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Seeing the forest for the trees—and the grasses: revisiting the evidence for grazer-maintained grasslands in Madagascar's Central Highlands

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Today, grasslands cover approximately 80% of Madagascar [1,2], but their extent prior to recent landscape modification remains elusive. Numerous studies converge to suggest that forest cover was much more widespread greater than 1000 years ago and even 100 years ago [3–7]. While researchers initially regarded grasslands as primarily anthropogenic (e.g. [8–10]), the view has been challenged by the diversity and age of endemic grass lineages. This shift in perspective started when Bond *et al*. [1] suggested that C_4 grasses have existed on Madagascar since the late Miocene (e.g. [11]). These inferences were based on (i) C_4 grasses, including endemic species, being remarkably diverse in Madagascar, (ii) the species composition of grassy biomes varying geographically (following climate and elevational gradients similar to South Africa), and (iii) grassy biomes including endemic graminoid, herbaceous and woody species. Bond *et al*. [1] also observed that Malagasy invertebrate and vertebrate groups have grassland specialists. Hackel *et al*. [12] found support for a Miocene to Pliocene origin of Madagascar's grassy biomes, while Vorontsova *et al*. [2] demonstrated that roughly 40% of Madagascar's grass species are endemic. There is particularly high diversity and spatial and ecological turnover of endemic grasses in Madagascar's Central Highlands, a region generally considered highly anthropogenically modified and biologically impoverished [4].

Solofondranohatra *et al*. [13] confirmed that endemic grasses in central Madagascar are phylogenetically diverse and found both fire- and grazer-adapted assemblages. They reasoned grassy biomes were maintained by fire and native grazers before humans arrived, and that cattle may have replaced native grazers. They further argued that the importance of grassy biomes has been underappreciated and the Malagasy unnecessarily vilified in the traditional deforestation narrative; efforts to reforest with exotic species are misguided. We agree with these basic arguments. However, two fundamental questions remain unresolved: (i) which now-extinct taxa maintained grazer-adapted grasses? (ii) How extensive were grasslands before human arrival?

As Solofondranohatra *et al*. [13] note, published isotope data for Madagascar's Central Highlands are taxonomically limited (favouring lemurs) and scattered across multiple sources and sites [14–19]. We seek to help rectify this gap by summarizing existing radiocarbon and $\delta^{13}C$ data and providing new data for lemurs, hippos and a euplerid carnivoran from the ecoregion (figure 1; electronic supplementary material, table S1). Sample preparation and analysis followed [18]. Raw isotope data were normalized using internal reference materials following [20]. Analytical precision and accuracy were 0.29 and 0.27‰, respectively. We compared $\delta^{13}C_{collagen}$ values with expected values for pure C_3 and mixed C_3–C_4 consumers. To do this, we assumed that most grasses

