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Introducing IsoMad, a compilation of isotopic datasets for Madagascar

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We present the first open-access, island-wide isotopic database (IsoMad) for modern biologically relevant materials collected on Madagascar within the past 150 years from both terrestrial and nearshore marine environments. Isotopic research on the island has increasingly helped with biological studies of endemic organisms, including evaluating foraging niches and investigating factors that affect the spatial distribution and abundance of species. The IsoMad database should facilitate future work by making it easy for researchers to access existing data (even for those who are relatively unfamiliar with the literature) and identify both research gaps and opportunities for using various isotope systems to answer research questions. We also hope that this database will encourage full data reporting in future publications.

Background

Madagascar's remarkable biodiversity is threatened, and accessible data regarding the distribution, habits, and conservation status of endemic species are key to effective conservation planning[1]. Isotopic research with modern biological materials from the island has helped both to characterize endemic biodiversity and to identify ecological interactions that affect the spatial distribution and abundance of species. For example, researchers have used isotopic data to confirm photosynthetic pathways of endemic plants[2], identify plant and animal responses to human activities such as forest fragmentation[3–5], investigate diets of both endangered and introduced animals[6–8], evaluate spatial partitioning and movement of animals among habitats[7,9,10], and infer the structure of food webs within terrestrial, freshwater, and nearshore marine environments[11–15]. Isotopic data from modern material can also be integrated with data for ancient organisms to investigate resources used by extinct taxa[16–19] and reconstruct past changes in the behavior of extant animals[4,20].

To date, publication of isotopic data has been somewhat haphazard. Some researchers have provided minor compilations of relevant raw isotope data in supplementary files (e.g.[19,21,22]). However, the metadata structure of these partial compilations tends to vary according to specific research questions and among research groups, which hinders reuse. We present the open-access IsoMad (Isotopic Data of Madagascar) database, which is the first compilation to include the majority of known isotopic data for modern materials on the island and in the coastal marine environment. This database follows from several motivations that include the FAIR data principles[23]. First, the initiative eases data accessibility by compiling data that were previously difficult for some researchers to access given journal paywalls, or because authors presented data only as text and summary statistics. We also have >5,000 previously unpublished measurements. Second, the structure of IsoMad makes the data easily searchable and accessible to users who are relatively unfamiliar with the literature. Consequently, the compilation should facilitate future isotopic research by making it easy to identify both research gaps and opportunities for using various isotope systems to answer a given research question. This initial unveiling of IsoMad is meant to be the first step in an ongoing initiative, where researchers will be able to continue adding to the database in perpetuity. It is our hope that the structure of the compilation will serve as a guide for more complete data reporting in future publications.

Methods

Dataset S1 includes data from multiple different isotopes (δ^{2}H, δ^{13}C, δ^{15}N, δ^{18}O, δ^{34}S, and ^{87}Sr/^{86}Sr), from various plant parts (e.g., leaves and fruit), animal tissues (e.g., fur, muscle, bone, and feathers), other organic material (e.g., feces), and water samples that were collected within the past 150 years. Detailed metadata are provided in Dataset S2. We did not include measurements from living archives (e.g., δ^{13}C and δ^{18}O data from tree ring

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records spanning hundreds of years) given that these are better suited for a separate database for older specimens that we are in the process of compiling.

The assemblage of published isotopic data from modern materials took place between November 2021 and November 2023. We relied on current professional networks, bibliographies, and internet search engines (e.g., Google Scholar) to locate relevant publications. Search terms included different combinations of keywords such as "Madagascar," "stable isotope," "isotopic," "nitrogen," "carbon," and "ecology." For all journal articles and book chapters published within the past 20 years, we contacted the corresponding authors to request published data and gather outstanding metadata. Not all authors responded or were willing or able to share their published data; a list of the publications that describe data or include summary data and are currently not included in IsoMad is provided in Dataset S3. In addition to published data, we were able to include a relatively large number of previously unpublished isotopic data. Please see Supplementary Information - Methods S1 for details regarding the pre-treatment and analysis of the samples that resulted in these data.

