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Arrivals and Extinctions

Madagascar is renowned for its unique and varied biodiversity, which spans dry grasslands, wet rain forests, mangroves and deserts. This variety, combined with the island's isolation and size, has fostered distinctive assemblages of plants and animals, including the country's famous lemurs and baobab trees.

Yet until relatively recently, Madagascar was even more diverse. Species like the elephant bird, dwarf hippo and giant lemurs inhabited the island within the past 2,000 years. The causes and timeline of their extinctions are intertwined with the arrival of humans and the animals we brought with us, a topic that has challenged scientists for decades. Now this is the focus of two studies led by UC Santa Barbara anthropology doctoral student Sean Hixon.

"Madagascar's remarkable biodiversity is threatened, yet people have lived on the island for over a millennium," Hixon said. "A long-term understanding of how people and introduced species shaped Madagascar's ecosystems gives important context to the current crisis."

"Because this is an island that has so much biodiversity, and so much of that biodiversity is native only to Madagascar — is highly endemic — the question has always been what impact has human arrival had on this large, biodiverse island," added co-author Kristina Douglass, an archeologist at Pennsylvania State University.

The new studies have finally answered some of these questions by analyzing different isotopes of nitrogen and carbon in ancient animal remains. In the process,

the team nearly doubled the number of reliably radiocarbon dated traces of past human activity from the island.



A fosa, Cryptoprocta ferox.

The most recent study, which appears in the Proceedings of the Royal Society B, establishes an overlap between the arrival of domesticated herbivores and the continued existence of some of the region's megafauna. It then compares the animals' ecological niches and discusses how they may have influenced one another. The other paper, published in Frontiers in Ecology and Evolution, details how dogs interacted with Madagascar's ancient ecosystems and compares them to the island's native top predator, the fosa.

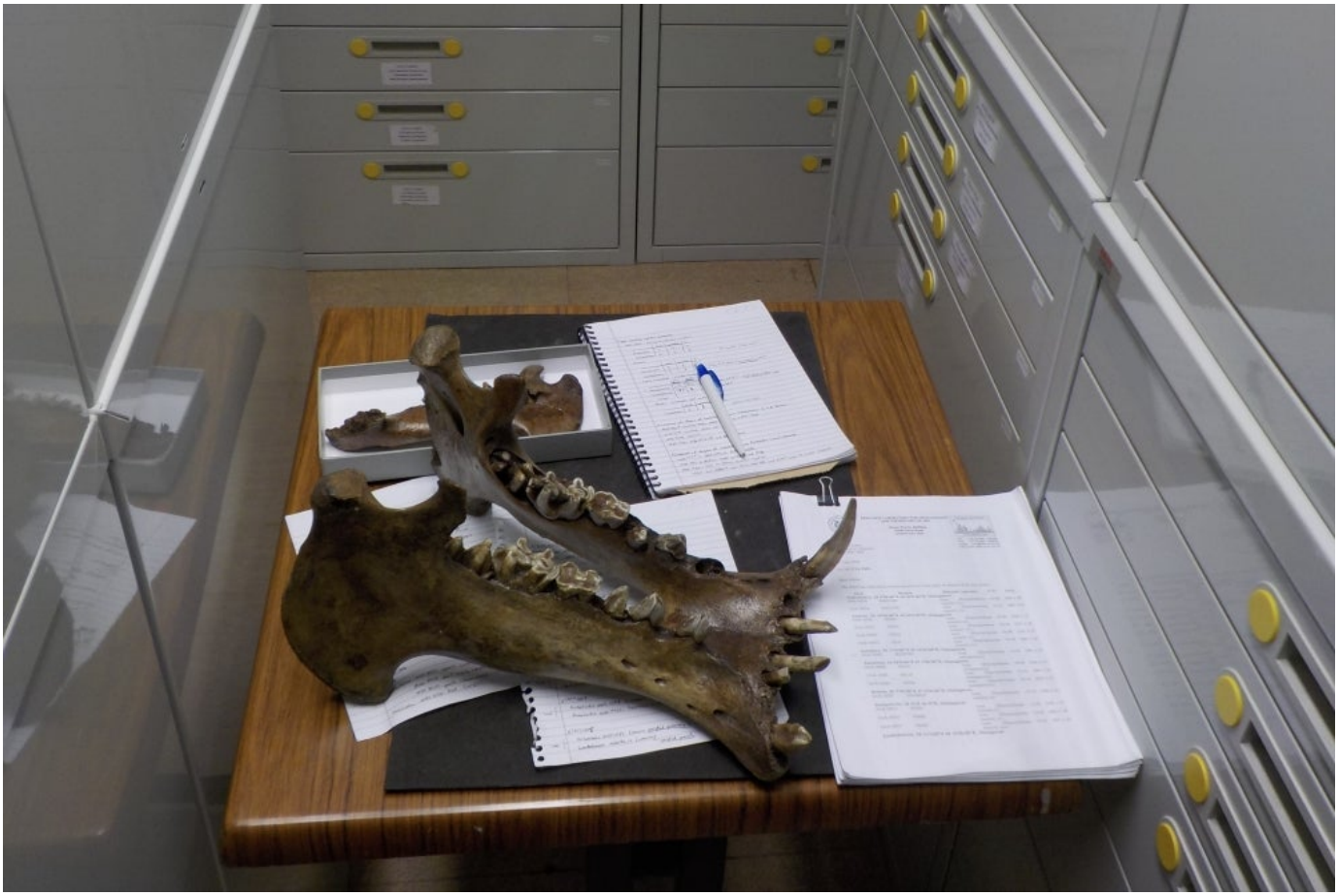
"The extinction of large-bodied animals sometime in the past 1,000 years has always been a very contentious debate," Douglass explained. "And what we've done in this paper, for the first time, is really look at how much interaction there was between animals that people brought and those that ended up going extinct to see if any kind of competition or interactions played a role."