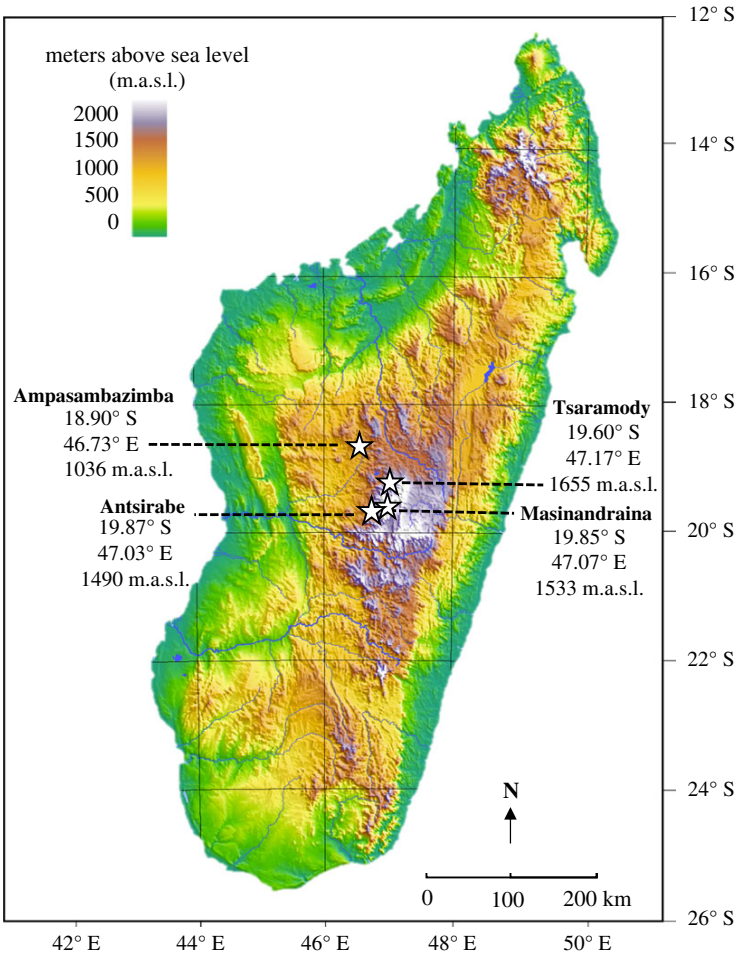

Figure 1. Map of Madagascar showing Central Highland subfossil sites included in this study. Basemap modified from commons.wikimedia.org. (Online version in colour.)

in Central Madagascar use the C_4-photosynthetic pathway, based on species lists for the Central Highlands (e.g. [1]), and a valid assumption for tropical and subtropical sites worldwide. No isotope data exist for grasses from central Madagascar. However, globally, C_4 plants have a narrow range of $\delta^{13}C$ values (−13.1 ± 1.2‰ [21]). For C_3 plants, we used $\delta^{13}C$ values for plants from Tsinjoarivo (−24.7 to −32.1‰ [22]), a protected area in the eastern Central Highlands 1300–1675 metres above sea level (m.a.s.l.). After accounting for the isotopic difference between tissue and diet (+5‰ for bone collagen; see [23]), as well as isotopic changes in atmospheric CO_2 following the industrial revolution (the Suess effect, −1.2‰; see [23]), animals with pure C_3 diets should have collagen $\delta^{13}C_{Suess}$ values < −19.7‰ while higher values require a mixed C_3–C_4 diet.

We explored temporal and spatial trends in the isotope data. We broke data down into two elevational bins: high (greater than 1300 m.a.s.l.) and mid-elevation (800–1300 m.a.s.l.). This cutoff is based on differences in climate (higher elevations have cooler temperatures and receive more precipitation), vegetation (mid-altitude versus montane and sclerophyll forest) and considerably reduced bird and mammal species richness above 1300 m.a.s.l. (e.g. [24,25]). We also broke the data into three temporal bins: greater than 19 000 calendar years before present (cal BP), which encompasses the Last Glacial Maximum (LGM); 19 000–11 700 cal BP, which covers the last deglaciation interval; and less than 11 700 cal BP, which covers the Holocene.

At high-elevation sites (Antsirabe, Masinandraina and Tsaramody), there are no $\delta^{13}C$ data for animals greater than 19 700 cal BP. However, there were shelducks and sheldgeese (*Alopochen* and *Centrornis*) at Antsirabe during and just after the LGM, which supports wetland conditions (figure 2). Just one datum exists for the last deglaciation, a hippo from Tsaramody with a $\delta^{13}C_{Suess}$ value suggesting a mixed C_3–C_4 diet (−15.9‰). More data are available for the Holocene. Hippos (all from Antsirabe) had a narrow isotopic range reflecting pure C_3 diets (−26.7 to −26.1‰). However, elephant birds (*Aepyornis hildebrandti*) had elevated $\delta^{13}C_{Suess}$ values both at Antsirabe and Masinandraina (−18.3 to −14.6‰), suggesting a mixed C_3–C_4 diet. A single extinct Malagasy 'aardvark', *Plesiorycteropus*, had a $\delta^{13}C_{Suess}$ value close to the expected threshold for pure C_3 consumption (−19.9‰).

At mid-elevation Ampasambazimba, water birds (*Alopochen*) were also present greater than 19 700 cal BP (figure 2). A single *Archaeolemur* dating to 33 168 ± 3563 cal BP had a $\delta^{13}C_{Suess}$ value of −16.7‰, supporting some reliance on C_4 resources. However, during the last deglaciation and Holocene, lemurs had $\delta^{13}C_{Suess}$ values reflecting pure C_3 diets (−25.6 to −20.5‰). The carnivoran *Cryptoprocta ferox* also consumed C_3 resources (−21.1‰), while hippopotamuses had variable $\delta^{13}C_{Suess}$ values, with some relying on a mixed diet (−24.2 to −14.7‰).

