) pottery fragments (Burney and Burney 2007).

C. *Methods*

Sediment Collection & Archaeological Survey

We retrieved duplicate cores for analysis and storage with lengths of 237 and 243 cm from Lake Ranobe (S 23.03120°, E 43.60483°, Fig. 2) in September 2017. A sediment-water interface core (upper 65 cm) was collected using a piston corer that employs a 2¾"-ID polycarbonate core barrel (Fisher, et al. 1992). These uppermost, poorly consolidated sediments were maintained in a vertical position, extruded, and sampled in the field at 2-cm intervals. Deeper, more consolidated sediments were collected in sizes up to 1-m-long segments using a Colinvaux-Vohnout-type corer, modified to employ clear polycarbonate core barrels (2" ID). The deeper core segments were shipped intact to the US and opened at the University of Florida (UF), where they were split lengthwise, photographed, and sampled at 1-cm resolution for geochemical and charcoal analyses. Sediment sample collection and export were completed with authorization of the Ministry of Mines, the Ministry of the Environment, the National Office for the Environment, the Ministry of Higher Education and Scientific Research, the Ministry to the Presidency in Charge of Mines & Petroleum, and the University of Tulear's CEDRATOM Museum.

Bones used in this study came from both existing collections and our surface archaeological survey in the vicinity of Lake Ranobe. We worked with the Morombe Archaeological Project during September 2019 to survey ~2.4 km^2 of land in the vicinity of Lake Ranobe (Fig. 1). A crew of 10, each spaced ~10 m apart, walked E-W transects, and collected all surface bones, ceramics, shells, iron, and imported glass and stone (Dataset S1). Survey samples were stored at the University of Tulear's Cedratom Museum, and bone samples were shipped to Pennsylvania State University (PSU) for ^{14}C analysis.

Chronology

We ^{14}C dated 15 samples from the Lake Ranobe sediment core, which included macrobotanical remains such as charcoal and seeds (n=12), bulk sediment organic matter (n=1), terrestrial bird eggshell carbonate (n=1), and ostracod carbonate (n=1, Dataset S3). All samples were pretreated and graphitized in the PSU Stable Isotope Geochemistry Laboratory and analyzed on the PSU AMS. We removed contaminating humates and carbonates from macrobotanical remains and bulk sediment organic matter prior to analysis by pre-treating samples with acid/base/acid (ABA) washes that involved 20 min at 60°C with 1N HCl and 1N NaOH (for charred remains) or 0.1N NaOH (for uncharred remains). We pre-treated carbonate samples with a 10% acid etch in 0.01% HCl solution for 20 min at 60°C. We calibrated all dates in OxCal 4.4 using SHCal20 (Hogg, et al. 2020) and developed an age-depth model using the R package Bacon (v2.4.3, Johnson 2002, Dataset S4). Four ^{14}C dates run on aquatic plant remains or bulk sediment are subject to an unknown freshwater ^{14}C reservoir, appear to be anomalously old or young outliers, and were thus excluded from the final age-depth model based on 11 dates. Specifically, bioturbation, different depositional pathways, or ^{14}C reservoir effects in lake water may account for the date reversals in the sequence, but it is not possible to determine with certainty which process was responsible. Shells of burrowing planorbid snails (cf. *Segmentorbis angustus*) exist throughout the sequence. However, distinct layers, stratigraphic correlation between overlap and nonoverlap core sections, and comparable ages of charcoal from overlap (PSUAMS-3523, 600±20 BP, 126 cm depth) and nonoverlap core segments (PSUAMS-6328, 460±20 BP, 126.5 cm depth), suggest consistent stratigraphy and relatively little or no bioturbation. It is possible that charcoal and terrestrial seeds require more time than aquatic plant remains and ostracods to enter the sediment record, yet "too-old" outliers in the sequence were confidently identified as aquatic plant seeds (*Najas* sp. from 115.5 cm depth, PSUAMS-5153, 1560±15 BP and *Najas* sp. & Potamogetaceae from 180.5 cm depth, PSUAMS-5155 1875±25 BP). A ^{14}C-depleted reservoir of dissolved inorganic carbon (DIC) in lake water may yield ^{14}C dates for aquatic plant remains and ostracods that are hundreds to thousands of years older than their true age (Philippsen 2013). However, comparable ages for ostracod (PSUAMS-6334, 650±20 BP) and charcoal fragments (PSUAMS-6328, 460±20 BP) from 126.5 cm depth suggest that the DIC in Lake Ranobe, at least at that time, was not substantially ^{14}C-depleted. Because no single mechanism explains all the aquatic and mixed organics outliers in our core chronology, we chose to exclude the two youngest and two oldest outliers to develop the age-depth model.

We obtained ^{14}C and stable carbon isotope (δ^{13}C) and nitrogen isotope (δ^{15}N) data from archaeological remains of zebu (*Bos indicus/taurus*, n=8) and stable isotope data from modern bones of four individuals from three mammal taxa: zebu (n=1), ovicaprids (n=2), and bush pig (*Potamochoerus larvatus*, n=1). Prior to collagen extraction and stable isotope analysis, we extracted lipids from the four modern bone samples using 3× sonication in 2:1 DCM:MeOH, followed by rinses in DI water (modified from Guiry, et al. 2016). Collagen extraction for both modern and ancient samples involved demineralization in 0.5N HCl followed by gelatinization in 0.01N HCl at 60°C for 10 hr. We purified crude collagen extracts from ancient samples through ultrafiltration (Brown, et al. 1988; D. Kennett, et al. 2017; McClure, et al. 2010) or XAD resin column chromatography (Lohse, et al. 2014; Stafford, et al. 1988; Stafford, et al. 1991). We determined δ^{13}C, δ^{15}N, and C:N values on collagen from all 12 individuals at the Yale Analytical and Stable Isotope Center and the University of New Mexico's Center for Stable Isotopes, where the mean precision of δ^{13}C and δ^{15}N standard measurements across runs was ≤0.1‰. All eight of the samples that we ^{14}C-dated at the PSU AMS facility had good preservation and displayed absence of contaminants as evaluated by C:N, δ^{13}C, and δ^{15}N values (Beaumont, et al. 2010; DeNiro 1985; D. Kennett, et al. 2017; Van Klinken 1999). We calibrated all bone dates in OxCal 4.4 using SHCal20 (Hogg, et al. 2020), and we corrected δ^{13}C values for the Suess Effect, following the approach of Crowley and Godfrey (2013, Dataset S2).

We supplemented this dataset with previously published bone data from animals recovered within ~30 km of Lake Ranobe (Anderson, et al. 2018; Crowley 2010;

Crowley, Godfrey, et al. 2012; Hansford, et al. 2018; Hixon, et al. accepted). Reliable previously published data came from introduced animals (13 total: *Bos indicus/taurus* n=12 and *Canis familiaris* n=1) and endemic animals (44 total: extinct *Palaeopropithecus ingens* n=13, *Hippopotamus lemerlei* n=11, *Archaeolemur majori* n=7, *Megaladapis* spp. n=7, *Pachylemur insignis* n=2, and *Aepyornis* cf. *maximus* n=1, and the extant *Lemur catta* n=3). We used the ^{14}C data to estimate extirpation and introduction events for animals with sufficient sample sizes (n≥5) with a Bayesian approach to event estimation (Buck and Bard 2007).

Geochemical Data

We measured weight percent carbon (TC) and nitrogen (TN) on bulk sediment samples (n=215) at 1-2-cm resolution with a Carlo Erba NA 1500 C/N/S Analyzer at the UF Stable Isotope Laboratory (Dataset S5). We determined weight percent inorganic carbon (TIC) in bulk sediment by coulometry on a UIC-Coulometrics coulometer, coupled with an Auto-Mate automated carbonate preparation device (AutoMateFX.com). We subtracted TIC from TC values to obtain estimates of percent total organic carbon (TOC). We assumed that all inorganic carbon was bound as $CaCO_3$ and that organic carbon constitutes 40-50% of organic matter mass when we calculated total percent $CaCO_3$ (TIC*8.33) and total percent organic carbon (TOC*2.25). To measure $\delta^{13}C$ in sediment organic matter, we first acidified samples in 1N HCl overnight to dissolve carbonates. Following acidification, samples were centrifuged and rinsed in DI water 3×, freeze-dried, and packed in tin capsules for analysis on a Delta V isotope ratio mass spectrometer (IRMS). Precision of $\delta^{13}C$ and $\delta^{15}N$ measurements, established by analysis of standards across runs was 0.08‰ and 0.07‰, respectively. The average offset of the standard $\delta^{13}C$ and $\delta^{15}N$ measurements relative to known values was 0.3‰ and 0.5‰, respectively.

To analyze lacustrine carbonates, we washed samples in a 150-µm sieve and picked multiple monospecific ostracod shells from each of the 169 samples. We analyzed samples with a Kiel carbonate device and Delta V IRMS, and the precision in $\delta^{13}C$ and $\delta^{18}O$ measurements of standards across runs was 0.03‰ and 0.06‰, respectively. The average offset of the standard $\delta^{13}C$ and $\delta^{18}O$ measurements relative to literature values was 0.2‰ and 0.3‰, respectively. We determined relative abundances of heavier elements in bulk sediment at PSU with an Olympus DeltaX model X-ray fluorescence core scanner and Geotek MSCL 7.9, at sample intervals of 2 cm, exposure times of 80 s, a voltage of 40 kV, and a current of 23 mA. Small amounts of material in the sediment-water interface core precluded XRF analysis of deposits from above 50 cm depth.

We used principal components analysis (PCA) and a correlation matrix to identify covariance structure in the lake sediment record, and we applied Bayesian change point analysis (BCPA) to both Lake Ranobe and other Indian Ocean records to identify significant changes in long-term mean values of measured variables. BCPA is used to identify the partition (change points) in the sequence that leads to intervals that each have values that can be approximated reasonably well by a single mean. This approach uses the Markov Chain Monte Carlo method at each point k to approximate the posterior probability that k is a change point given the sequences of values that precede and follow the point (Barry and Hartigan 1993). To create a composite paleoclimate record for comparison with the combined herbivore bone dataset, we interpolated records at 1-year increments (based on our age-depth model), averaged z-scores from each record, and smoothed the average z-score record with a 100-year running mean (Dataset S6). We used Spearman correlation coefficients to assess the relationship between herbivore taxon-specific stable isotope records and composite paleoclimate record values that correspond to the mean calibrated age of the herbivore ^{14}C data. We also used Kruskal Wallis one-way ANOVAs and Dunn's method of pairwise multiple comparisons to identify differences in collagen stable isotope values among taxa.

D. Results

Lake Sediment Chronology

The ^{14}C ages from the Lake Ranobe cores suggest that sediment deposition in the basin has been continuous since ~1700-1590 cal BP (PSUAMS-6332, 1775±20 BP, Dataset S1). Our final age-depth model yielded an average, long-term linear sedimentation rate of 0.13 cm/yr (Fig. 3). Sedimentation was likely slow (0.06 cm/yr) between 155.5 and 126.5 cm depth (~1150 and 630 cal BP) relative to the underlying ~80 cm of sediment (0.14 cm/yr, ~1680 and 1150 cal BP) and overlying ~125 cm of sediment (0.18 cm/year, ~630 cal BP and present).

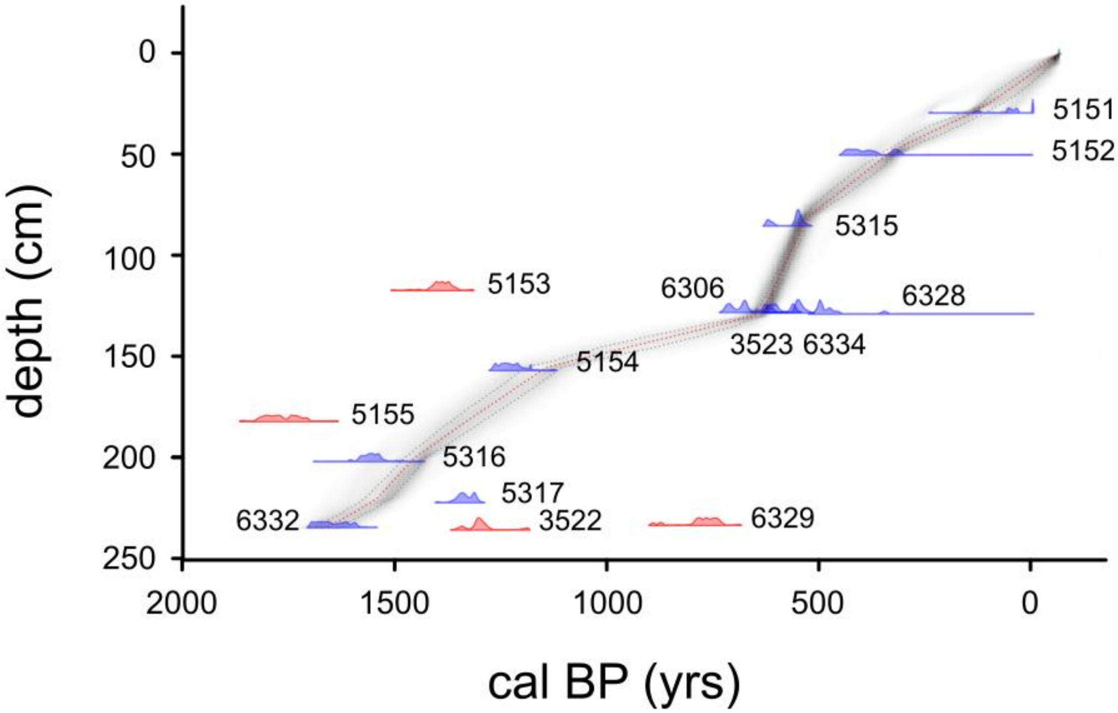


Figure 3. Lake Ranobe sediment core chronology, including probability distributions for ^{14}C dates (with PSUAMS numbers marked) calibrated with SHCal20. The age-depth model produced in R Bacon v2.4.3 is based on the blue dates (n=11). The red date outliers (n=4) come from bulk sediment organics or aquatic plant remains that might include an unknown ^{14}C reservoir effect. Apart from the ratite eggshell (PSUAMS 6332, 233.5 cm depth) and ostracods (PSUAMS 6334, 126.5 cm depth), dates used in the age-depth model come from macrobotanical remains.

Archaeological Survey

Survey around the coastal ponds near Ambohimailaka recovered sparse traces of human activity, such as shell-combed ceramics and recently deposited bone, which likely span, at most, the past several hundred years. In contrast, the archaeological record from around Lake Ranobe was substantial and included large clusters of animal bones, ceramics, and marine shells (Fig. 4). Similar clusters of artifacts from elsewhere in SW Madagascar are frequently considered the remains of villages or pastoralist camps that could have been occupied seasonally (Vérin and Battistini 1971). Marine shells came from well-known human foods and included the crowned turban shell (*Turbo coronatus*), giant mangrove whelk (*Terebralia palustrus*), trapezium horse conch (*Pleuroploca* *trapezium*), murex snail (*Chicoreus austramosus*), and bearded ark clam (*Barbatia foliata*). The largest cluster of human artefacts, which may be considered an archaeological site (possibly a past pastoralist campsite), is on the NE margin of the basin. An anomalously high concentration of historic glass in this cluster, and the shell-combed ceramics at this site, are consistent with human occupation during recent centuries (Douglass 2016). Current inhabitants of the nearby village of Avaradrova confirmed that a settlement at this site was abandoned during the past century. We focused on ^{14}C analysis of zebu bones from clusters on the south shore of Lake Ranobe because a variety of ceramic decorations, scarcity of historic glass, and the deflated sandy surface all suggest that these deposits span a relatively long period. Indeed, calibrated ages of eight bones from the southern margin of the lake span ~500 calibrated years (~600-100 mean cal BP, Fig. 4).

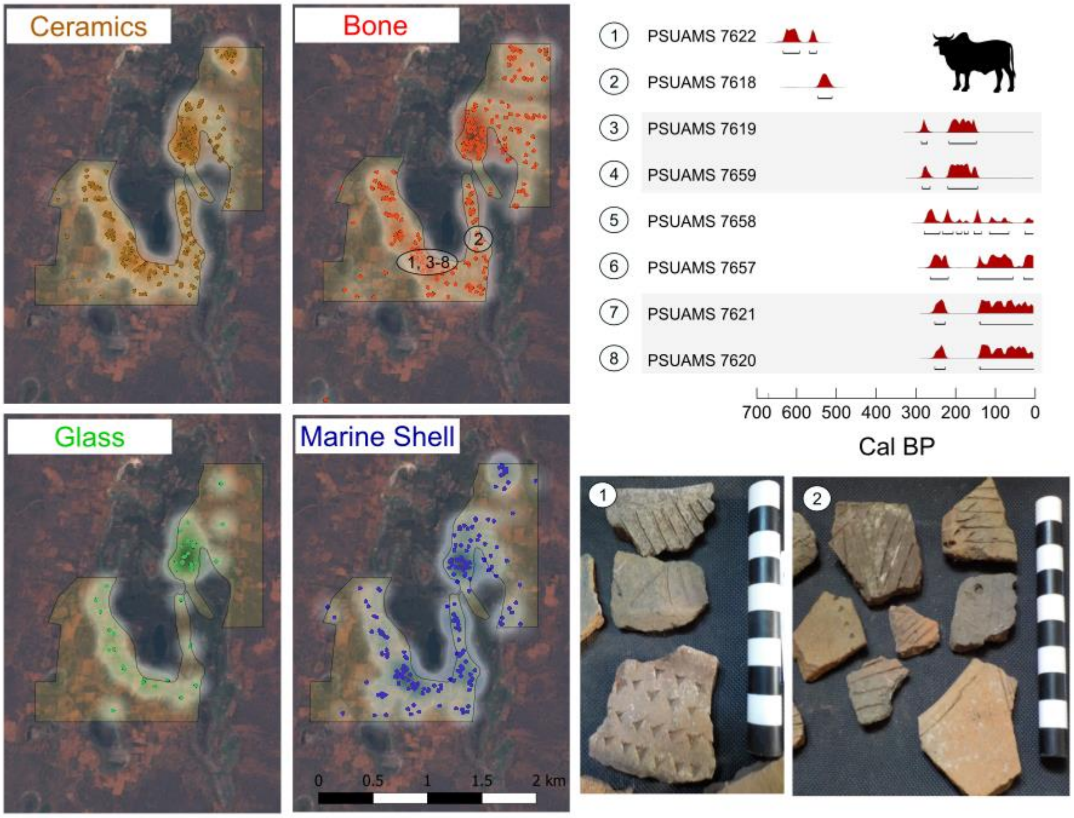


Figure 4. Distribution of surface scatters of ceramics (n=241), bone (n=252), glass (n=36), and marine shell (n=190) in the vicinity of Lake Ranobe, with point densities highlighted by heat maps. The parcel to the south yielded sparse scatters of bone (n=13) and ceramics (n=11) that are not shown. The calibrated ages of eight zebu bone fragments from the south shore of Lake Ranobe span the past 700 years and are associated with a variety of stamped and incised ceramics.

Geochemical Data

Smoothed ostracod $\delta^{18}O$ data from the sediment core display a succession of local maxima during the past ~1700 years. Values range between −7.2‰ and 4.9‰ ($\bar{x} \pm SD = -2.4 \pm 2.1$‰) and are positively skewed (0.6, Fig. 5). Surface water from Lake Ranobe, collected during September 2019, had a $\delta^{18}O$ value of −0.92‰. The fact that the $\delta^{18}O$ of our topmost ostracod sample (−2.5‰, 3 cm depth) is close to what would be expected given $\delta^{18}O_{water} = -0.92$‰ and $25^{\circ}C \leq T \leq 30^{\circ}C$ (expected calcite $\delta^{18}O$ range of −2.7-3.8‰), supports our assumption that ostracods in the lake secrete their shell carbonate near oxygen isotopic equilibrium.