Each entry in Dataset S1 was assigned a site name and georeferenced using decimal degrees in the WGS84 datum system. For freshwater and terrestrial entries, elevation (m above sea level), mean annual precipitation (MAP, mm/yr), and distance to closest coast (km) were estimated using QGIS 3.10.2. Elevation was sampled from the GEBCO-terrestrial raster, and MAP was extracted from the WorldClim2.1 30 s bio12 raster[24]. Distance to the closest coast was calculated by applying the NNJoin tool to sample locations and a trimmed outline of the island reprojected on the EPSG:8441 – Tananarive / Laborde Grid.

Each row is an entry for a unique specimen. Collection date and taxonomic description of each entry are specified as precisely as possible; uncertainties in collection date are indicated by ranges of years. The taxon sampled for analysis is typically identified at least to Kingdom and down to species whenever possible. However, some entries lack taxonomic description beyond common name or local Malagasy name (given in italics) or are mixtures of multiple materials (e.g. particulate organic matter) that cannot be assigned a taxon. Additional species attributes include specification of environment (e.g., "terrestrial" vs. "marine"), plant photosynthetic pathway ("C3", "C4" or "CAM"), and species status for terrestrial taxa (endemic or introduced, as indicated on the "Global Register of Introduced and Invasive Species – Madagascar"[25]).

Individual specimen attributes are also included to the highest degree possible based on publications and the unpublished notes of authors. This includes sex, body mass (kg), age category, collection method, collection setting, material type (e.g., "feather" vs. "leaf"), element (e.g., specifying bone or muscle component), subsample (for incremental or serially sampled specimens), and additional attribute notes. Given that some entries include isotopic data from multiple materials belonging to a single individual (e.g., fur, bone, and muscle from the same animal), isotopic data in the main material type groups are separated into multiple fields (e.g., "fur $\delta^{13}C$" and "muscle $\delta^{13}C$"). All stable isotope data are presented relative to international standards ($\delta^{2}H_{VSMOW}$, $\delta^{13}C_{VPDB}$, $\delta^{15}N_{AIR}$, $\delta^{18}O_{VPDB}$ or $\delta^{18}O_{VSMOW}$, $\delta^{34}S_{VCDT}$), and elemental weight %C:N values have been converted to atomic C:N values for consistency. We report water $\delta^{18}O$ values relative to VSMOW and $\delta^{18}O$ values from all other materials relative to VPDB. Full references are provided for each isotope system (e.g., "d15N_Source_Reference" versus "d34S_Source_Reference") for each data entry. This helps clarify sources for specimens that have had isotope data for different elements (e.g., C and N) published in different publications. Additional fields for combinations of material types and isotope systems (e.g. plant $\delta^{18}O$ values) not yet represented will be added to the compilation and associated metadata descriptions as needed during future updates.

Data Records

The IsoMad compilation currently includes 18,578 isotopic measurements from 9,508 specimens; 5,010 of the measurements for 2,725 specimens are reported here for the first time (Fig. 1a)[26]. Most data are $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 1a), with just 1,062 measurements (5.7% of total measurement number) from other isotope systems (H, S, O, & Sr). Most data in the compilation were published within the past 15 years, but the collection history of $\delta^{13}C$ data (paralleling that of $\delta^{15}N$ data during recent decades) extends over four decades (Fig. 1b). It is only since 2017 that researchers have published $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ data from biological materials collected on the island.

Most specimens in the compilation come from terrestrial organisms (Fig. 2a). Fur and muscle are the most commonly analyzed animal tissues (Fig. 2b), and leaves are the most commonly analyzed plant tissues (Fig. 2c). These specimens have a wide geographic distribution (Fig. 2d), although data are relatively limited from much of the western and northeastern parts of the island.

IsoMad is a partner of the IsoMemo network (isomemo.com). The compiled database (Datasets S1-3) is available for download through the IsoMad data community on the Pandora data platform[26]. Data are also accessible via online software developed within the Pandora and IsoMemo initiatives, which facilitates data queries, visualization, and analysis. The IsoMad data community is intended as a general warehouse of isotopic data from Madagascar and in the future may include additional datasets from ancient specimens and continuous archives (e.g., sequentially sampled speleothems). Updates to IsoMad will be made at least annually by both existing administrators (S.H., B.C., & R.F.) and future administrators who can contribute updates directly through the Pandora data platform. Researchers are encouraged to send new datasets to the existing administrators and inquire if interested in becoming administrators.