Although these data are still rather limited spatially, temporally and particularly taxonomically, they support the

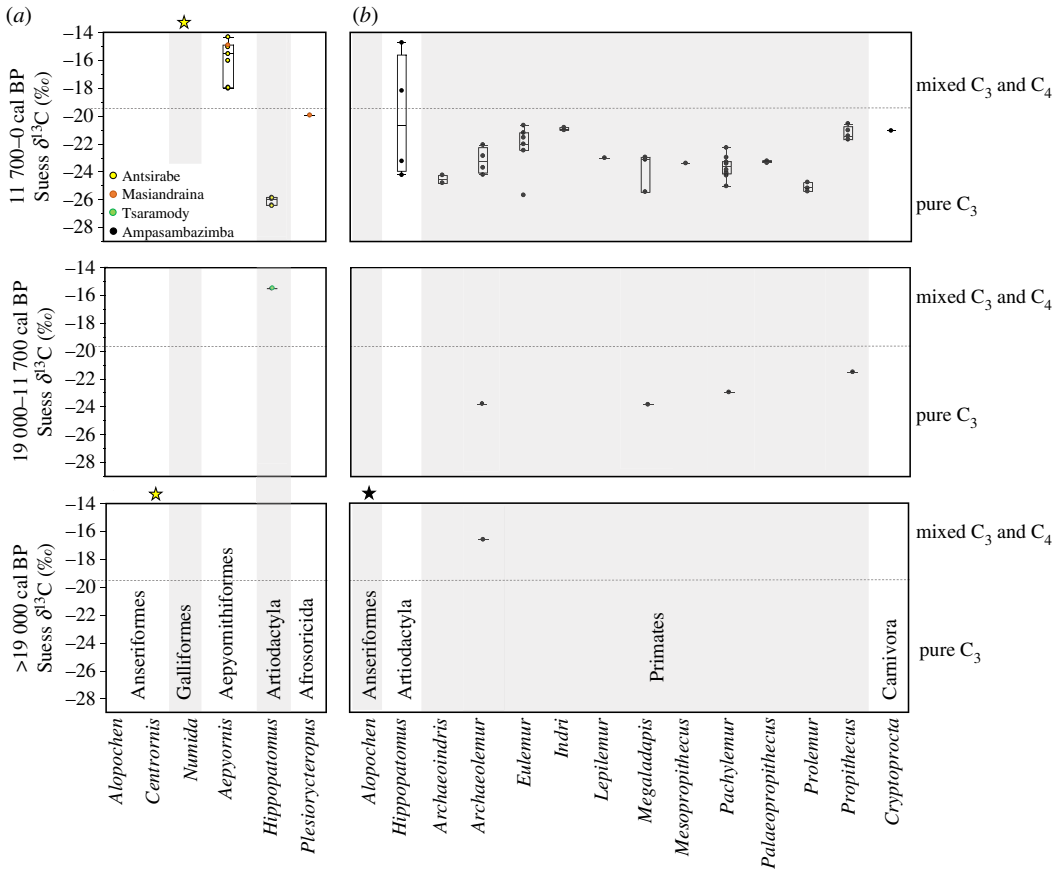

Figure 2. Boxplots showing $\delta^{13}C$ values for vertebrates during three time intervals at (*a*) three high-elevation sites (Antsirabe, Masiandraina and Tsaramody) and (*b*) one mid-elevation site (Ampasambazimba). Stars denote taxa with dates but no $\delta^{13}C$ values. (Online version in colour.)

notion that Madagascar's Central Highlands were not densely forested prior to and during the LGM. Available evidence for forest-dependent taxa at sites greater than 1300 m.a.s.l. and the elevated $\delta^{13}C_{suess}$ value for the *Archaeolemur* at mid-elevation are consistent with relatively open habitat at that time. Isotope data also support continued C_4 presence at high elevations after the LGM, and at both mid- and high-elevation sites during the Holocene. However, the abundance of lemur and other arboreal taxa implies significant tree cover from the last deglaciation through much of the Holocene.

Isotope and radiocarbon data do not obviate the presence of ancient grasslands in Madagascar. However, they also do not support widespread grasslands in central Madagascar throughout the past 30 000+ years. Instead, the data support a mosaic landscape, with fluctuating dominance of different biomes at different elevations and during different windows of time [5,26]. Factors beyond natural fire and grazing (including temperature, rainfall and anthropogenic fires) have probably contributed to the distribution of grassy biomes over time. Additional data will further elucidate the extent of grassy biomes in Madagascar's Central Highlands and which herbivores maintained grazer-dependent taxa. We look forward to helping solve these remaining unknowns so that appropriate management and conservation decisions can be made.

Data accessibility. All data included in this study are provided in the electronic supplementary material, table S1.

Authors' contributions. B.E.C. and L.R.G. designed research; K.E.S., L.R.G. and J.P.H. collected data; B.E.C., L.R.G. and J.P.H. analysed data; B.E.C. wrote the paper; L.R.G., K.E.S. and J.P.H. contributed to the interpretation and the revision of the work.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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