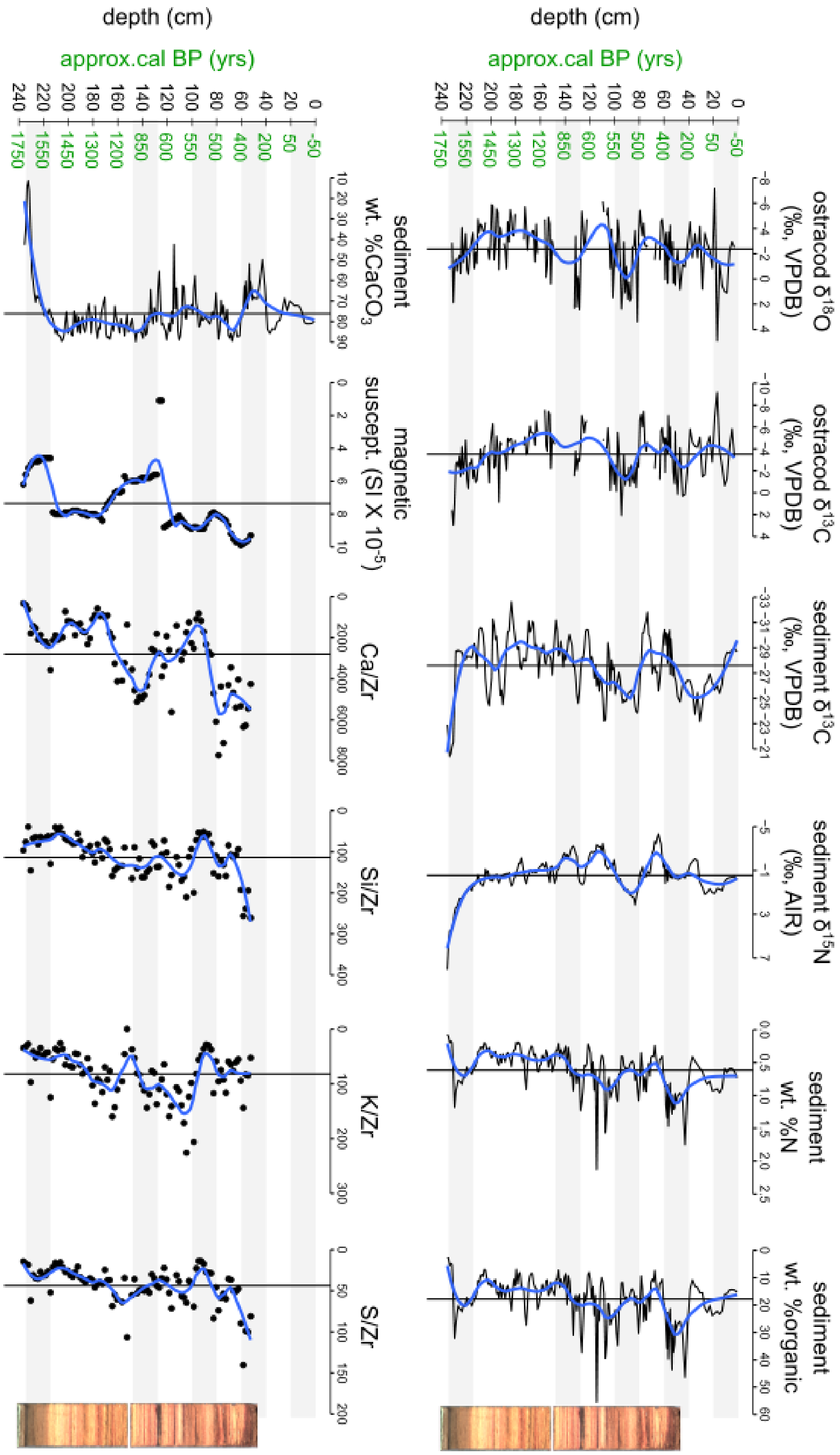


Figure 5. Geochemical records from the Lake Ranobe sediment core. Values are plotted versus depth (cm) and age (approximate cal yr BP). Blue loess curves are fitted to each record, horizontal lines mark the mean of each record, and depth intervals with above average ostracod δ^{18}O values are highlighted in grey. Scans of the more consolidated sediment in the deeper core sections appear at bottom.

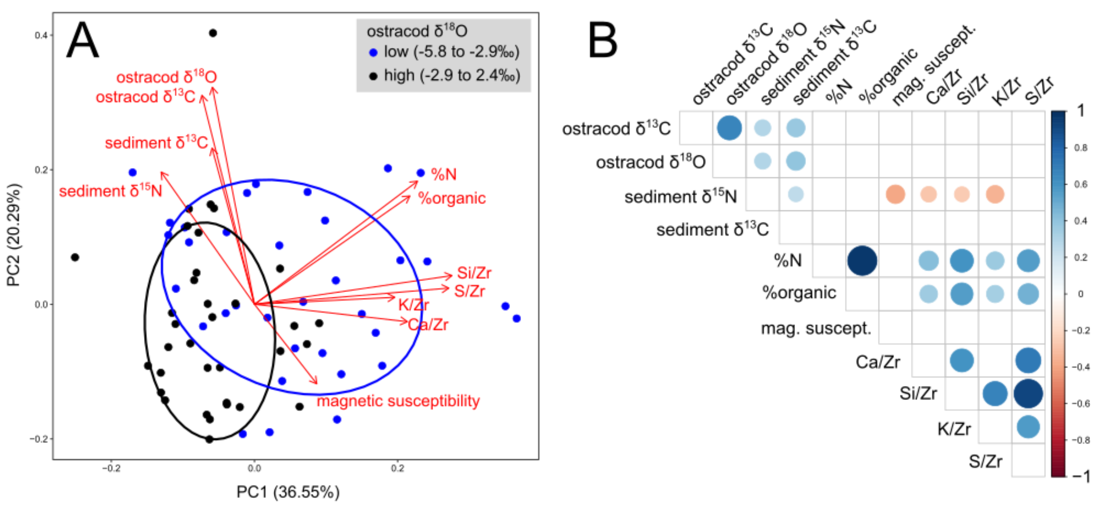


Figure 6. Principal components analysis (A) and correlation matrix (B) from the Lake Ranobe sediment core geochemical records. The PCA plot (A) includes loadings for each record in red and has samples grouped (with ellipses outlining 68% of each group) according to whether they share relatively low or high ostracod $\delta^{18}O$ values. The correlation matrix (B) displays only significant correlations as circles ($p<0.05$), with size scaled to p-values ($0.00<p<0.05$) and color scaled to Pearson correlation coefficients (scale at right).

The deepest ostracod datum (234.5 cm, ~1690 cal BP, $\delta^{18}O=-1.0$‰) overlies relatively consolidated grey sandy mud and is at approximately the same depth as an angular fragment of ratite (flightless bird) eggshell (233.5 cm, PSUAMS 6332, 1775±20 BP). Sediment geochemistry varies in the overlying sediment and is associated in some cases with fluctuations in the ostracod $\delta^{18}O$ record (Fig 6A). Generally, there are strong associations between 1) stable isotope values of sediment organic matter and ostracod tests (Fig. 6B), and 2) among the sediment organic content and the abundances of Ca, K, Si, and S, relative to Zr. High magnetic susceptibility is primarily associated with low sediment $\delta^{15}N$ values and is not consistently linked with sediment organic content.

The base of the core includes exceptionally high organic matter (acidified) $\delta^{13}C$ and $\delta^{15}N$ values (−22.9‰ and 8.1‰, respectively), and relatively low organic matter and $CaCO_3$ concentrations (2.8% and 42.6% of sediment weight, respectively). Among the heavier elements, Si, Zr, and Fe are particularly abundant at the base of the core, and Fe is mostly undetectable above ~216 cm depth (~1540 cal BP). The base of the core has relatively low magnetic susceptibility and abundant Zr, which drives low Ca/Zr, Si/Zr, K/Zr, and S/Zr values. The median Si/Zr throughout the Lake Ranobe sediment core (n=90, m=91.5) is only about 25% of that in the diatom-rich sediments of the Namonte Basin to the north, near Lake Ihotry (n=45, m=327.0, Mann-Whitney U=28.00, $p<0.001$). Diatoms are scarce throughout much of the Lake Ranobe core and are present in only ~25% of the 30 sediment samples collected between 240 and 50 cm depth (M. Velez pers comm.).

The first ~500 years of sediment deposition in Lake Ranobe (~1500-1000 cal BP) yielded ostracods with relatively low $\delta^{18}O$ values (−3.3±1.5‰). This sediment is composed primarily of $CaCO_3$ (~70-90 wt. %) but includes some thin (< 2 cm), dark layers that are relatively rich in N and organics. Si/Zr, K/Zr, and S/Zr values generally increase during this interval.

The period with relatively slow linear sediment accumulation (0.06 cm/yr), between ~1150 and 650 cal BP, includes scarce ostracods, which precludes approximation of continuous change. Several ostracod $\delta^{18}O$ values near the top of this interval (~700 cal BP), however, are relatively high (~2‰). This interval coincides approximately with local maxima in Ca/Zr and S/Zr values and minima in magnetic susceptibility and K/Zr values.

The last ~700 years of sediment deposition include approximately three maxima in ostracod $\delta^{18}O$ values (~550-500, ~400-200, and ~50-modern, with an average $\delta^{18}O$ value across these intervals of −1.3±2.2‰, n=47). The ~550-500 cal BP peak in ostracod $\delta^{18}O$ values coincides with local minima in Ca/Zr, Si/Zr, K/Zr, and S/Zr values, but heavy element abundance data do not span the two relatively recent peaks in ostracod

$\delta^{18}O$ values. Aside from ostracods that date to ~400-200 cal BP, ostracods relatively enriched in ^{18}O come from layers that tend to have little and less variable organic content. Application of BCPA to the Lake Ranobe ostracod $\delta^{18}O$ and sediment Ca/Zr values revealed change points that coincide approximately with change points in other Indian Ocean records (Fig. 7).

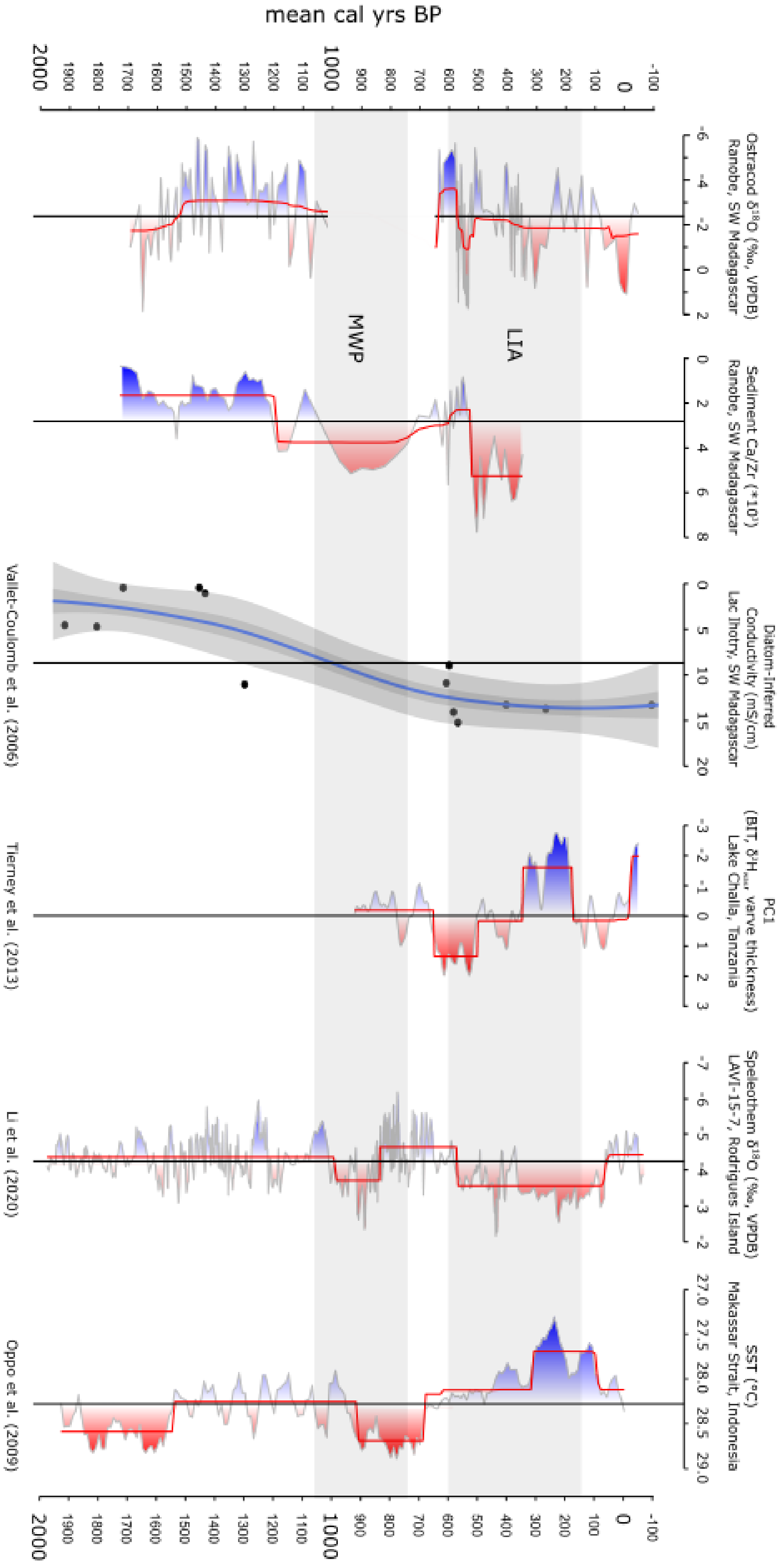


Figure 7. Records of Lake Ranobe sediment core Ca/Zr and ostracod δ^{18}O, with overall means marked by vertical lines, means between BCPA-inferred change points in red, and relatively high and low values shaded with red and blue, respectively. Regional context comes from records of diatom-inferred lake-water conductivity from Lac Ihotry, SW

Madagascar (with locally weighted smoothing, Vallet-Coulomb, et al. 2006), a variety of records from Lake Challa, Tanzania (Tierney, et al. 2013), a record of speleothem $\delta^{18}O$ values from Rodrigues Island (Li, et al. 2020), and a record of E Indian Ocean sea surface temperature inferred from a geochemical record from the Makassar Strait (Oppo, et al. 2009). Time periods that included the Medieval Warm Period (MWP) and Little Ice Age (LIA) are shaded in grey.

Herbivore Data

The disappearance of several megafauna taxa (pygmy hippos and three groups of extinct giant lemurs) from around Lake Ranobe (based on ^{14}C data from bone) coincided approximately with aridification, appearance of cattle, a rise in microcharcoal abundance, and a peak in sediment Cu concentration (Fig. 8). There are significant differences in median $\delta^{13}C$ values (H(4)=49.04, $p<0.001$) and median $\delta^{15}N$ values among herbivores (H(4)=22.24, $p<0.001$, Fig. 9). Pairwise comparisons indicate that the median cattle $\delta^{13}C$ value (n=21, m=−7.4‰) is significantly greater than values from giant lemurs *Paleopropithecus ingens* (n=14, m=−20.8‰), *Archaeolemur majori* (n=7, m=−20.6‰), and *Megaladapis* spp. (n=7, m=−21.0‰, $p<0.001$ for each). Such comparison also shows that the median pygmy hippo $\delta^{13}C$ value (n=11, m=−16.6‰) is significantly greater than that of *Megaladapis* spp. (n=7, m=−21.0‰, p=0.04). Finally, the median cattle $\delta^{15}N$ value (n=21, m=10.8‰) is significantly lower than that of *Paleopropithecus ingens* (n=14, m=14.4‰, $p<0.001$). All other differences in stable isotope values among herbivores were insignificant (Fig. 9). There are positive correlations between herbivore $\delta^{13}C$ values and records of regional aridity (composite Rodrigues and Ranobe $\delta^{18}O$ z-score record) for hippos (n=9, $r_s=0.76$, p=0.01) and cattle (n=21, $r_s=0.49$, p=0.02), and a negative correlation exists between cattle $\delta^{15}N$ values and records of regional aridity (n=21, $r_s=-0.45$, p=0.04, Fig. 9).

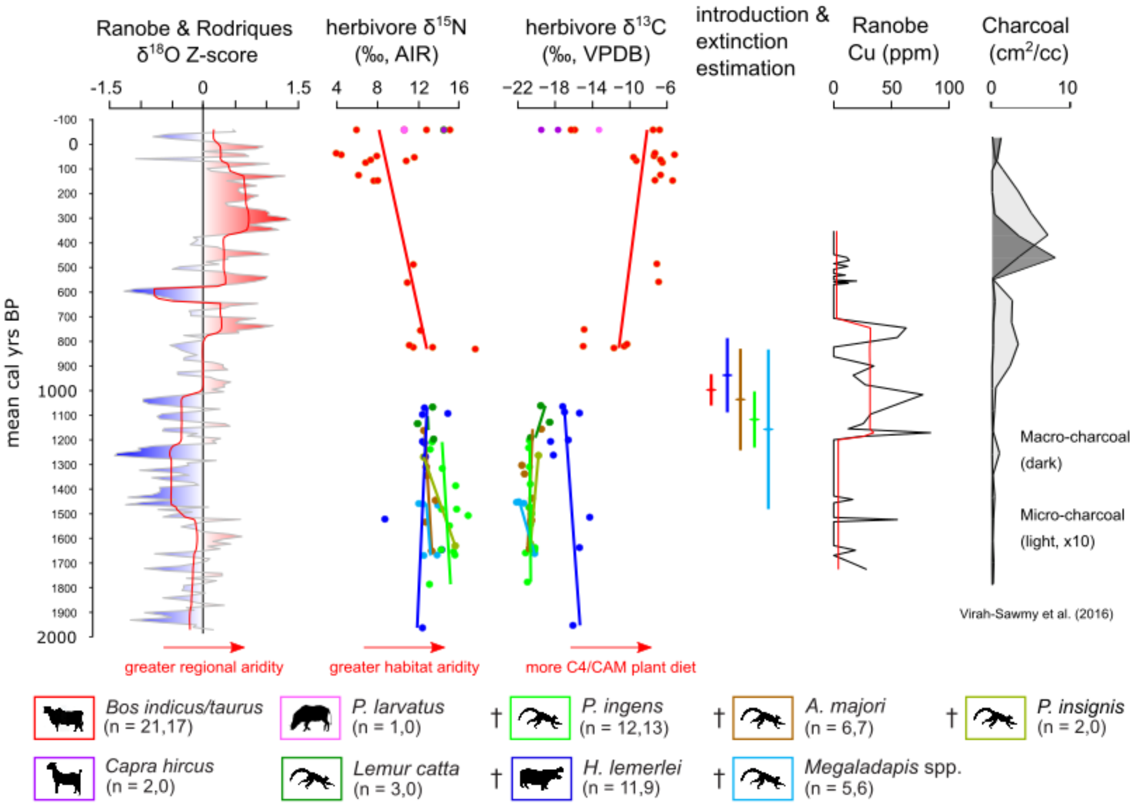


Figure 8. Regional climate (given as average z-score of the Lake Ranobe and Rodrigues Island δ^{18}O records), Ranobe animal bone stable isotope records, local extinction and introduction estimates, and anthropogenic records of Cu and charcoal deposition in lake sediments around Lake Ranobe. To create the composite paleoclimate record, the Ranobe and Rodrigues δ^{18}O records were interpolated at 1-year increments, z-scored, averaged, and then thinned to include 1 datum per decade. Bayesian change point analysis in the composite record (red line) identifies intervals that can be approximated reasonably well by a single mean. Introduced and extinct animal stable isotope data (n=63) plotted over time are fitted with lines, and Bayesian event estimates (μ±σ) for extinctions and zebu introduction are based on ^{14}C data (n=52) from taxa with n>5. Of the endemic taxa (hippos and lemurs), only *Lemur catta* is extant. Taxon-specific sample sizes of the form (n=[stable isotope sample size],[^{14}C sample size]) reflect the fact that extinction confidence intervals for pygmy hippos and giant lemurs consider all data from individuals since 3000 cal BP and that the introduction confidence interval for zebu data does not consider the 3 modern individuals with stable isotope data.