Technical Validation

Following data compilation, all sample attribute data were checked and modified as needed for consistency. This involved correcting misspelled or outdated taxonomic names, standardizing the spelling of site names, and confirming geographic coordinates. Given that the accuracy of coordinates varies according to collection method, we included a field ("Coordinate_Type") to specify the method associated with each entry (e.g., "collected with

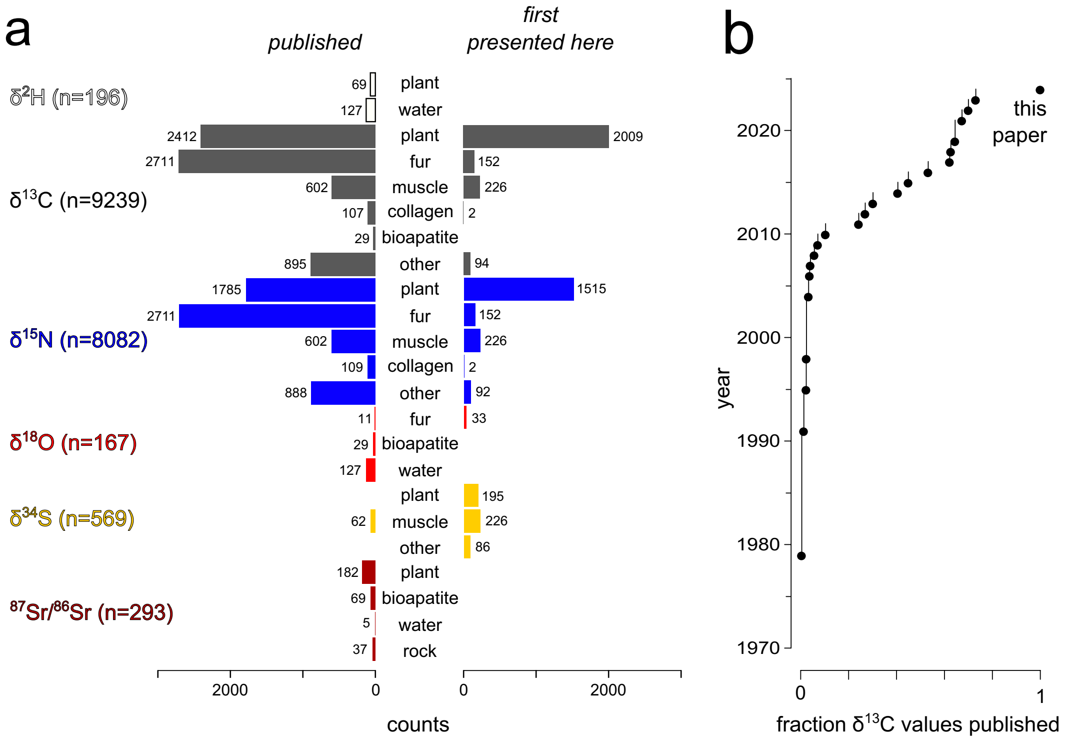

Fig. 1 Numbers of isotopic measurements separated according to isotope system, material type and whether or not data were previously published (**a**), and the publication history of the 9,239 δ^{13}C values (**b**), which mirrors that of δ^{15}N values (δ^{13}C and δ^{15}N data are typically acquired at the same time). The accumulation of δ^{13}C values over the past 50 years in frame b is presented as an empirical cumulative distribution function, which jumps up by x/N at each year when data were published, where N is the total number of published data entries and x is the total number published in the given year.

GPS", "reported by author", or "estimated from map"). We also included a field to indicate imprecise site coordinates ("Site_Radius_ > 50_km").

Previously unpublished data presented in this compilation for the first time are assigned a unique "Analysis_Code"; detailed sample collection and analytical methods for these entries are provided in Supplementary Information – Methods S1. Sample pretreatment and analysis can both impact isotopic data, but these impacts should be relatively minor (<1‰) in most cases[27–30].

Usage Notes

The IsoMad compilation of isotopic data from modern materials can be used to identify drivers of isotopic variability among primary producers, evaluate foraging niches of endemic and introduced animals, and serve as a modern reference when studying the subfossil record. As part of the Pandora & IsoMemo initiatives, data from IsoMad are connected with an R-based toolkit of applications for various types of analysis, including spatio-temporal modeling (https://github.com/Pandora-IsoMemo). We briefly illustrate potential uses of the data compilation through two examples involving data from entries 1 through 8,327: (1) Estimations of terrestrial consumer diets based on δ^{13}C data (using AverageR & ReSources); and (2) An exploration of the influences of abiotic and biotic variables on plant and mouse lemur (*Microcebus* spp.) δ^{15}N values (using the AverageR, OperatoR, and Bayesian Model Selection under Constraints (BMSC) apps).