Ultimately, the researchers confirmed that most of Madagascar's recently extinct megafauna briefly co-occurred with introduced species, meaning that the newcomers likely contributed to their demise. "We found that a series of disappearances of large endemic animals —including giant tortoises, elephant birds, pygmy hippos and giant lemurs — coincides with the arrival of goats, sheep, bush pigs and cattle in southern and western Madagascar between 1,200 and 700 years ago," Hixon said.

However, the results suggest that direct competition may not have been what drove the island's large herbivores over the edge. Rather, indirect impacts like changing habitats and an expanding human population could have had more pronounced effects.

A time and a place

Although the earliest traces of human activity on Madagascar are subject to debate, some estimates of human arrival suggest that people were perhaps present on the island as long as 10,000 years ago. At some point dogs and livestock joined them.



The authors sampled many bones, like this pygmy hippo mandible, from the National Museum of Natural History in Paris.

Photo Credit: SEAN HIXON

Hixon and his team sought to determine whether these domesticated animals even crossed paths with the island's megafauna. Settling this question required dating as many bone samples as possible, both from the field and from collections, using radiocarbon analysis.

Atoms of a given element all have the same number of positive protons; indeed, this number defines an element. But they can vary in the number of chargeless neutrons in their nuclei, giving the different isotopes slightly different weights. Scientists can glean a lot of information by analyzing these ratios.

For example, a living organism will have a similar proportion of stable carbon-12 to radioactive carbon-14 as its environment. However, after death, the creature can no longer replenish the decaying ^{14}C. So, scientists can use the ratio between the two isotopes to estimate the age of organic matter.

Hixon and his colleagues used this approach to date 83 introduced animals (dogs and livestock) and 75 endemic animals. They found that the two groups did overlap in time and space, and statistical analysis suggests that all the regional extinctions occurred within the span of 500 years, between A.D. 800 and 1300. These are the first papers to show an overlap between human-introduced animals and Malagasy megafauna, Hixon and Douglass said.

This is a significant finding in a line of research that has been plagued by a paucity of data. Malagasy specimens are uncommon, and many are poorly documented, Hixon explained. What's more, carbon dating is expensive. Commercial services can cost more than $500 for a single sample. Fortunately, Penn State has the facilities to do this in house, and co-author Douglas Kennett (Hixon's advisor) has recently established a lab at UC Santa Barbara to prepare specimens for this technique.

Still, radiocarbon dating cost the team over $100 per specimen. Given the cost and facilities this requires, it's a significant issue in terms of scientific and cultural equity for researchers and communities in regions with fewer resources invested in the paleosciences, the authors said. These two studies alone have increased the number of reliably dated traces of past human activity from the island by more than 75%.

“So this is a massive contribution and increase in just building up the chronology for human arrival and activity in Madagascar,” Douglass said.