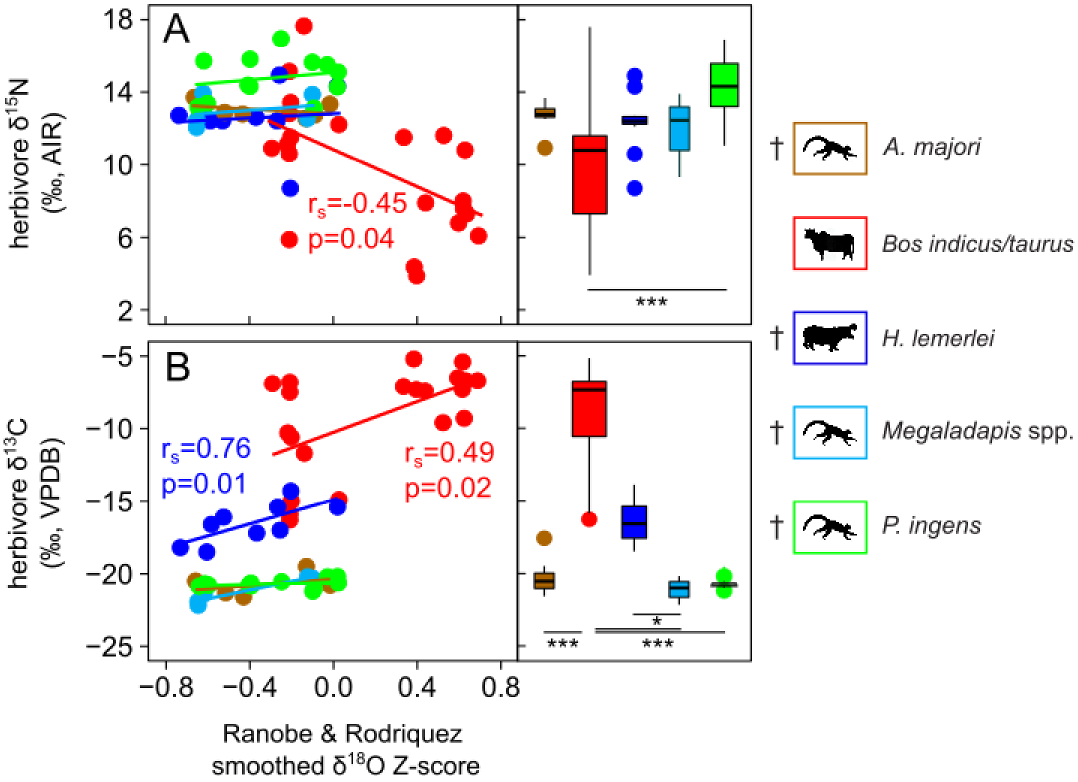


Figure 9. Herbivore δ^{15}N data (A) and δ^{13}C data (B) against 100-year smoothed paleoclimate composite data from Fig. 8. Herbivore data were matched to the smoothed composite record according to the mean calibrated age of individuals, and only significant ($p<0.05$) Spearman's correlation coefficients are given. The associated box plots at right compare the distributions of δ^{15}N and δ^{13}C values among taxa, with the width of boxes scaled according to sample size. Kruskal-Wallis one-way ANOVAs and Dunn's method of pairwise multiple comparisons suggest significant differences between taxa, with * marking $p<0.05$, and *** marking $p<0.001$.

E. Discussion

The Lake Ranobe ostracod δ^{18}O values, coupled with Ca/Zr and sedimentation rate data, identify a dry interval between ~1000 and 700 cal BP that coincided with 1) the disappearance of endemic pygmy hippos and giant lemurs and 2) the appearance of introduced livestock and possibly other evidence of human activities around the lake. Regional paleoclimate records suggest that this drought affected other parts of the Western Indian Ocean and was associated with positive-IOD conditions. Possible human settlement on the south shore of Lake Ranobe between ~700 and 500 cal BP coincided with a relatively wet interval that may have helped agropastoralists expand into inland sites. Stable isotope records from animals in the vicinity of Lake Ranobe reflect different responses to past aridification and possible drought sensitivity in cattle.

Drought and Relationships Among Climate Proxy Records

Relatively dry periods, characterized by high E/P and low lake levels, left relatively ^{18}O-enriched ostracods and associated geochemical evidence. The strong positive correlation between lacustrine carbonate (e.g., ostracod) δ^{18}O and δ^{13}C values is typical of closed basins (Talbot 1990) and can be explained by coupled changes in lake water δ^{18}O values and the δ^{13}C values of the lake's dissolved inorganic carbon (DIC) species (CO_2, HCO_3^-,CO_3^{2-}). Specifically, reduced freshwater inputs of ^{13}C-depleted DIC and relatively strong evaporation (driving increased partial pressure of CO_2 in the lake and increased loss of $^{12}CO_2$ to the atmosphere) can increase the δ^{13}C of the lake's remaining DIC during drought (Li and Ku 1997). The correlation between the Lake Ranobe sediment organic matter and ostracod δ^{13}C values suggests that ostracods used the lake's DIC for shell formation, and the sediment organics include primarily remains of aquatic plants that used the lake's DIC for photosynthesis.

Both the origin of the lake and subsequent changes in lake level can explain the association of sediment organic matter δ^{15}N and ostracod δ^{18}O values. When soil N is in short supply, plant uptake can leave soils enriched in ^{15}N (Amundson, et al. 2003), and preferential loss of ^{14}N to the atmosphere can also leave soils enriched in ^{15}N (particularly under arid conditions, Austin and Vitousek 1998). The infilling of Lake Ranobe (reflected by the transition from sandy soil to calcareous lake sediment at the base of the core) preserved organic-rich lacustrine sediment with high %N (Fig. 5). Relatively low δ^{15}N values in this lacustrine sediment likely reflects diminished loss of ^{14}N to the atmosphere and terrestrial plants. Thus, the associated early increases in lake volume and changes in N cycling likely explain the coupled low ostracod $\delta^{18}O$ values and sediment $\delta^{15}N$ values near the base of the core. Subsequent, relatively small increases in lake sediment $\delta^{15}N$ values may reflect shallowing of the lake, which could have contributed to warmer water temperatures, reductions in dissolved oxygen, increased microbe-driven denitrification, and ^{15}N-enrichment of the lake's remaining nitrate pool (Hecky 1993; Talbot 2002). The negative correlation between sediment $\delta^{15}N$ values and magnetic susceptibility may stem, in part, from increased deposition of ferromagnetic minerals via runoff during wet periods associated with relatively low sediment $\delta^{15}N$ values.

Variation in the organic content of the sediment is not consistently correlated with the stable isotope or magnetic susceptibility records, and the strong correlation between %organic matter and %N is expected. Relatively high Si/Zr and Ca/Zr values in organic-rich sediments suggest that aquatic plants and organisms with silica and carbonate skeletons flourished under similar circumstances and in many cases during times with relatively low ostracod $\delta^{18}O$ values (Fig. 5 & 6). Note, however, that both biogenic carbonate deposition during wet periods and chemical carbonate precipitation during relatively dry times can increase Ca/Zr values and complicate interpretation of the association between Ca/Zr and ostracod $\delta^{18}O$ values (Haberzettl, et al. 2007; Kylander, et al. 2011). Our observed correlation between %organic matter and S/Zr may follow from sulfur deposited in organic matter or from the deposition of S in pyrite (FeS_2) under reducing conditions (Moreno, et al. 2007). Finally, coupled K/Zr and magnetic susceptibility values may both follow from relatively intense periods of aeolian or fluvial erosion (Aufgebauer, et al. 2012; Kylander, et al. 2011; Piva, et al. 2008).

Chronology and Regional Comparison

1700-1500 cal BP: Freshwater filled the inter-dune swale that defines Lake Ranobe. Lacustrine carbonates and organic matter accumulated over underlying sand, as well as terrestrial animal remains such as *Mullerornis* sp. eggshell. A minimum $\delta^{18}O$ value at ~1650 cal BP in a W Indian Ocean speleothem from Rodrigues Island suggests the region may have been relatively wet at that time (Li, et al. 2020). Warm and wet conditions in that region today are connected with cooler than usual sea surface temperatures (SSTs) in the E Indian Ocean and W Tropical Pacific through the positive phase of the Indian Ocean Dipole (IOD, Li, et al. 2003). A shift towards relatively low SST in the Makassar Strait, Indonesia after 1600 cal BP is consistent with a coincident wetting trend in SW Madagascar (Oppo, et al. 2009).

1500-1000 cal BP: Relatively low ostracod $\delta^{18}O$ values reflect wet conditions, and a rise in K/Zr values may reflect increased detrital input via runoff. A series of peaks in sediment organic content and steady increases in Si/Zr and S/Zr attest to pulses of primary production in the lake during this interval. Decreased sedimentation rate after ~1150 cal BP, peaks in ostracod $\delta^{18}O$ values around 1150 and 1080 cal BP, a decrease in K/Zr values ~1100 cal BP, and possibly the local maximum in Ca/Zr values ~1150 BP attest to a drying trend at the end of this interval. An increase in Rodrigues Island speleothem $\delta^{18}O$ values between 1250 and 1150 cal BP suggests that other parts of the W Indian Ocean also experienced a drying trend at the end of this interval (Li, et al. 2020).

1000-700 cal BP: Relatively slow accumulation of sediment with lower organic matter content during the Medieval Warm Period attests to an interval of reduced primary productivity. A prolonged increase in Ca/Zr values may reflect authigenic carbonate precipitation during low lake levels associated with drought. Low lake levels could explain the absence of ostracods throughout most of this interval and were approximately coincident with salinization of Lac Ihotry (Vallet-Coulomb, et al. 2006), a maximum in speleothem δ^{18}O values from Asafora Cave (~100 km to the north, Faina, et al. in press), and palynological evidence from elsewhere in southern Madagascar for drought ~950 cal BP (Virah-Sawmy, et al. 2010). They are also consistent with indurated clay in Lac Ihotry from ~800 cal BP that blocked our coring efforts and with highest Ca/Zr values near the base of the Lake Namonte sediment core (Domic et al. in review). Drought during this interval is also recorded in Rodrigues Island speleothem δ^{18}O values (Li, et al. 2020), and elevated SST in the Makassar Strait suggests that this multidecadal drought in the W Indian Ocean occurred during positive IOD conditions (Oppo, et al. 2009).

700 cal BP to present: The return of ostracods with relatively low δ^{18}O values, along with a simultaneous decrease in Ca/Zr and increase in magnetic susceptibility at the start of this interval, likely indicate a return to relatively mesic conditions. This trend is matched by relatively low Rodrigues Island speleothem δ^{18}O values (Li, et al. 2020) and a decline in Makassar Strait SST (Oppo, et al. 2009). Makassar Strait SST continued to decline during much of this interval and notably during the Little Ice Age (Oppo, et al. 2009), and a coincident transition to mesic conditions around Lake Challa (Kenya/Tanzania) suggests there were widespread negative IOD conditions (Tierney, et al. 2013). The Rodrigues Island speleothem δ^{18}O values, however, remained high after 600 cal BP, and peaks in the Lake Ranobe ostracod δ^{18}O values, which punctuate the record since 600 cal BP, suggest episodic returns to dry conditions ~550, ~400-250, and 50 to −50 cal BP. The ~550 cal BP drying is associated with organic-poor sediment with high δ^{15}N values and low K/Zr, Si/Zr, Ca/Zr, and S/Zr values, and it is consistent with aridity recorded in sediments from Lake Challa (Tierney, et al. 2013) and the Rodrigues

Island speleothem (Li, et al. 2020). The aridity ~400-250 cal BP may have been less severe than that of ~550 cal BP, because the ~400-250 cal BP interval includes relatively low ostracod $\delta^{18}O$ peaks, high magnetic susceptibility, and average K/Zr values. The ostracod $\delta^{18}O$ peaks during this interval may, however, have been damped by anthropogenic deforestation documented by Virah-Sawmy et al. (2016). Fire and forest loss could contribute to: 1) faster recharge, thereby lowering lake water $\delta^{18}O$ values, and 2) greater erosion, which would have increased K/Zr and magnetic susceptibility during a time of comparable aridity. Unlike the most recent dry interval and that of ~550 cal BP, primary productivity was markedly high ~400-250 cal BP, as evidenced by a peak in organic matter content (also visible in core scans as darker layers) and some of the highest Si/Zr and S/Zr values.

Human and Herbivore Activity

The disappearance of megafauna from around Lake Ranobe coincided with the dry interval of 1000-700 cal BP, yet evidence for intensified human activity in the area confounds inference of drought-driven extirpation. The introduction of cattle during this interval (1080-960 cal BP) could have led to multiple forms of competition between livestock and endemic megaherbivores (Hixon, et al. accepted). Increasingly abundant microcharcoal particles during this interval likely reflect anthropogenic burning, and a coincident peak in Cu concentration (~1190-900 cal BP) may reflect smelting for metal tool production (Davies, et al. 2004; Guyard, et al. 2007). Approximately 1000-year-old bones from an extant lemur (*Propithecus verreauxi*) from the site of Taolambiby (Fig. 2), ~100 km SE of Lake Ranobe, include cutmarks likely produced by metal tools (Anderson, et al. 2018; Perez, et al. 2005), and our survey recovered slag fragments of unconstrained age from the south shore of Lake Ranobe.

The earliest directly ^{14}C-dated zebu from the vicinity of Lake Ranobe come from the paleontological deposits of Andolonomby/Ambolisatra (PSUAMS 5303, 1010±15 BP, Hixon, et al. submitted) and predate those that we recovered on the south shore of Ranobe by up to ~200 years. Zebu bones from the south shore of Ranobe are associated with ceramics decorated with triangle impressions, incised parallel lines, and circular holes (Fig. 4), which makes them similar to ceramics recovered from the inland archaeological site of Rezoky, a prehistoric pastoralist camp in the Mangoky Drainage (Fig. 2) ~140 km to the NE (Vérin and Battistini 1971), and from some coastal archaeological sites in the Velondriake region to the north (K.M.G. Douglass 2016). Directly ^{14}C-dated zebu and ovicaprid bones from Rezoky (n=8) span ~730-500 cal BP (Hixon, et al. accepted), which makes them approximately contemporary with the earliest ^{14}C-dated zebu bones from the south shore of Lake Ranobe. Lake records suggest that this interval was one of the wettest during the past millennium (Fig. 8), which could have helped agropastoralist populations expand into inland drainages.

The absence of positive correlations between the Ranobe-Rodrigues composite δ^{18}O record and herbivore δ^{15}N records (Fig. 9) suggests that none of the taxa we examined are drought-tolerant as envisioned in Figure 1. Consistent with the work of Crowley et al. (2012, 2017), we found relatively high δ^{15}N values in the collagen of extinct endemic megaherbivores and found no directional increase through time in δ^{15}N records from endemic megaherbivores. The earliest directly ^{14}C-dated cattle from around Ranobe had δ^{15}N values comparable to those of endemic megafauna, which suggests that they exploited similarly arid habitat. However, cattle that lived during subsequent dry times had relatively low δ^{15}N values, which suggests that they exploited relatively mesic habitat. The data suggest that cattle abandoned arid habitats during relatively dry times, which may indicate sensitivity to drought and/or strategic reliance of pastoralists on mesic patches. Historically, pastoralists are known to have relied on mesic refuges during droughts (Rasolondrainy 2019). Reliance by cattle on mesic habitat with relatively low $\delta^{15}N$ values during dry times within the past millennium suggests that the scarcity of mesic habitat did not contribute to megafaunal extinction, even in arid SW Madagascar.

Positive correlations between aridity records and $\delta^{13}C$ values in pygmy hippos and cattle suggest that these animals were able to cope with some vegetation change associated with aridification. During relatively dry times, these herbivores likely consumed more ^{13}C-enriched xerophytic C4 grasses and CAM succulents. Faina et al. (in press) found that ^{13}C-enriched vegetation flourished during relatively arid times, and deforestation contributed further to the rise of grasses and herbs in this region during the past millennium (Virah-Sawmy, et al. 2016). Today, endemic succulent vegetation (e.g. *Euphorbia stenoclada*) remains an important source of fodder that is maintained and used by pastoralists (Feldt, et al. 2017; Kaufmann and Tsirahamba 2006).

The data suggest that cattle managed to cope with past vegetation changes to a greater extent than pygmy hippos but may have been constrained to mesic patches during droughts. The relatively high pygmy hippo and giant lemur $\delta^{15}N$ values suggest that these animals exploited relatively arid habitat and are inconsistent with the idea that drought forced endemic megaherbivores into dwindling patches of mesic habitat. The regional disappearance of megafauna may be better explained by coincident forest clearance and other human disturbances such as hunting and the introduction of potential megaherbivore competitors. The following chapter further considers lengths of local co-occurrence among humans, livestock, and extinct endemic megaherbivores at another cluster of sites in SW Madagascar.

V. CH. 5: Disappearance of drought-tolerant endemic megafauna coincided with spread of pastoralism around Tampolove, SW Madagascar

A. Abstract

The previously-discussed research suggests that humans hunted Madagascar's endemic megaherbivores to extinction only when this hunting was facilitated by introduced livestock and dogs and possibly exacerbated in the SW by late Holocene aridification. However, the scarcity of sites with unambiguous traces of humans, livestock, and endemic megaherbivores make it difficult to compare the lengths of local cooccurrence among these groups, and differences in the tolerance of different herbivores to drought are uncertain. Here, we report the excavation of the margins of three coastal ponds in SW Madagascar (Tampolove, Ankatoke, and Andranobe), which include bones of extinct megafauna (giant tortoises [*Aldabrachelys* spp.], pygmy hippos [*Hippopotamus lemerlei*], and elephant birds [*Aepyornis* spp.]), extirpated fauna (Nile crocodiles [*Crocodylus niloticus*]), and introduced vertebrates (zebu cattle [*Bos taurus indicus*] and bushpigs [*Potamochoerus larvatus*]), as well as traces of human activity (modified pygmy hippo bone, processed estuarine shell, fish bone, and charcoal). Directly ^{14}C-dated bone of endemic megafauna indicates that hippos and giant tortoises continually occupied the vicinity of these small, ephemeral ponds in the dry forest during mid-Holocene aridification (rather than retreating up inland drainages), which suggests that they had some degree of drought tolerance. A modified but undated pygmy hippo bone stratigraphically removed from the main megafaunal bone bed at Tampolove suggests that people modified this bone within the past millennium and likely after the local disappearance of pygmy hippos. Episodic vegetation burns and the deposition of

estuarine shell, fish bone, and cattle bone also occurred likely only within the past millennium. However, an African bushpig (*Potamochoerus larvatus*) tooth directly dated to ~4,000 years ago suggests that these animals arrived on Madagascar well before introduced bovids possibly with the aid of people. The scarcity of cutmarks on megafauna bone and relatively late increases in the abundance of livestock bones and charcoal are consistent with the idea that it was forest clearance and the spread of pastoralism that drove the local disappearance of endemic megafauna, possibly after some period of local coexistence between humans and endemic megafauna.

B. Introduction

The last millennium witnessed the disappearance of a diversity of large animals endemic to Madagascar, which included elephant birds, giant lemurs, pygmy hippos, and giant tortoises (Crowley 2010). Early to mid-Holocene evidence of human arrival is the subject of debate (Anderson, et al. 2018; Dewar, et al. 2013; Hansford, et al. 2018; Mitchell 2019), but it raises the possibility that there was an extended period of coexistence between humans and endemic megafauna on the island (Douglass, et al. 2019). At least in SW Madagascar, some combination of drought and the spread of pastoralism could have contributed to the late Holocene pulse of extinctions (Burney 1993; Godfrey, et al. 2019; Hixon, et al. accepted; Virah-Sawmy, et al. 2016). Cause cannot be directly inferred from temporal coincidence, yet known sequences of events can constrain possible scenarios. We report the excavation of archaeological sites on the edge of three coastal ponds in SW Madagascar, and directly date traces of human activity, endemic megafauna, and human introduced species to establish a chronology for when each of these groups was present in the area during the past 6,000 years.

Such a chronology lacks the generality of a regional study, yet it can test key implications of the ideas that endemic megaherbivores were sensitive to 1) drought, 2) hunting, and 3) hunting in the presence of introduced domesticated species (e.g., cattle, sheep, goats, and dogs). Surface water can be particularly scarce in the arid spiny forests of SW Madagascar, and speleothem oxygen isotope records from Rodrigues Island (~2,000 km to the east) suggest that the drought that approximately coincided with the disappearance of Madagascar's megafauna during the Medieval Warm Period (~900 calibrated years before present [cal BP]) was only one of a long series of megadroughts during the last 5,000 years (for example, at around 4900, 3600, and 2800 cal BP, Li, et al. 2020). If some megaherbivores (e.g., pygmy hippos) were sensitive to climatic desiccation relative to others (e.g., giant tortoises), then we would expect the sensitive taxa to disappear from the vicinity of ephemeral coastal ponds and retreat up relatively mesic drainages during past megadroughts (Fig. 1A). Local persistence of megafauna during past megadroughts suggests either that these animals had some degree of drought tolerance or that these megadroughts had minor impacts on local water availability.

Cut-marked bone attests to past hunting of endemic megafauna (Godfrey, et al. submitted; Hansford, et al. 2018; Perez, et al. 2005), yet the contribution of hunting to past extinction is unclear. If megafauna were sensitive merely to the presence of human hunters on the landscape, then we would expect extirpation to have shortly followed the arrival of people (Fig. 1B). If megafauna were sensitive to human hunters only after human populations expanded in tandem with agropastoralism, then we would expect some period of coexistence between people and megafauna in the absence of a suite of introduced domesticated species (Fig. 1C). We focus our attention on the mixed archaeological/paleontological deposits in the vicinity of Tampolove and Lamboara, SW

Madagascar (Fig. 2), which have produced some of the oldest traces of human activity in the region (MacPhee and Burney 1991).

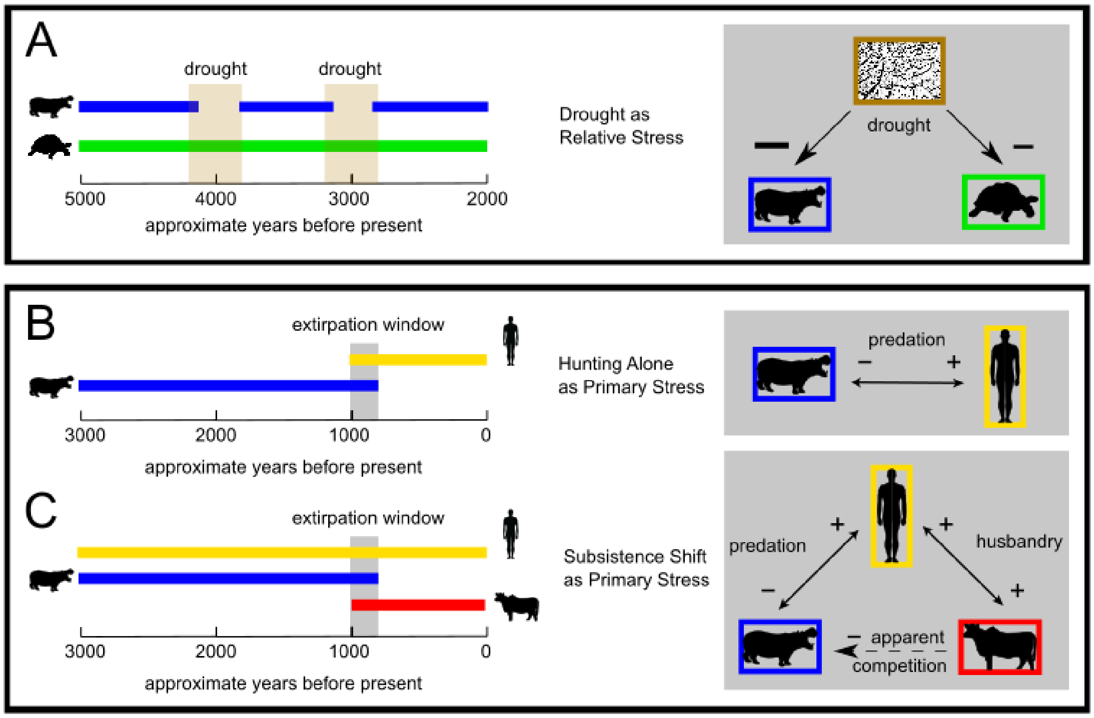


Figure 1. Potential past patterns of local arrival and disappearance, with examples of supported drivers of extirpation at right. Drought sensitive taxa are expected to disappear from the margins of shallow coastal ponds in the arid SW during past megadroughts (A), taxa sensitive to only human hunting are expected to disappear shortly after the arrival of people (B), and taxa sensitive to hunting only from expanding agropastoral populations may have an extended period of coexistence with humans but not introduced livestock (C).

Study Area

The coastal plains of SW Madagascar are composed of Quaternary alluvium, which forms dunes and lithified calcareous outcrops that are broken in the east by foothills of Eocene clayey limestone (Roig, et al. 2012). The excavations described here are on the margins of three shallow coastal freshwater ponds all 3-5 m asl: Tampolove [TAMP], Ankatoke [ANKA], and Andranobe [ANDR]. These represent a subset of a series of shallow depressions in calcareous crust that define the southern edge of a shallow coastal inlet known as the Bay of Assassins (Fig. 2). These ponds are bounded by mangrove swamp to the east and both active and ancient dunes to the west. Each pond is small (<0.01 km^2) and has a limited catchment (<1 km^2). The climate is semi-arid and typically includes <400 mm of annual precipitation, which falls during the austral summer (November – March, Dewar and Richard 2007). The fact that these ponds are near present sea level means that local water availability varies according to changes in both regional precipitation and relative sea level (Vallet-Coulomb, et al. 2006). SW Madagascar likely shared episodes of climatic drying with other western Indian Ocean Islands since at least the mid-Holocene (Li, et al. 2020). However, the hydro-isostatic response of Madagascar's landmass and the surrounding oceanic crust to early Holocene sea level rise produced an anomalous marine highstand (~2 m above present sea level) around 2000 cal BP that raised coastal water tables (R Battistini 1971; Camoin, et al. 2004).

The excavated ponds are currently shallow enough to permit the growth of emergent plants (plants rooted in lake bottom) throughout, and water levels track variation in rainfall both seasonally and interannually. During the dry season, the relatively verdant ponds are hubs of activity for people and livestock, and other ponds the area dry completely. People have constructed spiny bush enclosures around at least parts of each of these ponds to protect the cultivation of crops for human consumption (e.g., sweet potatoes) and emergent plants for fodder and thatching (e.g., reeds such as *Phragmites mauritianus*). The surrounding spiny thicket includes a diversity of endemic baobabs (e.g., *Adansonia grandidieri*), as well as stem succulents belonging to Didiereaceae (e.g., *Didierea madagascariensis*) and Euphorbiaceae (e.g., *Euphorbia stenoclada*).

TAMP and ANKA are located immediately SE of a coastal village of Vezo fishers known as Tampolove, and ANDR is located immediately SE of a village of Masikoro agropastoralists known as Andalambezo. These villages are less than 10 km west of the Mikea National Park, which has existed since 2012. The nearest regional population center (~50 km to the NE) is Morombe.

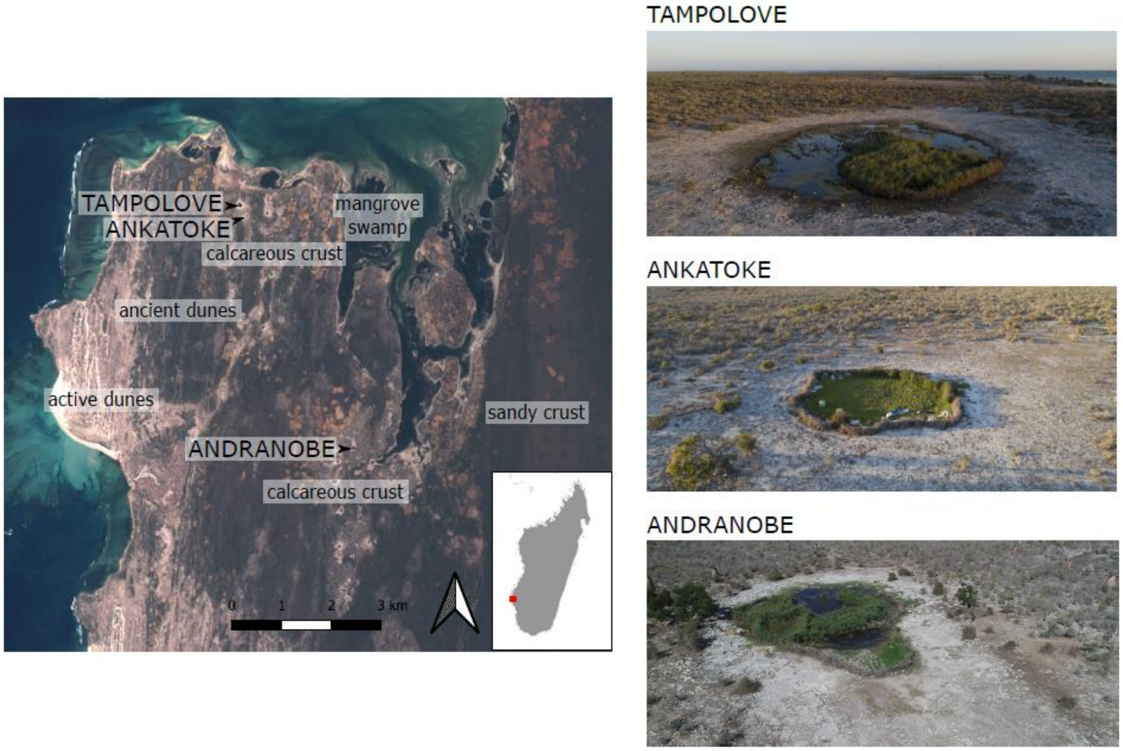


Figure 2. Locations of excavated ponds in the vicinity of Tampolove, SW Madagascar. Sandy limestone surrounds each of the basins, but the region includes dunes and mangrove swamps. Each pond is at least partly enclosed for modern cultivation, and only Ankatoke was completely dry during excavation in September, 2019.

Research History

Coastal ponds in the vicinity of Tampolove were the focus of productive paleontological collections of the late 19th and early 20th century that unfortunately lacked stratigraphic context. Shortly before the French colonization replaced the rule of the Sakalava Kingdom over much of western Madagascar, J.T. Last visited “basin-like depressions, now silted up" near the village of "Itampúlu-bé" and recovered abundant remains of elephant bird, pygmy hippo, crocodile, cattle, bushpigs, and other mammals and birds (Last 1895:245). Many of these specimens were sold to the Natural History Museum in London. In the late 1890's and early 1900's, Eugène Bastard and Guillaume Grandidier made additional collections from the same taxa in the area for the National Museum of Natural History in Paris, and this included the excavation of coastal ponds ~6 km north of Tampolove and at a site called Lamboharana (near the modern village of Lamboara) (G Grandidier 1905). The last expedition to expand museum collections in Europe came through the Vernay-Archbold Expedition of 1929, during which E.I. White excavated a pond in the vicinity of "Itàmpolové" while M. Ramamonjy of the Académie Malgache led additional excavations at Lamboharana/Lamboara (White 1930).

Though Charles Lamberton omitted Itampolove/Tampolove from his map of Malagasy subfossil sites (Lamberton 1934) and created some confusion between the sites of Itampolove and Itampolo, which is 300 km to the south (Tattersall 1987), bones recovered from Itampolove/Tampolove and the nearby site of Lamboharana/Lamboara significantly shaped our understanding of Malagasy prehistory. Specifically, drilled teeth of the extinct giant aye-aye (MacPhee and Raholimavo 1988) and a couple of modified femora of extinct pygmy hippos directly dated to ~2000 cal BP (MacPhee and Burney 1991) from Lamboharana/Lamboara give some of the earliest evidence of interactions between humans and megafauna on the island. However, both sets of modified bone lack stratigraphic context, and the perimortem status of the hippo bone marks has been questioned based on observation that metal blades of excavators can produce clean chopmarks on bone embedded in stiff sediment (Anderson, et al. 2018). Additionally, the Lamboharana/Lamboara hippo chop marks cut through the entire femoral shaft, which may be more characteristic of tool production than butchery damage (Anderson, et al. 2018). Past bone tool use is undescribed on Madagascar but known from the archaeological records of other islands. For example, on New Zealand, the Maori used moa bone to create fish hooks (Teviotdale 1929) and whale bone to manufacture a variety of artifacts (Cunliffe and Brooks 2016).

The bone assemblages from the vicinity of Tampolove document significant changes in the composition of faunal communities. Specifically, aquatic birds and large, permanent bodies of fresh water are currently scarce. However, the diverse assemblage of subfossil bird bones from Lamboharana/Lamboara, including the extinct Malagasy shelduck (*Alopochen sirabensis*) and Malagasy crowned eagle (*Stephanoaetus mahery*) as well as the extirpated yellow-billed stork (*Mycteria ibis*) and African spoonbill (*Platalea alba*), reflects a community that likely exploited habitat with relatively abundant surface water during recent millennia (Goodman and Rakotozafy 1997). Additionally, direct dating of megaherbivore bone from past excavations suggest that the arrival of zebu cattle approximately coincided with the local disappearance of pygmy hippos and giant tortoises ~1000 cal BP (Hixon, et al. accepted). Both the past extent of human activity around Itampolove/Tampolove and the local persistence of extinct megaherbivores during past megadrought are uncertain.

C. Methods

Survey & Excavation

During July, 2019, ten members of the Morombe Archaeological Project (MAP) completed archaeological survey over an area of ~7 km^2 in the vicinity of Tampolove. Crew members walked N-S transects while spaced ~10 m apart and systematically recorded and collected surface bones, ceramics, and ratite eggshell (Fig. 3). Survey samples were stored at MAP headquarters in Andavadoaka. Opportunistic survey during August and September 2019 targeted the recovery of megafaunal bone from the surface sediments of coastal rockshelters and the margins of other coastal ponds in the vicinity of Tampolove (Fig. 4).

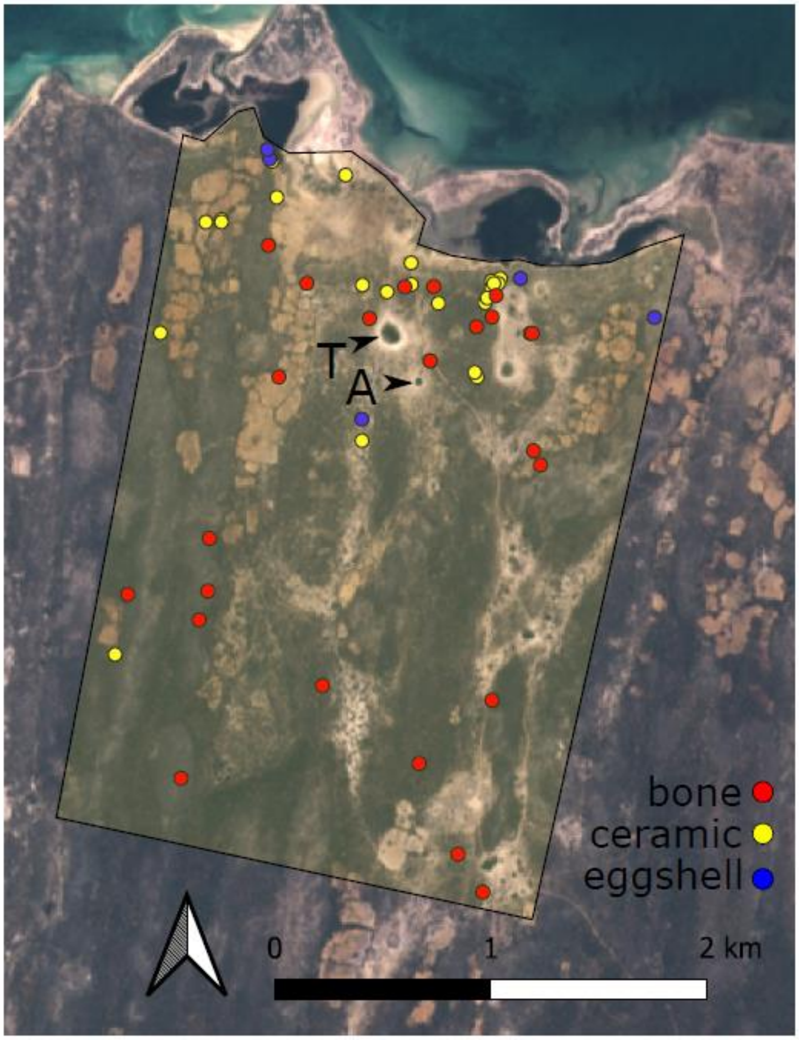


Figure 3. Survey in the vicinity of Tampolove, with material type color coded and Tampolove and Ankatoke excavation sites marked with “T” and “A.”

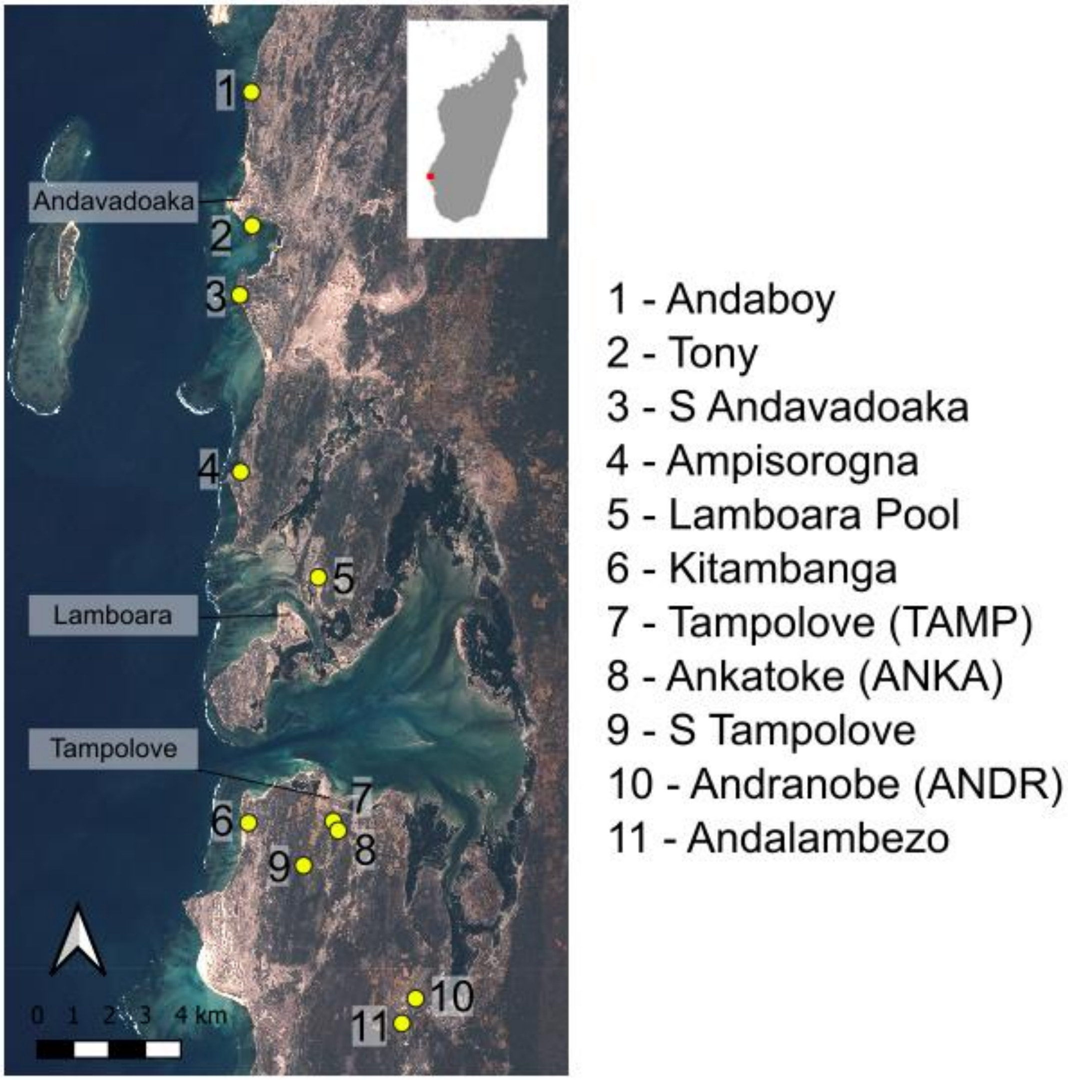


Figure 4. Map illustrating locations of excavated ponds (TAMP, ANKA, ANDR) relative to the modern towns of Andavadoaka, Lamboara, and Tampolove and other sites that produced directly ^{14}C dated bone that is discussed in the text (numbered from N to S).

During August, 2019, we excavated a 1 × 1 m pit at TAMP and 1 × 2 m pits at ANKA and ANDR (Fig. 5). Excavations on the edge of each pond reached ≤120 cm depth below surface (~5 m^3 of sediment excavated total). We chose to excavate at random on the muddy margins of each pond to minimize flooding. Groundwater consistently filled pits once we dug below ~50 cm, but this flow was not rapid enough to require routine use of our suction pump. During excavation, we recorded the provenience of all charcoal, unburnt wood, bones, ratite eggshell, keratin, and artifacts. We noted the provenience of individual bone fragments when they were scarce. Otherwise, both small bone fragments and any material >2 mm recovered during the wet screening of excavated sediment were assigned to their corresponding layers. We defined layers based primarily on sediment qualities and in some cases on artificial boundaries. Given abundant traces of bioturbation throughout the pond sequences, we used a coarse 10 cm sampling interval during the collection of sediment samples for laboratory analysis. In the field, we noted contacts and fresh sediment Munsell color and used a 14× triplet magnifier to estimate other changes in sediment quality (i.e., grain size, composition, rounding). The bulk of the most common material (megafaunal bone) was labelled, photographed, and stored in plastic bags at MAP headquarters in Andavadoaka. The excavation and export of samples was completed with authorization of the University of Toliara, the Ministry of Mines (permit No 1396/MMRS/SG/DGM/DGAM/PCMAIVT), and regional political offices. All sediment samples, charcoal, wood, representative samples of artifacts, small animal bones, and bone samples of introduced and endemic animals targeted for chemical analysis were exported to Pennsylvania State University (PSU). Specimens were photographed before destructive analysis, and the 3D form of a cutmarked pygmy hippo bone (recovered from TAMP and described in detail below) was recorded through structure from motion mapping.