Diets and interactions

The pathways differ slightly in their tendency to incorporate different carbon isotopes into biomass: C3 plants have a lower ratio of carbon-13 to carbon-12 compared to their C4 and CAM relatives. By analyzing a sample’s ^{13}C to ^{12}C ratio, the researchers could learn about an herbivore’s diet and the type of ecosystem it likely inhabited: open grasslands or dense forests. They could also extend this information to carnivores, like dogs and fosa, by extrapolating from the types of herbivores they ate.The team also analyzed ratios between two stable isotopes of both carbon and nitrogen to investigate the ecology of ancient animals. Ratios of carbon isotopes are sensitive to the type of photosynthesis different plants employ. Woody plants, like trees and shrubs, tend to use C3 photosynthesis. Grasses and the succulents of the island’s southwest tend to employ C4 and CAM photosynthesis, respectively, which use different enzymes.

The nitrogen isotopes also provided the team with information on animals’ ecological niches. Animals higher on the food chain tend to have tissues enriched in heavier ^{15}N, as opposed to ^{14}N.

The stable isotopes revealed a mixture of overlapping and non-overlapping niches between the endemic megafauna and the introduced herbivores. For example, goats appear to have eaten similar forage to the island’s giant tortoises and pygmy hippos. Zebu and sheep likely relied significantly more on succulents and grasses than did any of the island’s endemic megafauna, especially the giant lemurs and elephant birds.

Meanwhile, the analysis reveals stark contrasts between introduced dogs and endemic fosa. Ancient fosa primarily consumed forest-dwelling animals, while dogs relied more heavily on prey from relatively open habitats and possibly food scraps from people. “Dogs certainly arrived in time to help people hunt megafauna,” Hixon said, “and could have interacted with some of the extinct giant lemurs. But the data suggests that dogs weren’t consistently eating any of the extinct megafauna.”

Despite the often distinct diets of introduced and endemic animals, the introduction of new species to the island could still have contributed to the extinction of Madagascar's megafauna. It is easy to construct a simplified concept of extinctions based on direct impacts like overhunting or direct competition, but the process can be much more subtle. "People are extremely good at settling new places, in the sense of creating a niche that suits them," Douglass said. "And not only just suits people, but suits the animals that people rely on."



A herd of zebu cattle in coastal southwest Madagascar. Recent estimates from the World Bank suggest that a little over half of the island's surface is dedicated to pastoralism.

Photo Credit: SEAN HIXON

For instance, expanding zebu herds could have impacted the island's native animals even if they ate different plants. Their presence may still have threatened the megafauna through indirect competition if people were clearing land for grazing and occasionally hunting megafauna. And the success of the zebu would have fostered human population growth, with all the impacts it entails. Indirect interactions such as these could account for a period of coexistence between humans and Malagasy

megafauna.

Understanding a process like extinction will require looking at many different angles. “It’s not just that people arrived on Madagascar, it’s that people arrived and then were experimenting with different kinds of livelihoods,” Douglass added. “And each of those different livelihoods had different types of impacts on the environment.”

Continuing to unravel the past

There’s evidence that Madagascar was also experiencing climatic changes around the time of human arrival. The recent studies don’t exclude the possibility that environmental changes may have contributed to the demise of the island’s megafauna. In fact, the team just submitted a paper investigating how endemic and introduced herbivores responded to drying conditions in the island’s southwest during the past 1,600 years. And competition between plants, as well as human land use, could have contributed to historical vegetation changes.



Zafy Chrysostome excavates a coastal archeological site in in the Velondriake Marine Protected Area of southwestern Madagascar. Chrysostome had been a core member of team for nearly 10 years before his sudden passing last year.

Photo Credit: GARTH CRIPPS

Hixon, Douglass and their co-authors have many plans for future research. To start, they want to look at specimens from more areas of the island. These papers were mostly limited to the country’s arid southwest, where specimens preserve well. However, Madagascar hosts an astounding diversity of ecosystems that researchers have yet to fully explore.

Hixon plans to further investigate the island’s ancient food webs. He is curious to learn more about when introduced mice and rats arrived on the island, how they likely interacted with endemic small mammals, and how they responded to past

vegetation and climate change.

Douglass’ lab has begun using remote sensing technology to predict the locations of undiscovered archeological settlements and signatures of land use change in the Southwest. She’s curious if pastoralists living in particular places for generations have altered the soil chemistry and distribution of different vegetation types.

This research also has potential applications beyond its importance in documenting the culture, history and ecology of the island. As a biodiversity hotspot, Madagascar’s ecosystems are critical areas for conservation, and there is ongoing work to rewild parts of the island. For instance, giant tortoises have already been reintroduced to western Madagascar from Aldabra Atoll in the western Indian Ocean.

“The type of work that we’re doing is important for the long-term success of efforts like this,” Hixon said, “because if we don’t understand why the animals disappeared in the first place, it’s pretty unlikely that reintroduction efforts will work.”

About UC Santa Barbara

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