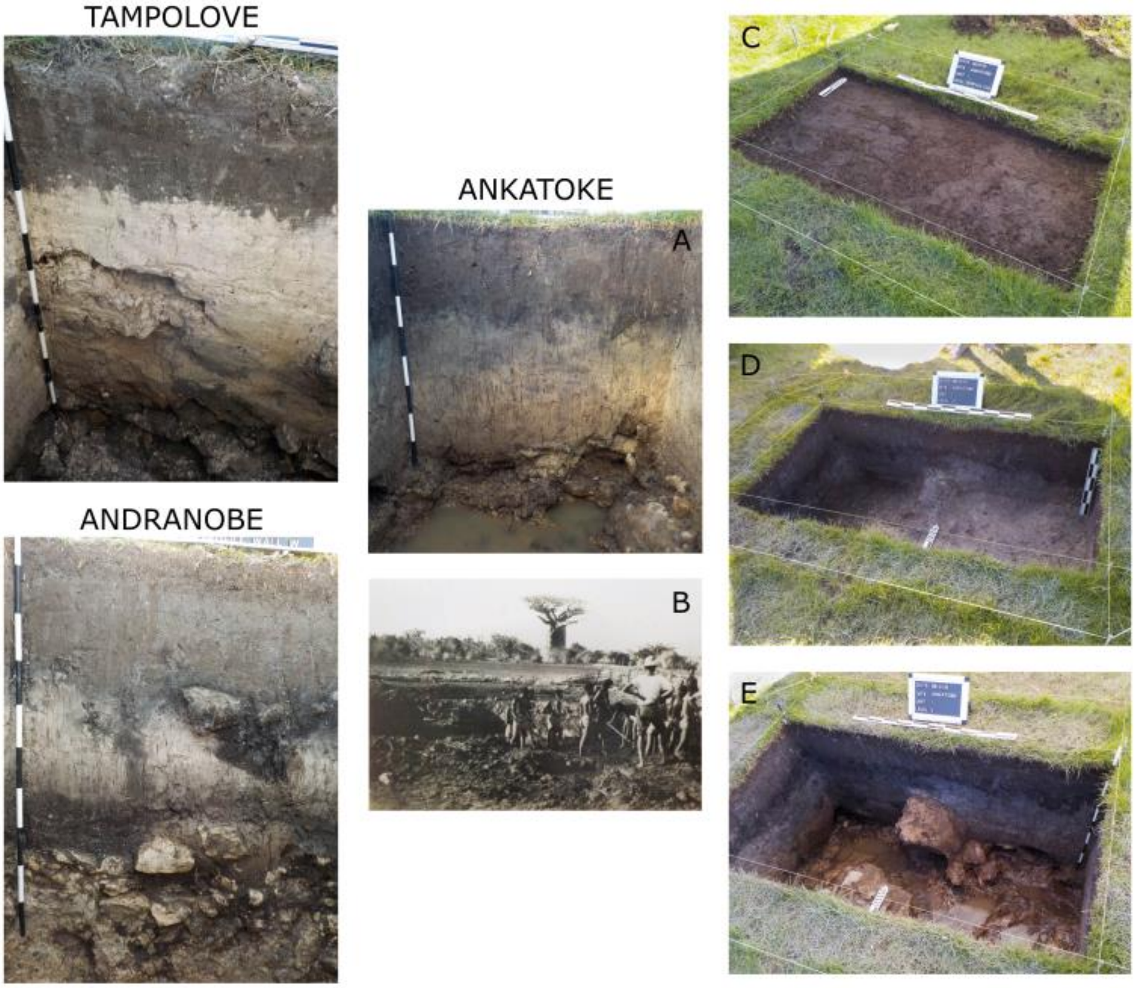


Figure 5. Profiles of Tampolove (W wall), Ankatoke (E wall), and Andranobe (W wall). Errol White likely made extensive excavations at Ankatoke in 1929 (B), and we excavated here a 1 × 2 m trench that passed through surface soil (C), clay (D), and sandy mud around pebbles to boulders (E). Figures 6-8 give cartoons of each profile with full field notes on sediment and organic remains.

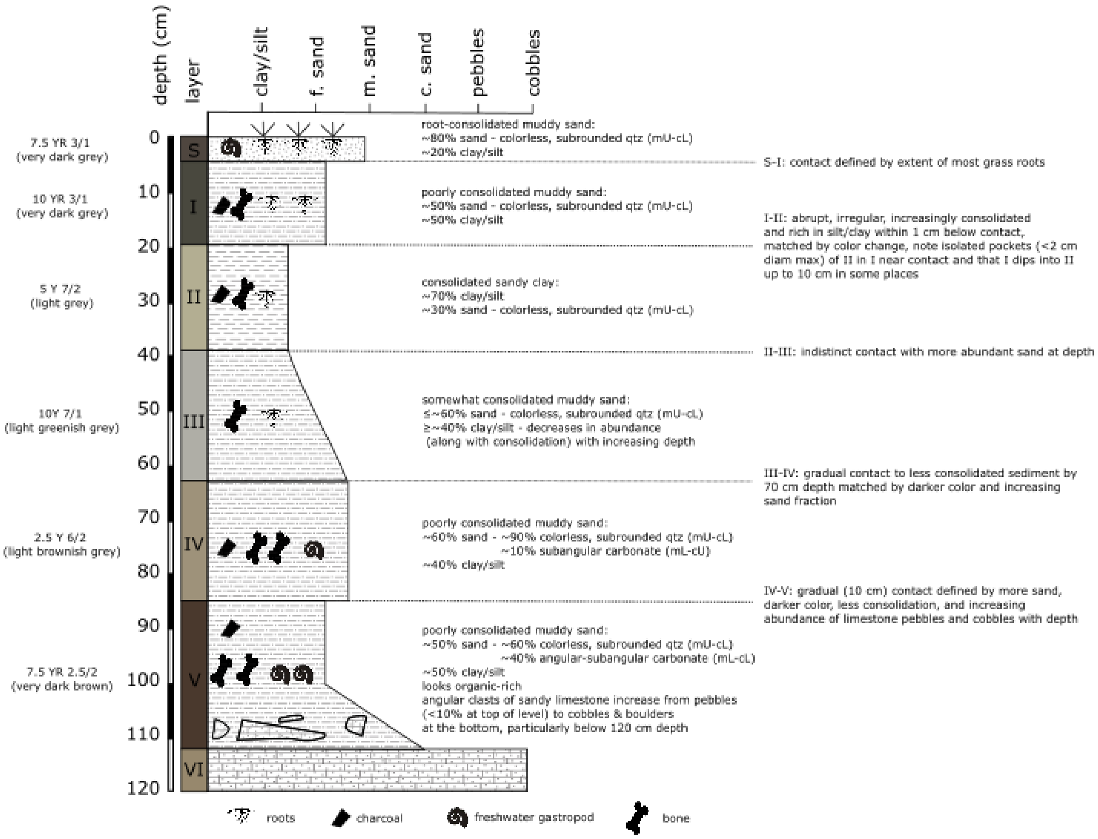


Figure 6. Tampolove stratigraphic profile from the SW corner of the pit, with full field notes on sediment and organic remains.

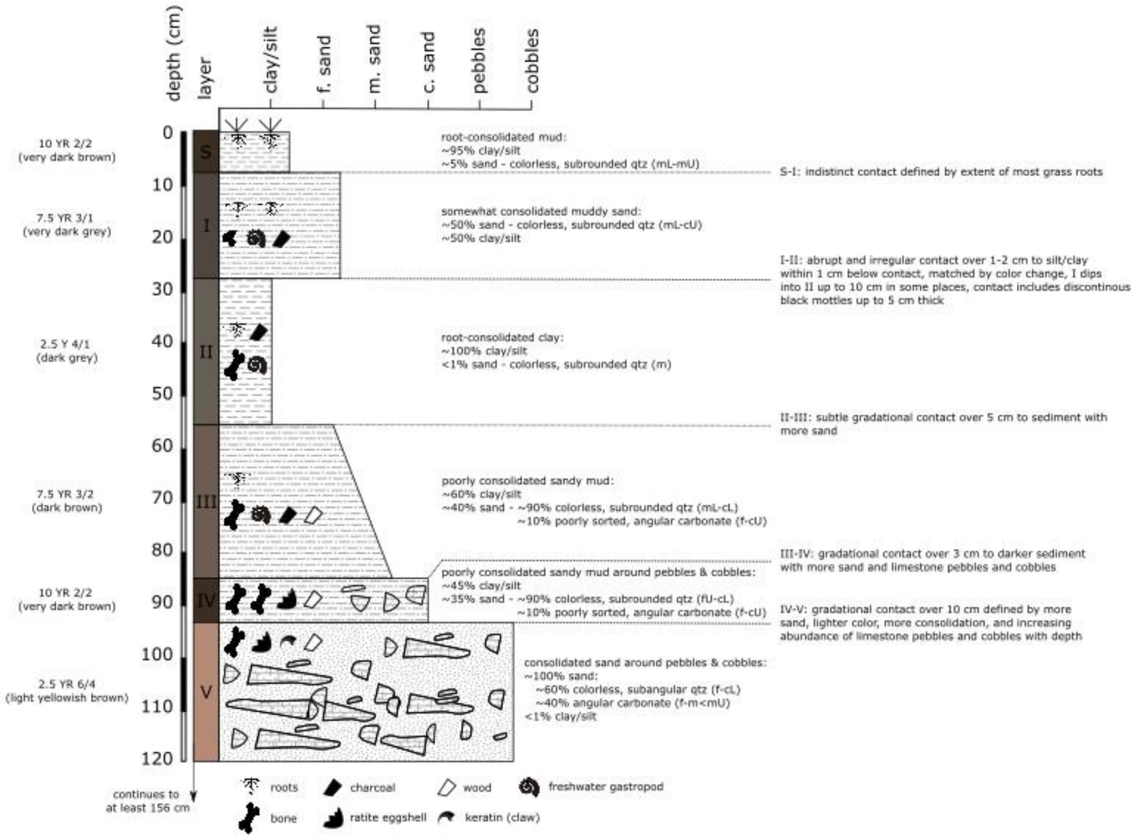


Figure 7. Ankatoke stratigraphic profile from the NE corner of the pit with full field notes on sediment and organic remains.

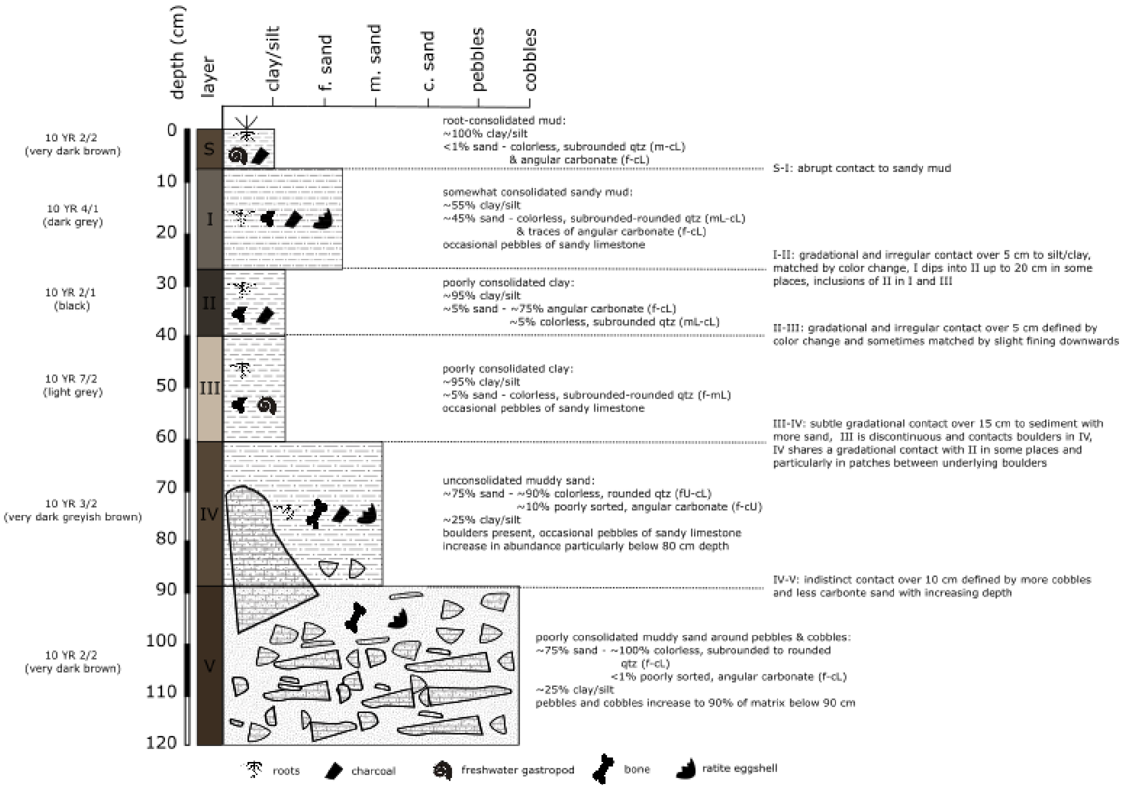


Figure 8. Andranobe stratigraphic profile from the SW corner of the pit, with full field notes on sediment and organic remains.

Sample Analysis

Analyses of excavated sediment took place at PSU. Elemental abundance data from excavated sediment were produced using an Olympus DeltaX model x-ray fluorescence (XRF) core scanner and Geotek MSCL 7.9 Multisensor Core Scanner Innoux 1776 at PSU. The trace element composition of sediment is sensitive to a variety of physical and chemical processes that may help explain changes in the diversity of associated plant and animal remains. Specifically, dry conditions and low lake levels may drive relatively more Ca deposition (Haberzettl, et al. 2007; Kylander, et al. 2011). Deposition of biogenic silica can drive higher Si concentrations (Agnihotri, et al. 2008; Dickson, et al. 2010), and times with greater physical relative to chemical weathering are more likely to deposit mobile elements such as K (Aufgebauer, et al. 2012; Piva, et al. 2008).

We obtained high resolution imagery of key finds (e.g. shallow megafaunal bone fragments and cutmarks on pygmy hippo femur) using a Keyence VHX-7000 laser scanning digital microscope, and we used a portable Artec Space Spider (Artec 3D, Luxembourg) to create a 3D mesh of the cutmarked pygmy hippo femur before destructive sampling. Charcoal and bone selected for ^{14}C analysis (n = 7 for charcoal, 76 for bone) was pretreated at the PSU Stable Isotope Geochemistry Laboratory and analysed at the PSU AMS Laboratory. We removed contaminating humates and carbonates from charcoal prior to analysis by pretreating samples with acid/base/acid (ABA) washes that involved 20 min at 60°C with 1N HCl and 1N NaOH followed by repeated rinses in nanopure water (Kennett, et al. 2014). Bones destined for ^{14}C analysis were mechanically cleaned, demineralized in 0.5 N hydrochloric acid (HCl) under refrigeration, and gelatinized in 0.01 N HCl at 60°C. Of the 76 bone samples, 29 failed protein extraction during demineralization, and 3 required more confident taxonomic ID before continuing analysis (Table 1). We purified crude collagen from the remaining 44 samples through ultrafiltration (Beaumont, et al. 2010; Fernandes, et al. 2021; D. J. Kennett, et al. 2017) or XAD resin column chromatography (Lohse, et al. 2014; Stafford, et al. 1988; Stafford, et al. 1991).

Prior to graphitization and ^{14}C analysis of bone samples, we confirmed sample quality and collagen preservation using both our percent collagen yield and atomic C:N data gathered from the Yale Analytical and Stable Isotope Center (Beaumont, et al. 2010; D. Kennett, et al. 2017; Van Klinken 1999). Residual contaminants can have distinct C:N, and this was the case for 8 samples (Table 1). This left 36 specimens for ^{14}C

analysis, 4 of which were suspected of being duplicates from the same individuals as other specimens (given that they could be fragments of the same bone or different bones from the same individual), and 3 of which required more confident taxonomic ID before continuing analysis. We ultimately chose to ^{14}C date 31 specimens that likely come from 29 individuals: A single pygmy hippo from TAMP likely produced a ^{14}C-dated right femur (PSUAMS 8666, 1880±20 ^{14}C BP) and the fused vertebrae (PSUAMS 8730, 1865±15 ^{14}C BP) that we chose to date, and a single giant tortoise from the same site likely produced both a ^{14}C-dated plastron fragment (PSUAMS 3955, 3955±25 ^{14}C BP) and carapace fragment (PSUAMS 8670, 3925±25 ^{14}C BP) that we chose to date.

Table 1. Summary of bone specimen counts and attrition during pretreatment for ^{14}C analysis. Of 76 specimens selected for analysis, 31 were directly dated. When combined with previously-published ^{14}C data, the total analyzed sample from the vicinity of Tampolove includes data from 66 bone specimens. See main text for explanation regarding the date count from TAMP (*), which includes two duplicate specimens, and note that five previously-published ^{14}C dates from Tony (Fig. 4) come from ratite eggshell calcite.

Site	**Sample Sizes**					
	Starting	Failed Extraction	C:N>3.5	To ID	Duplicates	^{14}C dated
Tampolove (TAMP)	30	14	2	1	3	12*
Ankatoke (ANKA)	21	6	2	4	0	9
Andranobe (ANDR)	7	1	3	0	1	2
Multiple - Survey	18	8	1	1	0	8
Multiple - Prev. Pub.	-	-	-	-	-	35
TOTAL	76	29	8	6	4	66

To expand our subfossil ^{14}C dataset, we compiled ^{14}C data from all specimens previously collected along a ~30 km stretch of coast around Tampolove (Fig. 4, Douglass, et al. 2019; Hixon, et al. accepted). This includes data from identified specimens previously gathered in the vicinity of Itampolove/Tampolove (n=5), Lamboharana/Lamboara (n=13), Andavadoaka (n=10), and multiple sites near Andavadoaka (Andaboy, Tony, Ampisorogna, n=7).

Data Analysis

We normalized XRF elemental profiles to Ti, except in the case of Fe, which we normalized to Mn to serve as a ‘palaeo-redox indicator’ given that reduction and release of Mn from sediments precedes that of Fe (Haberzettl, et al. 2007). We used principal components analysis of normalized data to help synthesize consistent trends in elemental profiles across sites.

We calibrated all charcoal and bone dates in OxCal 4.4 using SHCal20 (Hogg, et al. 2020), or the post-bomb atmospheric SH3 curve (Hua, et al. 2013) for three specimens that yielded $>^{14}$C modern ages. We used Fisher’s exact test to compare the proportions of directly dated megafaunal individuals (hippos and giant tortoises) that died during relatively wet and dry intervals inferred from previously-published records from SW Madagascar and the Mascarene Islands (Camoin, et al. 2004; Li, et al. 2020; Vallet-Coulomb, et al. 2006).

D. Results

Survey

Surface survey in the vicinity of Tampolove recovered a somewhat even spread of surface bone, while ceramics and ratite eggshell fragments were concentrated relatively close to the shore (Fig. 3, Dataset S1). Zebu were most commonly represented in the surface bone scatters, but small tortoises, small reptiles, and ovicaprids or bushpigs were also collected. Only one bone of extinct megafauna was recovered from the surface within this study area, and it was a giant tortoise carapace fragment found under an inland limestone ledge. Local informants from Tampolove shared stories of zebu that occasionally became entrapped in the thick sediment of nearby coastal ponds and mentioned that large bones not belonging to zebu occasionally surface on the margins of these ponds during cultivation.

Opportunistic survey of other coastal rock shelters near Kitambanga (Fig. 4) and Andavadoaka recovered three additional specimens of giant tortoise carapace. Similar surface survey of coastal ponds near Andalambezo and Lamboara recovered bone fragments of pygmy hippo, giant tortoise, crocodile, and zebu. A local guide led us to the pond near Andalambezo where he had unearthed pygmy hippo and giant tortoise bone fragments while cultivating sweet potatoes. We recovered megafaunal bone fragments at Lamboara on the surface of eroding heaps of sediment immediately adjacent to hollowed depressions in the limestone.

Excavated Sediment

Fossiliferous sandy marine limestone defines the base of each profile (Fig. 6-9, TAMP VI, ANKA V, ANDR V). This limestone crops out on the margin of each pond, and the fossils include primarily marine gastropods at TAMP and ANKA but also ratite eggshell at ANDR. The extent of this limestone below 120 cm depth at TAMP is unknown due to a boulder that blocked excavation. This sandy limestone occurs as relatively friable cobbles at ANKA, and we recovered no terrestrial bone from the light yellowish brown sand between these cobbles at 120 and 105 cm depth. The same is true of the very dark brown muddy sand between these cobbles at ANDR.

The stratigraphy of the overlying soft sediment includes shared patterns among TAMP, ANKA, and ANDR. This is most visibly exemplified by a layer of clay (zone 2 in Fig. 6-9), which separates the surface soil formation (zone 1) from the underlying fossiliferous muddy sand and bedrock (zone 3). Each zone has a distinct lithology and elemental composition, and these differences are consistent among sites.

Zone 3. Relatively high Fe/Mn and organic content distinguish zone 3 (TAMP IV-V, ANKA III-IV, ANDR IV) from the overlying sediment (Dataset S4), and the sand in this muddy sediment includes both quartz and carbonate grains. The colorless quartz component is invariably dominated by rounded medium-coarse sand, which is similar to what forms the dunes to the west. The relatively small carbonate component is poorly sorted and angular, with some clasts that come from the underlying limestone and some fragments of planorbid snail shell. Sulphur was detected only at TAMP and only in zone 3 of this site's sequence. Decreasing limestone clasts up zone 3 at all sites contributes to a fining trend toward the top of this zone.

Zone 2. A gradational contact that spans 5-10 cm separates the sediment of zone 3 from the light grey consolidated clay of zone 2 (TAMP II-III, ANKA II, ANDR II-III). The clay has high Ca/Ti and scarce organics. It includes a substantial quartz sand component only at TAMP, and the carbonate sand component of zone 3 is almost entirely absent.

Zone 1. Intermediate Ca/Ti values, coupled with relatively high Si/Ti and K/Ti values, characterize the surface sediment and soil formation of zone 1 (TAMP S-I, ANKA S-I, ANDR S-I). An abrupt and irregular contact separates the surface sediment from the underlying clay of zone 2, yet clay inclusions from zone 2 (≤5 cm diameter) occur in zone 1 immediately above the contact. The sediment in zone 1 includes a relatively abundant component of quartz sand, but this is indistinct in the muddy root mat that forms the surface of each profile.

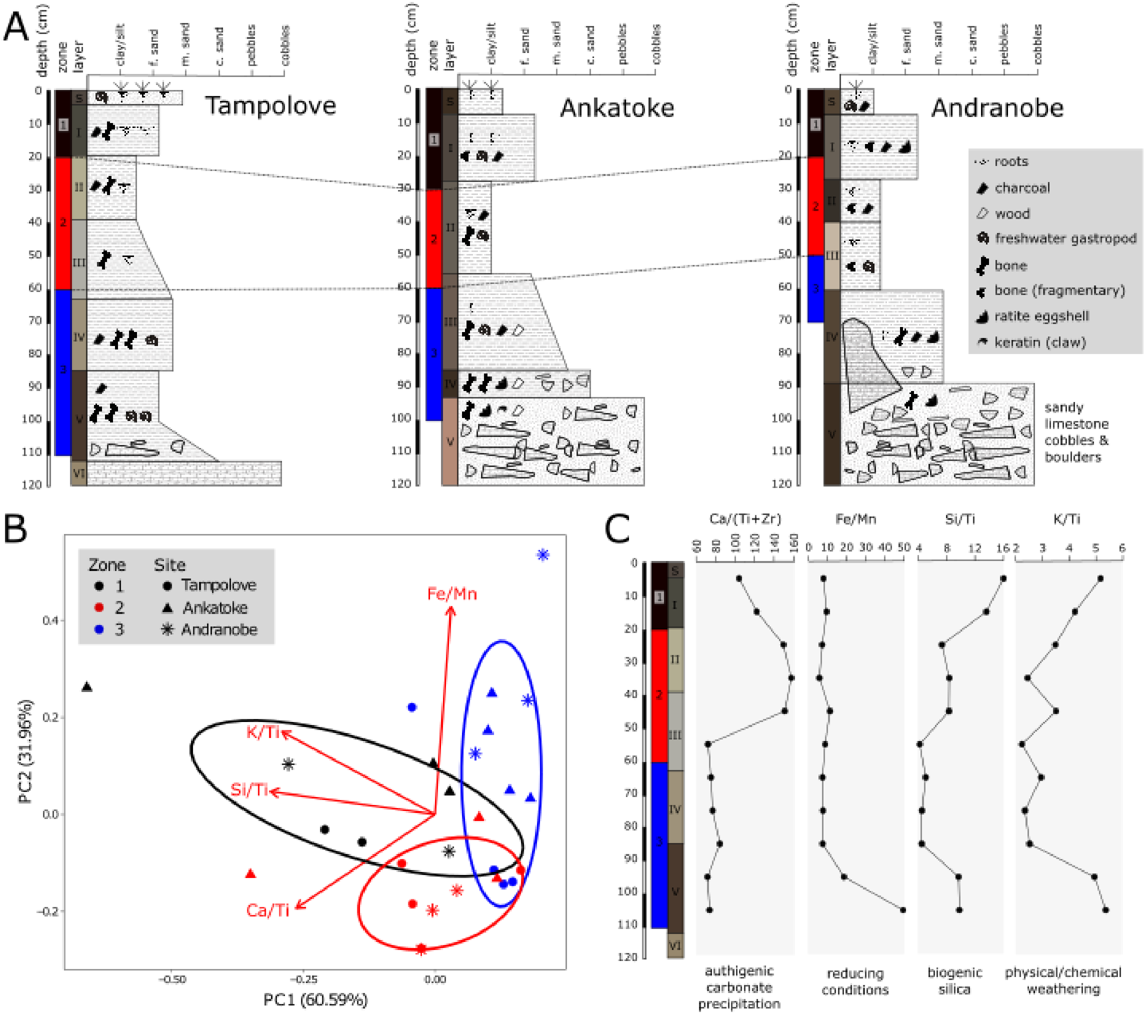


Figure 9. Lithology of excavated pond sediments, including stratigraphic profiles (A), principal components analysis of sediment XRF data with ellipses that outline 68% of the data from each group (B), and XRF profiles from Tampolove for example (C). Each sequence in (A) includes a relatively fine-grained, consolidated, and grey unit (zone 2) that separates underlying megafaunal bone beds (including zone 3) from overlying soils (zone 1). These zones are similar across sites and are geochemically distinct (B). XRF data from Tampolove are representative and plotted for reference (C). Note that the depth of sediment layers varies by up to ~10 cm across each excavated trench, so stratigraphic profiles for Tampolove and Andranobe represent the SW corner of the trench, and that for Ankatoke represents the NE corner of the trench.

Chronology and Subfossils

Deposits of pond margin sediments that span a greater depth include bones that span a relatively long period of time (Figs. 10-12, Dataset S2). This span ranges from ~6,000 years at TAMP (~120 cm sediment sequence) to ~2,500 years at ANDR (~100 cm sediment sequence). The average sedimentation rates at TAMP and ANKA since the mid-Holocene are comparable (~2 cm/century) and possibly half that at ANDR during the late Holocene (~4 cm/century).

Zone 3. Most bones in this layer are only somewhat fragmentary and include readily identifiable pygmy hippo long bones and cranial fragments (e.g., Fig. 13a,f), giant tortoise carapace and plastron fragments (Fig. 13d), ratite eggshell and long bones (Fig. 13c,m), and crocodile scutes, cranial fragments, and teeth (Fig. 13b, Dataset S3). The widespread success of collagen extraction from these bones attests to the excellent preservation of organics in this zone. ANKA also includes keratin (mostly in the form of crocodile claws, e.g., Fig. 13i), as well as a couple of rounded agates found in association with ratite eggshell (Fig. 13m). The epiphyses of some of the pygmy hippo long bones have gnaw marks (Fig. 13f), and none of the bones include immediately noticeable chopmarks. In association with these bones towards the top of this zone are some large (>1 cm diameter) charcoal fragments and scarce bones of bushpig (Fig. 13k,l) and zebu (Fig. 13e). This zone at TAMP and ANDR also includes occasional mangrove whelk (*Terebralia palustris*) shells (Fig. 13g). These whelks currently live at least ~500 m distant from these ponds, and whelk shells at ANDR each have an irregular hole above the operculum that is analogous to holes that people currently create to extract the snails from their shells. The span of time represented by bones in this layer ranges up to ~4,000 years (~6000-2000 cal BP at TAMP, Fig. 10). There are multiple examples of directly ^{14}C-dated bone in close stratigraphic association that nonetheless differ in age by >1,000 years, and there are a couple of examples of bones from the same individual that are separated stratigraphically. For example, the aforementioned giant tortoise carapace and plastron fragments from TAMP that have indistinguishable ^{14}C ages are separated by 22 cm of sediment (PSUAMS 8670 comes from 112 cm depth, and PSUAMS 8668 comes from 90 cm depth).

Zone 2. Bones in this layer are relatively scarce, fragmentary, and chalky, yet they include readily identifiable fragments of hippo (Fig. 13h), giant tortoise, crocodile, and zebu. TAMP zone 2 (Fig. 10) includes both a chopped distal fragment of a pygmy hippo right femur (Fig. 14) and an associated scatter of marine fish bones (cranial fragments, vertebrae ~1 cm in diameter, and spines), one of which (a vertebra) includes a chop mark (Fig. 13j). Unfortunately, both chopped pygmy hippo fragment and associated fish bones failed ^{14}C analysis due to the exceptionally poor preservation of bone protein. Charcoal fragments with provenience in zone 2 come from only ANKA and ANDR, and shells of the mangrove whelk are relatively abundant in ANDR zone 2. The preservation of bone proteins in the clay of zone 2 is mostly very poor, particularly at TAMP. The only directly dated collagen from zone 2 (extracted from a fragmentary pygmy hippo molar from ANKA, 55 cm depth, PSUAMS 8733, 3555±20 ^{14}C BP, 3880-3700 cal BP) is >2,000 years older than a closely associated charcoal sample (38 cm depth, PSUAMS 8849, 575±30 ^{14}C BP, 630-510 cal BP), which makes this molar comparable in age to bone from zone 3. Directly dated charcoal that brackets zone 2 spans the past millennium.

Zone 1. A fragment of iron (from TAMP, 16 cm depth) and sparse ceramic fragments (from ANKA, 3 & 9 cm depth) are present only in zone 1. Small fragments of non-identifiable bone and charcoal (mostly ≤ 1 cm diameter) are also present at all three sites, and three ^{14}C dates from TAMP and ANKA suggest that these specimens span the past ~200 years.

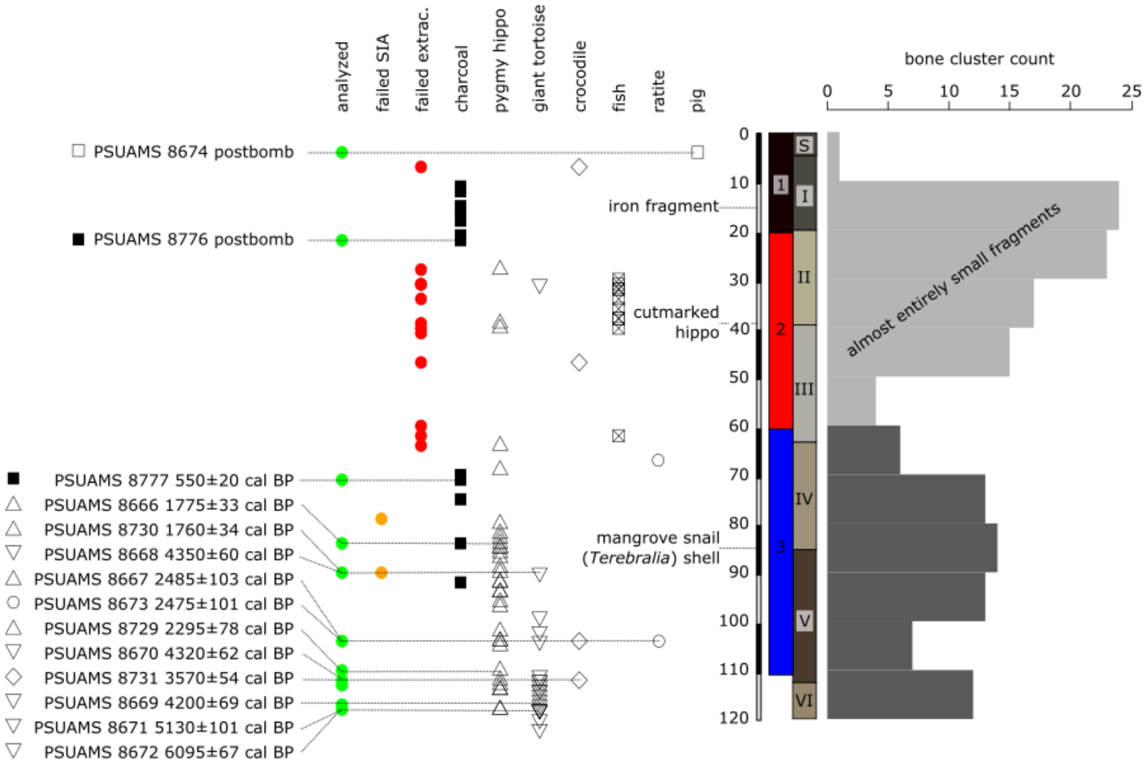


Figure 10. Faunal and charcoal occurrence and ^{14}C data from Tampolove, with colored layers and zones from Fig. 9 for reference. Green circles mark depths of ^{14}C-dated plant and animal remains, orange circles mark depths of bones that yielded collagen with signs of contamination, and red circles mark depths of bones that failed collagen extraction. Depths of only confidently-identified bones are shown, and points are shaped according to taxon. Associated ^{14}C data are given at left with ages (μ±σ) calibrated using SHCal20. Note that two directly dated pygmy hippo bones have indistinguishable ^{14}C dates and may come from the same individual, and the same is true for two directly dated giant tortoise bones. The histogram at right gives counts of depth-recorded bone clusters binned at 10 cm increments. Note that very few of the small bone fragments in the upper section of the sequence can be confidently identified and that the cutmarked hippo referenced in this figure corresponds to TAMP-1-2-61 in Fig. 14.

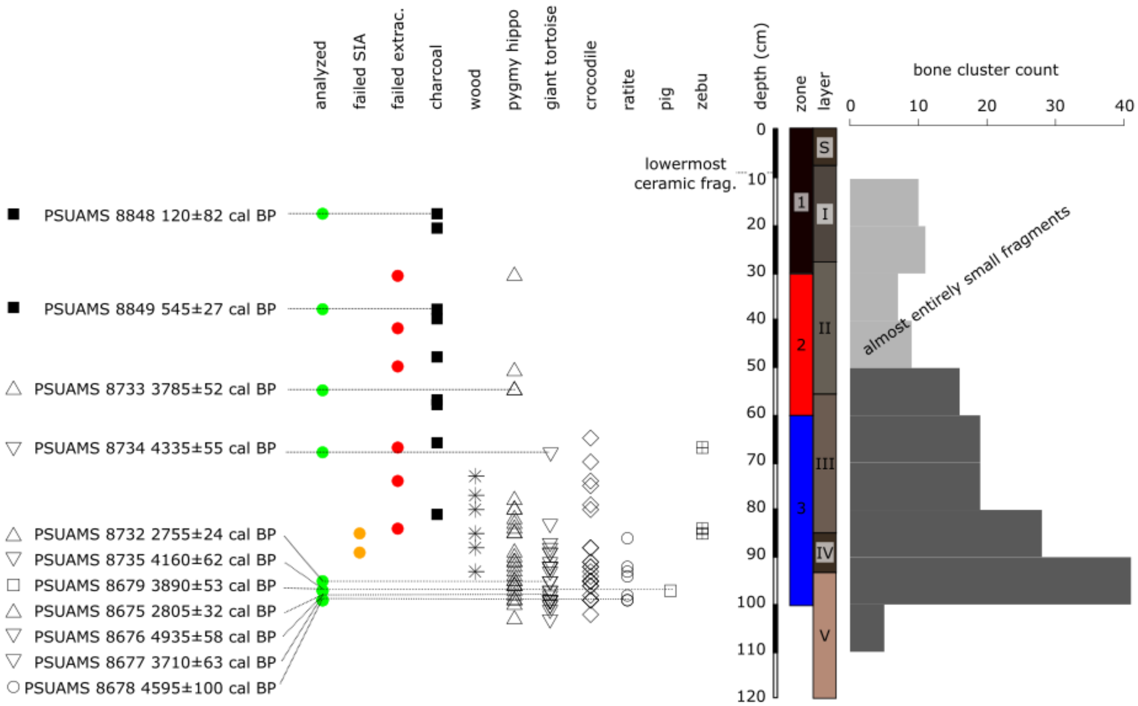


Figure 11. Faunal and charcoal occurrence and ^{14}C data from Ankatoke, with colored layers and zones from Fig. 9 for reference. Green circles mark depths of ^{14}C-dated plant and animal remains, orange circles mark depths of bones that yielded collagen with signs of contamination, and red circles mark depths of bones that failed collagen extraction. Depths of only confidently-identified bones are shown, and points are shaped according to taxon. Associated ^{14}C data are given at left with ages (μ±σ) calibrated using SHCal20. The histogram at right gives counts of depth-recorded bone clusters binned at 10 cm increments. Note that very few of the small bone fragments in the upper section of the sequence can be confidently identified.

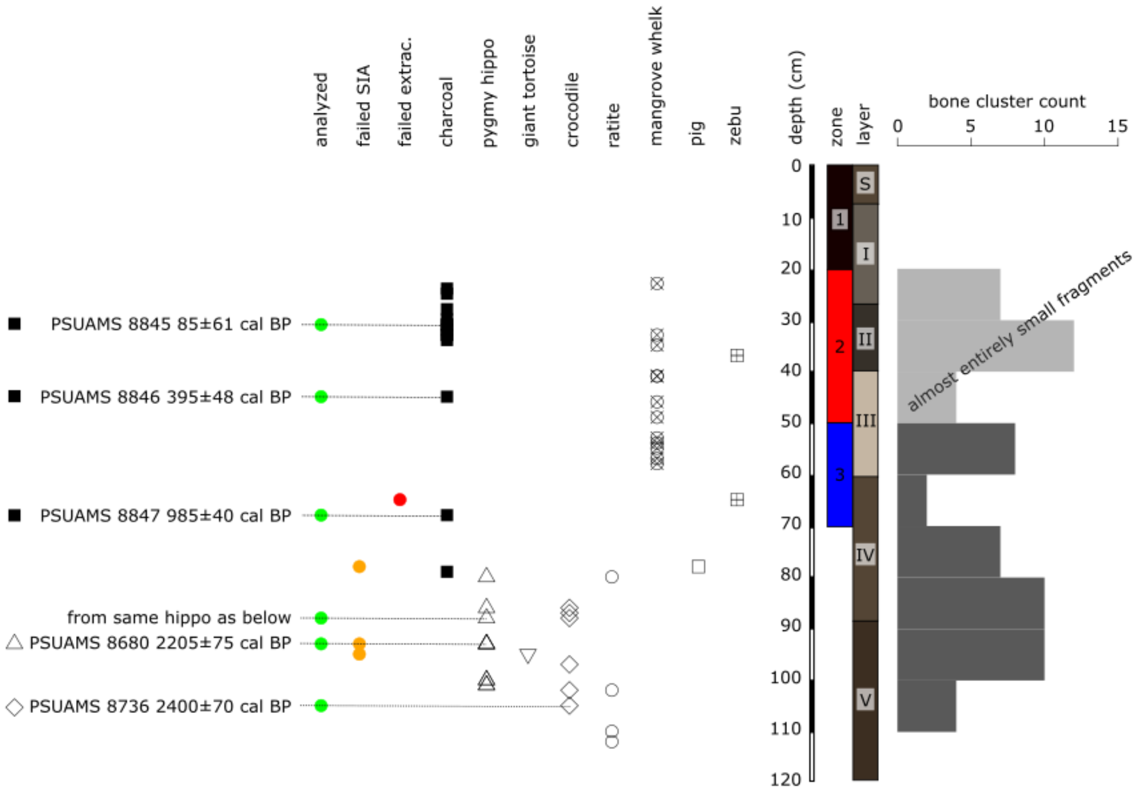
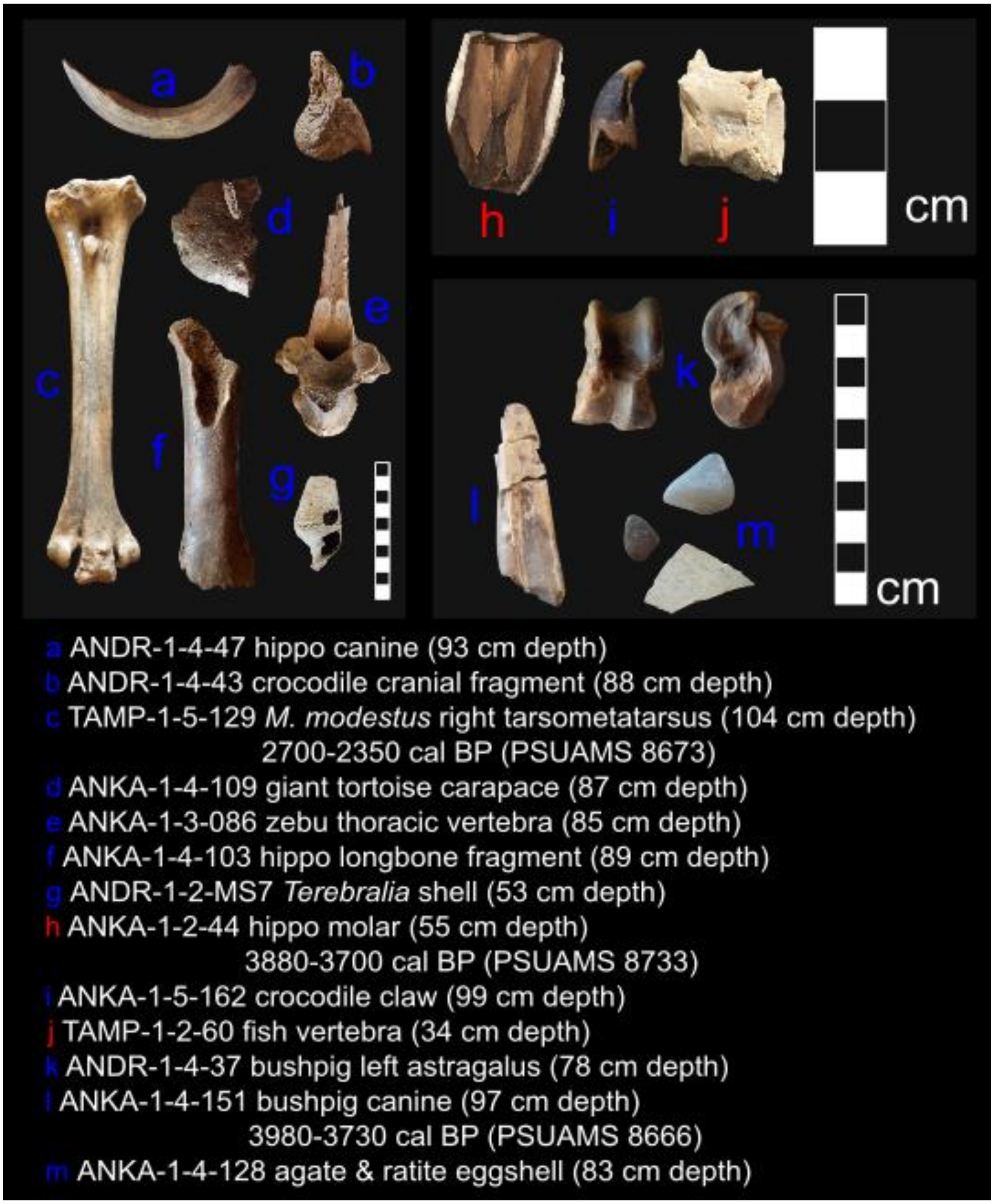


Figure 12. Faunal and charcoal occurrence and ^{14}C data from Andranobe, with colored layers and zones from Fig. 2 for reference. Green circles mark depths of ^{14}C-dated plant and animal remains, orange circles mark depths of bones that yielded collagen with signs of contamination, and red circles mark depths of bones that failed collagen extraction. Depths of only confidently-identified bones are shown, and points are shaped according to taxon. Associated ^{14}C data are given at left with ages (μ±σ) calibrated using SHCal20. The histogram at right gives counts of depth-recorded bone clusters binned at 10 cm increments. Note that very few of the small bone fragments in the upper section of the sequence can be confidently identified.



a ANDR-1-4-47 hippo canine (93 cm depth)
b ANDR-1-4-43 crocodile cranial fragment (88 cm depth)
c TAMP-1-5-129 *M. modestus* right tarsometatarsus (104 cm depth)
2700-2350 cal BP (PSUAMS 8673)
d ANKA-1-4-109 giant tortoise carapace (87 cm depth)
e ANKA-1-3-086 zebu thoracic vertebra (85 cm depth)
f ANKA-1-4-103 hippo longbone fragment (89 cm depth)
g ANDR-1-2-MS7 *Terebralia* shell (53 cm depth)
h ANKA-1-2-44 hippo molar (55 cm depth)
3880-3700 cal BP (PSUAMS 8733)
i ANKA-1-5-162 crocodile claw (99 cm depth)
j TAMP-1-2-60 fish vertebra (34 cm depth)
k ANDR-1-4-37 bushpig left astragalus (78 cm depth)
l ANKA-1-4-151 bushpig canine (97 cm depth)
3980-3730 cal BP (PSUAMS 8666)
m ANKA-1-4-128 agate & ratite eggshell (83 cm depth)

Figure 13. Examples of material recovered from Tampolove (TAMP), Ankatoke (ANKA), and Andranobe (ANDR) and discussed in the text. These come from stratigraphic zones 2 and 3 (red and blue, respectively), with corresponding 2σ calibrated age ranges for three directly specimens and depths below surface given in parentheses.

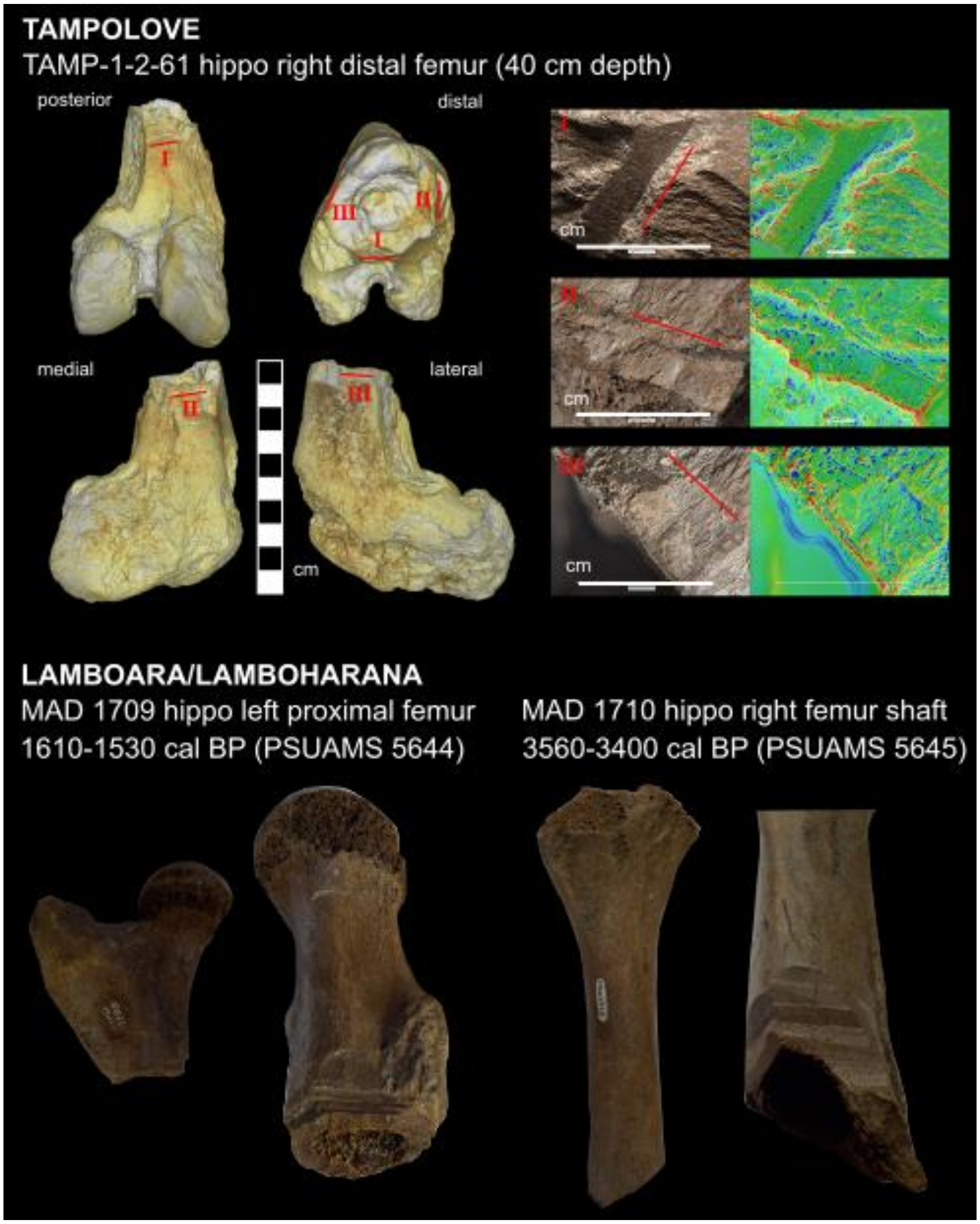


Figure 14. Cutmarked pygmy hippo femur recovered from Tampolove during recent excavation at ~40 cm depth (TAMP-1-2-61, above), and previously-recovered and directly ^{14}C-dated (~3500 and 1600 cal BP, MacPhee and Burney 1991) cutmarked pygmy hippo femora from the nearby site of Lamboara/Lamboharana that are currently housed in the National Museum of Natural History in Paris (MAD 1709 & MAD 1710, below). Four views highlight three locations of cutmarks on the broken shaft of TAMP-1-2-61, and the inset frames show 20× magnification of these areas, with corresponding orientations given by red lines. Note that the false color insets of TAMP-1-2-61 are meant to highlight linear edges and crevices, and the overview photos of all three femur fragments are on the same scale.

Directly dated bones of two pygmy hippos and three giant tortoises recovered during surface survey from other coastal ponds and rock shelters in the area span the time period represented in zone 3. Two giant tortoise carapace fragments from rockshelters near Tampolove (PSUAMS 8727, 1280±15 ^{14}C BP, 1260-1075 cal BP) and Andavadoaka (PSUAMS 8665, 1190±20 ^{14}C BP, 1180-960 cal BP) are relatively recent, and a zebu maxilla fragment from a rockshelter near Andalambezo (PSUAMS 7656) has postbomb ^{14}C content.

Hydrological Context

The deposition of bones in zone 3 spans marine transgression and multiple 'megadraughts' that likely affected SW Madagascar during the middle Holocene (Fig. 9, Camoin, et al. 2004; Li, et al. 2020). These droughts are inferred from above-average oxygen isotope values in a speleothem from Rodrigues Island, particularly during intervals of ~6,000-4,500, 4,000-3,500, 3,000-2,500, and 1,000-0 years ago (Li, et al. 2020). The proportions of ^{14}C-dated pygmy hippos (n=18) and giant tortoises (n=22) that died during these dry intervals (~33% and ~23%, respectively) are statistically indistinguishable (p=0.50, Fisher's exact test). However, the proportions of ^{14}C-dated pygmy hippos and giant tortoises that died before sea levels surpassed their present level ~4000 cal BP (0% and ~36%, respectively) are significantly different (p=0.005, Fisher's exact test).

The transition between sedimentary zones 3 and 2 (~2000-1000 cal BP) occurred both during a drought recorded in high δ^{18}O values in a speleothem ~30 km E of Tampolove (Asafora, Faina, et al. in press) and during the salinization of a pan in the coastal plains ~40 km NE of Tampolove (Lac Ihotry, Vallet-Coulomb, et al. 2006). This parallel is discussed below. The salinization of Lac Ihotry occurred during marine regression (Camoin, et al. 2004) and approximately coincided with the Medieval Warm Period (MWP) 'megadrought' of ~900 cal BP (Li, et al. 2020). Most directly-dated traces of human-introduced taxa follow the transition to sedimentary zone 2, but a bushpig from zone 3 (PSUAMS 8679 3620±20 ^{14}C BP, 3980-3730 cal BP) may represent an earlier example of past species introductions.

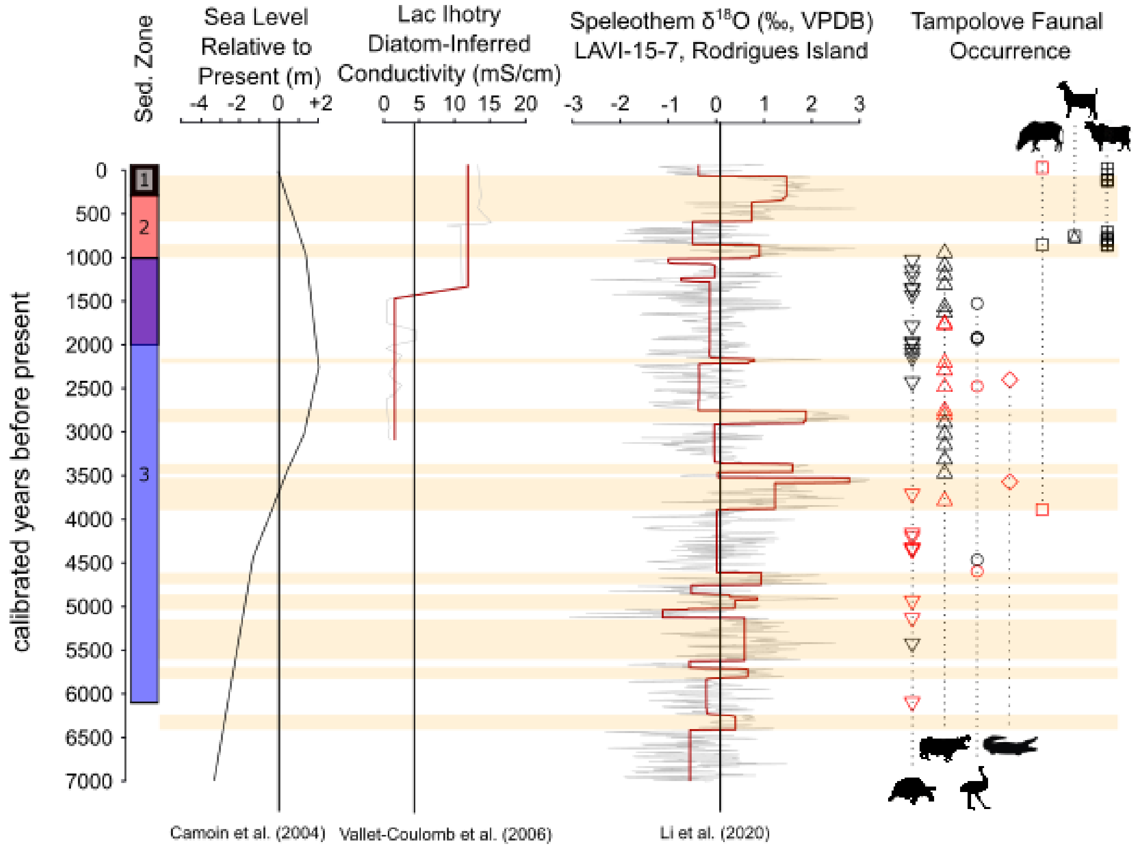


Figure 9. Occurrence of Tampolove fauna on a scale of absolute time relative to local sedimentary zones, approximate changes in relative sea level on Madagascar (Camoin, et al. 2004), a record of diatom-inferred conductivity from Lac Ihotry (~40 km NE of Tampolove Vallet-Coulomb, et al. 2006), and a composite record of speleothem δ^{18}O from Rodrigues Island (Li, et al. 2020). A radiocarbon datum from an elephant bird eggshell of 9420 mean cal BP (OxA-34217) is not shown, which leaves data from 65 specimens on display. Note that ^{14}C dated individuals recovered from TAMP, ANKA, and ANDR are marked in red, the plot includes two pygmy hippos and two giant tortoises that are likely duplicate specimens, and one of the tortoises from 2420 cal BP may come from a relatively small species. Bayesian change point analysis (BCPA) in the Ihotry and Rodriques records (dark red lines) identify intervals that can be approximated reasonably well by a single mean, and the overall means of these records are given by black vertical lines. Intervals with above average Rodrigues speleothem δ^{18}O values highlighted by

BCPA (indicative of relatively arid conditions) are highlighted with brown horizontal bars for reference.

E. Discussion

Overview of Key Findings

Paired paleohydrological and faunal occurrence data suggest that both pygmy hippos and giant tortoises had some degree of drought tolerance during the mid to late Holocene but that a novel combination of hydrological stressors could have contributed to the local disappearance of pygmy hippos during the MWP. The bushpig tooth from ANKA directly dated to ~4000 cal BP suggests that people had arrived on the island by this time, but confidently dated traces of human activity in the subsequent 3,000 years are limited. A chopmarked pygmy hippo femur may further attest to past cooccurrence between humans and extinct megafauna. However, the context of the marked bone (sedimentary zone 2 of TAMP, Fig. 10, bracketed by charcoal that spans the past ~550 years) leaves the possibility that past people modified bone of earlier subfossils. Consistent with regional patterns, faunal and charcoal records from this study indicate that the disappearance of endemic megafauna coincided with the late arrival of pastoralists ~ 1000 cal BP who cleared the forest through burning and foraged a mixture of endemic resources (e.g., marine fish and mangrove whelks).

Chronology and Regional Context

6000-1500 cal BP (Zone 3). The marine limestone bedrock in the vicinity of Tampolove formed during a Pleistocene highstand, and fragmentary limestone from the base of TAMP, ANKA, and ANDR likely reflect past karst collapse and basin formation. Though the earliest ^{14}C dated bone from ANDR (Fig. 12, a crocodile from ~1 m depth, PSUAMS 8736, ~2400 cal BP) is consistent with the idea that these depressions formed during the maximum of the Flandrian transgression (~3700 cal BP, Battistini 1964), the relatively early deposition of giant tortoise carapace fragments from TAMP (Fig. 10, e.g., PSUAMS 85672, ~6100 cal BP) suggest that at least some of these depressions could have formed earlier.

The lowermost sediments of TAMP and ANKA include limestone cobbles and megafaunal bone fragments (giant tortoises and elephant birds). These fragments are closely associated yet span ~2,000 years (during ~6000-4000 cal BP). Relatively low sea levels and high speleothem $\delta^{18}O$ values from Rodrigues suggest that this time could have been relatively dry (Camoin, et al. 2004; Li, et al. 2020). Additionally, the onset of a hiatus in sediment deposition at the site of Andolonomby/Ambolisatra (~100 km S of Tampolove) at ~5500 cal BP coincides with a decline in arboreal taxa (e.g., *Uapaca* cf *bojeri*) and the expansion of xeric spiny bush (Didiereaceae), which further suggests that the region was dry ~6000-4000 cal BP (Virah-Sawmy, et al. 2016). Consequently, the slow sedimentation during this interval may reflect the early absence of aquatic ecosystems in these coastal basins.

It is only after sea level rose above present levels ~ 4000 cal BP that hippos and crocodiles entered the subfossil record around Tampolove (though the earlier absence of crocodiles could easily be explained by limited sample size). Wind very likely imported the subrounded quartz sand that exists throughout each pond sequence, but associated organic-rich mud and planorbid snail shells indicate that deposition of most megafaunal bone in zone 3 between ~4000 and 2000 cal BP occurred in freshwater sediment. The depositional environment in the ponds was likely reducing, which explains both the high Fe/Mn values and excellent collagen preservation in zone 3.

There are multiple ^{14}C-dated giant tortoises and pygmy hippos that attest to the fact that these taxa did not abandon the coastal plains around Tampolove during 'megadroughts' that occurred during ~4000-3500 and 3000-2500 cal BP. It was only after the first of these 'megadroughts' that an open freshwater lake (Lac Ihotry) formed ~40 masl in the coastal plains ~40 km NE of Tampolove. However, relatively high coastal water tables could have somewhat compensated for climatic drying at coastal sites during these intervals. Note that, while TAMP is currently ~700 m from the beaches of the village of Tampolove, it is only ~300 m from a break in the bedrock that likely defined the coastline during the late Holocene marine highstand. The deposition of sulphur in TAMP zone 3 is consistent with reducing conditions (Sluijs, et al. 2008), but sulphur deposition can also follow from inputs of marine organic matter.

It was during the wet intervals of zone 3 that the aquatic birds of Lamboharana/Lamboara likely flourished (Goodman and Rakotozafy 1997), and these sediments may include early traces of human presence. For example, a mangrove whelk possibly deposited by people at TAMP was associated with megafaunal bone dated to ~1800 cal BP (Fig. 10), and introduced zebu bones from ANKA that failed direct dating were associated with megafaunal bone that ranged in age between ~4800 and 2800 cal BP (Fig. 11). However, the evidence for extensive bioturbation in zone 3 and redeposition of megafaunal bone in zone 2 makes the associations with megafaunal bone almost meaningless for bracketing ages. Directly dated charcoal records from all three sites are free of age reversals and may give more accurate possibilities for dating by association. Also note that a couple of well-rounded agate pebbles (one of which is banded) recovered beneath the charcoal of ANKA (Fig. 11 & 13m) are exotic to the region and were possibly deposited by people. However, the close association of these pebbles with angular fragments of ratite eggshell (Fig. 11) leaves the possibility that ratites deposited these pebbles as gizzard stones.

The bushpig tooth with a date of 3980-3730 cal BP (PSUAMS 8679) deposited at ANKA may reflect regional human presence by ~4,000 years ago. Bushpigs are typically considered a human-introduced species on Madagascar and other islands in the western Indian Ocean (Boivin, et al. 2013), but analysis of ancient DNA from bushpig bones would help confirm when Malagasy bushpig populations diverged from those in mainland Africa. Based on similarity in the Malagasy word for bushpig (*lambu*) and the Malay word for cattle (*lembu*), Blench (2007) suggests that people who arrived on Madagascar from SE Asia ~1000 cal BP encountered an unfamiliar population of feral pigs made possible through earlier human arrival from E Africa. Genetic data from modern specimens across East Africa and Madagascar confirm that Malagasy bushpigs belong to *Potamochoerus larvatus* (Lee, et al. 2020), which is frequently hunted and widely distributed south of the Sahel. The possible existence of subspecies endemic to Madagascar may attest to a long history of *P. larvatus* on the island (Blench 2007), but there is no genetic evidence for this. Holocene dispersal of *P. larvatus* to Madagascar without the aid of humans is unlikely given that ocean currents became less favorable for rafting by dispersal-disadvantaged taxa (terrestrial animals that aren't flighted, e.g., bushpigs and hippos) from mainland Africa to Madagascar after ~15 million years ago (Samonds, et al. 2012). The early Cenozoic fossil record of terrestrial vertebrates on Madagascar is unfortunately poor, but the datum presented here is consistent with the idea that humans introduced bushpigs to Madagascar possibly during the mid-Holocene. It is possible that the helmeted guinea fowl (*Numida meleagris*) was another early human-aided introduction, for it is dispersal-disadvantaged and has bones from SW Madagascar dated to over 10,000 cal BP (Goodman, et al. 2013)

1500 cal BP-present (Zone 1 & 2). Though none of the ^{14}C-dated extinct megafauna from TAMP, ANKA, or ANDR postdate 1500 cal BP, data from other deposits attest to the fact that pygmy hippos and giant tortoises persisted along the adjacent 30 km stretch of coastline until at least ~1000 cal BP. It was around this time that endemic megafauna disappeared from subfossil records across SW Madagascar (Crowley 2010; Hixon, et al. accepted). The deposition of clay-rich sediment with scarce planorbid snail shells and possible evidence of authigenic carbonate precipitation (high Ca/Ti) suggest that the start of this interval (1500-1000 cal BP) was relatively dry. Bioturbation and repeated wetting and drying of ephemeral ponds likely contributed to the fragmentary and poorly preserved bone assemblage left in this layer of clay. This distinct stratigraphic unit is likely widespread in coastal ponds around Tampolove, for J.T. Last also noted “a thick layer of white or greyish loam” under the surface soil that he excavated, and the same is true of E.I. White, who noted beneath the surface in pond sediment near Tampolove a “whitish chalky layer about six inches or a foot thick” (White 1930, 221). The diatom-inferred salinization of Lac Ihotry indicates that other coastal bodies of freshwater contracted during this time (Vallet-Coulomb, et al. 2006).

The novel combination of marine regression and climatic desiccation during the Medieval Warm Period may explain why only this most recent of the ‘megadroughts’ present in the Rodrigues record is reflected so dramatically in the stratigraphy of silted-in coastal ponds around Tampolove. Given that pygmy hippos were clearly present around Tampolove only when sea levels were higher than they are today, this novel combination of hydrological stressors could easily explain the local disappearance of these animals.

However, the early local persistence of giant tortoises in the area despite relatively low coastal water tables and periods of dry climate during the mid-Holocene suggests that they were not as sensitive to late Holocene aridification.

Large, ^{14}C-dated fragments of charcoal reflect periodic burning during the past millennium (~1000, 500, 300 cal BP), and local first occurrence data from zebu (UCIAMS 224208, 1010±15 ^{14}C BP, 930-800 cal BP) and an ovicaprid (PSUAMS 3764, 900±20 ^{14}C BP, 800-730 cal BP) confirm that livestock were present during this interval. Data from elsewhere in SW Madagascar also attest to the presence of sheep and dogs by this time (Hixon, et al. accepted). The people who occupied this area within the past millennium left traces of marine resource consumption (age bracketed by charcoal) both in coastal middens (Douglass et al. 2018) and in the zone 2 sediments that we excavated from TAMP (cutmarked fish bone) and ANDR (modified *Terebralia* shells).

The only clear case of a human-modified megafaunal bone that we excavated is the cutmarked pygmy hippo femur from TAMP (Fig. 14). Like the previously excavated specimens from Lamboharana/Lamboara (G. Grandidier 1905; MacPhee and Burney 1991), the shaft of our pygmy hippo femur is entirely cut through. This similarity, and the care with which we managed to excavate our specimen, is consistent with the idea that past excavators did not necessarily damage the specimens from Lamboharana/Lamboara. The smooth faces cut into the TAMP specimen were likely produced when the bone was relatively fresh, for the bone is currently chalky and crumbles easily. The preservation of organics in the TAMP specimen is exceptionally poor, as evidenced by the absence of collagen in the cutmarked femur and associated fish bone in TAMP zone 2.

However, the stratigraphic context of the cutmarked TAMP specimen raises the possibility that the cutmarks on this specimen were not perimortem. Specifically, the ages of the cutmarked Lamboharana/Lamboara specimens fit within the age range of bones recovered from zone 3 (~6000-1500 cal BP), and it is likely that our cutmarked pygmy hippo from TAMP zone 2 originated from zone 3. This is because 1) a large (>2 cm diameter) charcoal fragment over 20 cm below the cutmarked TAMP specimen dates to 620-530 cal BP (PSUAMS 8777, hundreds of years after the last directly dated hippo from the island died), and 2) at least one of the other scarce fragments of megafaunal bone from zone 2 (the molar fragment from ANKA of 3880-3700 cal BP [PSUAMS 8733]) also has a date consistent with zone 3. Such anomalously old bone is likely the product of bioturbation or late deposition through runoff from sediment surrounding the basin. It is also worth noting that bones of possibly extirpated megafauna would have been readily available to people throughout the past millennium. People still regularly unearth megafaunal bone while cultivating the margins of these ponds. Thus, the context gives several reasons to question the perimortem status of the cutmarks on the TAMP pygmy hippo femur. The context of the cutmarked Lamboharana/Lamboara specimens may differ, but, regardless of the age of the specimen, the modified pygmy hippo femur from TAMP cannot be taken as evidence for local cooccurrence between humans and pygmy hippos.

The dated charcoal beneath the cutmarked TAMP specimen is significant, for it suggests that the top half of the sediment sequence (~70 cm) was deposited within the past 500 years. This deposition is much faster than that at ANKA and ANDR, and it raises the possibility that TAMP zone 2 represents a massive deposition event. People could have been responsible, for cultivation within the past centuries very likely accounts for the sharp and uneven contacts between the surface soil formation of zone 1 and the underlying clay of zone 2.

The scarcity of cutmarks on extinct animal bone at Tampolove and several sites elsewhere in SW Madagascar (Anderson, et al. 2018) gives the impression of limited human predation on these animals. This scarcity is particularly unexpected if we consider humans to have been present since ~4000 cal BP, as possibly evidenced by the ANKA bushpig tooth of 3980-3730 cal BP, stone tools from northern Madagascar (Anderson 2019; Dewar, et al. 2013), and cutmarked elephant bird bone (Hansford, et al. 2018). However, taphonomic reasons can explain at least some of this scarcity, because we know that 1) humans subsisted heavily on coastal resources near Tampolove since at least ~1400 cal BP (Douglass, et al. 2018) even though very few processed shells and cut fish bone entered the excavated pond sediments of TAMP, ANKA, and ANDR within recent millennia, and 2) livestock are routinely butchered and their bones are widespread along the modern coast around Tampolove (Dataset S1), yet few have entered the uppermost sediments of coastal ponds. Therefore, the present study suggests merely that any endemic animals butchered in the region were not butchered and recovered on the immediate margin of the coastal ponds that we excavated. Future excavations may reveal whether people used megafaunal bone during past tool production in the vicinity of coastal ponds and whether early coastal middens include small fragments of cutmarked megafaunal bone.

Conclusions

When matched against paleohydrological records, faunal occurrence data from Tampolove are consistent with the idea that some extinct and extirpated megafauna (pygmy hippos and possibly crocodiles) were more sensitive to late Holocene drought than others that persisted locally (giant tortoises and possibly elephant birds, as in Fig.

1a). These different sensitivities suggest that aridification cannot explain the simultaneous disappearance of all of these groups from Tampolove and the broader region of SW Madagascar by ~900 cal BP. Future work should compare the magnitudes of the MCA and the earlier 'megadraughts' that the megafauna of SW Madagascar endured without retreating up relatively mesic drainages. Consistent with the work of Godfrey et al. (2019), the sequence of bones, charcoal, and artifacts excavated from Tampolove suggest that forest clearance through burning and growing human populations (facilitated by pastoralism) better explain the simultaneous disappearance of megafauna around Tampolove. Future research should clarify the status of bushpigs and other animals (e.g., helmeted guinea fowl, *Numida meleagris*) that were possibly introduced by humans (Douglass, et al. 2019; Goodman, et al. 2013). Additional fieldwork and the analysis of ancient DNA will be required to test this hypothesis. If the ANKA bushpig tooth with a date of ~4000 cal BP is taken as evidence of human presence by this time, then this finding favors the scenario depicted in Fig. 1c by clarifying the spread of pastoralism ~1000 cal BP as a much later shift in human subsistence. Given the scarcity of such early traces of human activity (Douglass, et al. 2019), these types of finds raise many questions on the nature of human activity on Madagascar between 4000 and 1500 cal BP. Fieldwork in other parts of Madagascar is essential for clarifying the extent of human activity on the island before the spread of pastoralism and pulse of megafaunal extinction that happened in the SW.

VI. CH. 6 CONCLUSION

A. *Context review*

This dissertation helps address a grand challenge in archaeology to characterize how past human activities and climate change have shaped Earth's biological systems (Kintigh, et al. 2014). A long-term perspective on these interactions gives useful context to modern biodiversity conservation and sustainable land use practice in the face of ongoing climate change. This context is particularly important on biodiverse islands such as Madagascar and in dry areas such as SW Madagascar. For example, to help generate expectations for how the mobility of modern pastoralist populations will respond to projected aridification (Tadross, et al. 2008), it is useful to understand where pastoralists lived during past dry and wet intervals. Additionally, to help ensure the success of efforts to reintroduce giant tortoises to Madagascar (Pedrono, et al. 2013), it is useful to consider how past human activity contributed to their earlier disappearance. The research described here contributes to our knowledge of this type of context by studying the past series of vertebrate arrivals and disappearances in SW Madagascar.

Madagascar's biodiversity is matched by its cultural diversity, which is drawn from across the Indian Ocean and helps complicate an assessment of whether it was an East African or a SE Asian who first set foot on the island. The earliest possible traces of human activity on Madagascar are a cutmarked bone dating to ~10,000 years ago (Hansford, et al. 2018) and stone tools from ~4,000 years ago (Dewar, et al. 2013), both of which are the subject of ongoing debate (Anderson, et al. 2018; Mitchell 2019). Regardless of origin, early people on Madagascar over a millennium ago encountered a remarkable array of endemic large herbivores (Goodman, et al. 2014), and early settlers from mainland Africa may have been struck also by the absence of endemic bovids. However, by the time of European arrival ~500 years ago, populations of the island's extinct megafauna had crashed (Crowley 2010), and Madagascar became sometimes known as 'Zebu Island' in the early 20th century due to the abundance of zebu cattle (Kaufmann and Tsirahamba 2006). As outlined in the Introduction, the research presented in this dissertation helps answer the following questions:

- Did the spread of pastoralism coincide with the expansion of human populations, and was there potential for negative ecological interactions between introduced livestock and now extinct megaherbivores?

  Radiocarbon and stable carbon and nitrogen isotope data from the bone collagen of 66 introduced herbivores and 68 extinct endemic megaherbivores, combined with a compilation of preexisting data 282 endemic megaherbivores (total sample drawn from 45 sites), help test the potential cooccurrence among various taxa in SW Madagascar during the past several thousand years and clarify aspects of the habitat and diet of these animals (Chapter 1).

- What was the potential for introduced predators, such as dogs, to contribute to the hunting of megafauna, and was there potential for competition between dogs and endemic carnivorans?

  Radiocarbon data from 17 dog bone samples from 13 site across Madagascar confirm the antiquity of dogs on the island, and comparisons in the stable isotope composition of dog, fosa, and prey collagen clarify the potential for dietary overlap between dogs and fosa (Chapter 2).

- How did climate change during the past spread of pastoralism, and how did livestock and endemic megafauna respond to past environmental change?

  Geochemical records from a lake sediment core from Ranobe, SW Madagascar identify intervals of climatic drying during the past ~1,600 years, and associated archaeological survey helps identify local traces of past pastoralist activity (Chapter 3). Coupled lake sediment and bone collagen stable isotope data characterize the extent to which zebu and extinct pygmy hippos and giant lemurs relied on arid habitat and xerophytic plants during past dry intervals.

- What were the relative sensitivities of livestock and endemic megafauna to drought since the mid-Holocene?

  Coupled pond sediment and faunal occurrence data from mixed archaeological/paleoecological deposits reveal whether certain megafauna persisted around ephemeral coastal ponds during past 'megadraughts' while others lived in the vicinity of these ponds only during relatively wet intervals (Chapters 4).

The following summary of key findings are organized by topic, with the past potential for various interspecific interactions (all chapters) discussed before the effects of hydrological stressors on different taxa (Chapters 3 and 4). Each section ends with notes on limitations of the current research and areas for future work.

B. *Interspecific interactions*

Brief temporal overlap between introduced livestock (zebu, sheep, and goats) and extinct megafauna, both around Tampolove (Chapter 4) and throughout SW Madagascar (Chapter 1), supports the possibility that some form of competition contributed to the nearly simultaneous regional disappearance of giant tortoises (*Aldabrachelys* spp.), pygmy hippos (*Hippopotamus lemerlei*), elephant birds (*Aepyornis* sp.), and certain giant lemurs (*Archaeolemur majori* & *Pachylemur insignis*). The mostly distinct stable isotope content of zebu and sheep collagen (Chapter 1) indicates that there was limited potential for direct forms of competition between these livestock and endemic megaherbivores. However, multiple lines of evidence suggest that animal husbandry facilitated human population growth starting ~1,000 years ago (Godfrey, et al. 2019; Pierron, et al. 2017), and human hunting of bushmeat brought livestock into indirect competition (apparent competition) with endemic taxa, regardless of herbivore diet. Additionally, repeated burning and loss of spiny forest followed the expansion of pastoralist populations around at least two sets of coastal ponds (Chapters 3 & 4), which could have deprived endemic megaherbivores of their preferred browse. Dogs were also present on Madagascar during the early spread of pastoralism and clearance of endemic forest, and they could have aided human-led hunts of lemurs and other fragmented megafaunal populations that persisted after 1,000 years ago (Chapter 2). Predators such as dogs and humans can also interact negatively with native carnivorans, such as fosa. For example, dogs could have competed with fosa over shared prey, yet limited overlap in the stable isotope content of dog and fosa collagen suggest limited potential for exploitation competition between these predators (Chapter 2). The many past potential interactions among introduced and endemic predators and herbivores could have followed an extended period of coexistence between humans and endemic megafauna (Dewar, et al. 2013; Hansford, et al. 2018). A directly dated introduced bushpig tooth dated to ~4,000 years ago from Tampolove may suggest that people arrived on the island by this time. Such early traces of human activity could indicate that it was not merely the presence of human hunters on the landscape that contributed to the pulse of Late Holocene extinctions.

Any work with the fragmentary material record faces the limitation of small sample size, and this is particularly true on tropical islands such as Madagascar. For example, the ^{14}C-dated subfossil records of introduced goats, bushpigs, cats, and rats are particularly scarce. We can always learn more about how these taxa shaped Madagascar's modern ecosystems through analysis of additional bones spread across time and space. The spatial component is particularly important on Madagascar, where the forces that shaped ecosystems in the SW are unlikely to be identical to those that shaped relatively mesic ecosystems in the central highlands and eastern humid forests.

Existing bone collections from SW Madagascar should be targets for the exploration of ancient DNA preservation given that aDNA from past introduced species can help trace past human population movements that may be otherwise cryptic in regional archaeological records. This is particularly true for taxa such as bushpigs (*Potamochoerus larvatus*), helmeted guineafowl (*Numidia meleagris*), and pied crow (*Corvus albus*) given the questionable status of these animals as human introduced. Stable isotope data from this dissertation also point to future areas of research. For example, overlapping collagen stable isotope values for goats, giant tortoises, and pygmy hippos raise the possibility that these animals competed for resources. Additional studies in SW Madagascar with relatively fine spatial and temporal resolution will improve our understanding of past herbivore cooccurrence, and refined reconstructions of past fire regime and water availability may help isolate some of the past impacts of herbivory on vegetation.

C. Hydrological stressors

Environmental conditions can determine the strength and outcome of interspecific interactions, and this is particularly true when vital resources, such as water, are in short supply. Geochemical records from lake sediments in coastal SW Madagascar confirm that the disappearance of endemic megafauna and arrival of pastoralism approximately coincided with climatic desiccation (Chapters 3 & 4). Livestock stable isotope and occurrence data further suggest that zebu closely tracked mesic habitat during the past millennium, which may indicate a possible sensitivity to past and ongoing drought (Chapter 3). However, stable carbon isotope data from both zebu and pygmy hippo collagen also suggest that these animals coped to some extent during dry times by consuming more xerophytic C4 and CAM plant material. Additionally, occurrence data from small coastal ponds around Tampolove document the local persistence of pygmy hippos despite what might have been a series of mid-Holocene megadroughts (Chapter 4). Still, unlike giant tortoises, pygmy hippos could have been sensitive to the combination of climatic drying and marine regression that occurred ~1,000 years ago. This pattern highlights the fact that hydrological stressors could explain some but not all of the Late Holocene disappearance of endemic megafauna in SW Madagascar. In fact, the apparent drought tolerance of giant tortoises raises the possibility that water scarcity conferred a relative benefit to these animals over other, relatively drought-sensitive taxa, such as livestock and pygmy hippos.

The conclusion that drought fails to explain past island-wide extinctions on Madagascar is well supported by this and previous research (Crowley, et al. 2017; Hixon, et al. 2018). However, more could be done to characterize the relative drought tolerance of different taxa, which is particularly relevant to modern concerns regarding the sustainability of agropastoralism in the face of ongoing drought. Exploring applications of other isotope systems to the subfossil record (e.g., strontium and sulphur) may help us better identify where livestock and endemic fauna lived during past droughts, and whether they relied heavily on freshwater resources (e.g., emergent plants). The analysis of ancient DNA from the bones of livestock and megafauna could also allow us to infer changes in effective population size that coincided with past megadroughts. Additionally, when informed by refined regional paleoclimate records, models of past freshwater availability could enable past species distribution modelling, which may be tested using faunal occurrence data from present and future excavations.

D. Conclusions in context

Conclusions on past interspecific interactions and hydrological stressors in SW Madagascar help clarify key aspects of the region's environmental history narrative. The early pastoralists who temporarily occupied inland sites such as Andranosoa managed a suite of introduced animals (cattle, goats, sheep, and dogs) at least a millennium ago, and these animals could have initially arrived at approximately the same time through coastal entrepôts such as Mahilaka. These pastoralists very likely encountered a diversity of now-extinct megafauna, but existing data suggest that this encounter was brief. While dogs could have aided human-led hunts and goats could have directly competed for browse with pygmy hippos and giant tortoises, indirect interactions better explain the simultaneous decline of endemic megafauna and success of introduced grazers like sheep and cattle. For example, pastoralists were likely responsible for past fires that cleared forest habitat for herbaceous plants favored by livestock, and animal husbandry likely contributed to the inferred acceleration of human population growth during the past millennium.

Aridification coincident with the Medieval Warm Period can account for the disappearance of only certain taxa from only certain coastal sites (e.g., pygmy hippos from Tampolove), and existing data attest to the past drought tolerance of giant tortoises. This suggests that factors other than climate drying negatively impacted now-extinct megafauna. Other factors, such as habitat clearance and negative interactions involving introduced species likely pose a relatively great threat to the viability of reintroduced giant tortoise populations and possibly to populations of extant endemic taxa, such as fosa. If anything, projected drought may be a greater concern to modern pastoralists in SW Madagascar, for existing data suggest that cattle closely tracked limited wet habitat even during dry intervals of the past millennium.

Madagascar has a history of colonization and extinction that may span the Holocene, and the environmental transformation of SW Madagascar during the past millennium may not be representative of earlier human-environment interactions. Undisputed traces of human activity on the island date to at least 1,500 years ago, and scarce finds of cutmarks, artifacts, and likely introduced species may suggest that the past millennium encompassed only a portion of the human history of the island. Human occupation of Madagascar well before the start of the past millennium is significant because it demonstrates an unexpected case of extended coexistence between highly versatile predators (people) and naïve endemic megaherbivores before the spread of food production systems that define the modern subsistence economy.

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