Example 1. Inferring consumer diet using isotopic data requires (1) knowing different possible dietary sources, and (2) confirming these possible sources are isotopically distinct. Although many types of organisms (e.g., anthropods and fungi) are underrepresented in the IsoMad database, the compilation improves our ability to evaluate diet, such as in the nearshore marine environment around Toliara in southwestern Madagascar (Fig. S1). Given the extensive spatial coverage of isotopic data from terrestrial plants, we are also able to estimate the degree to which consumers from different parts of the island rely on C_3 plants (mostly woody taxa) and C_4 plants (mostly grasses)[31]. We assumed for simplicity that the contribution of dietary carbon from CAM succulent plants was minimal. It is possible to use AverageR to generate interpolated surfaces of plant δ^{13}C values that can then be used to extract estimated average δ^{13}C values for both C_3 and C_4 plants at particular sites across the island (Fig. 3a). We corrected plant δ^{13}C values for isotopic changes in atmospheric CO_2 since the Industrial Revolution (the Suess Effect[32]) according to collection year[16]. We emphasize that it is essential that this type of correction is considered during future comparisons, especially those involving δ^{13}C values from both modern and ancient material. As expected, there is considerable geographic variability in C_3 plant δ^{13}C values, with lower values in mesic central and northern Madagascar, and higher values in the arid southwest. This reflects differences in water

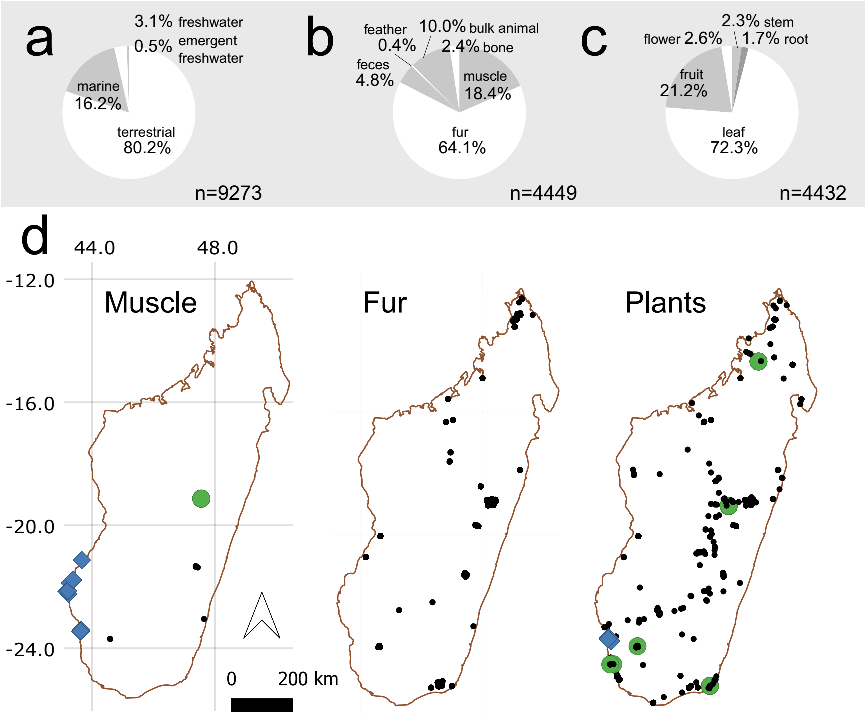

Fig. 2 Pie charts showing the relative breakdown of all database entries categorized according to environment (**a**), animal tissue types (**b**), and plant tissue types (**c**), and maps showing the spatial distributions of sampling locations for select material types (**d**), where blue diamonds = marine, green circles = freshwater, black circles = terrestrial. We note that the number of data for plant tissue samples (n = 4,432 entries) and animal tissue samples (n = 4,449) do not sum to the database total (n = 9,508); this is because the database also includes other organisms, such as fungi, and specimens not assigned to Kingdom. Also note that frame b excludes 12 individuals that have data for multiple tissue types, that frame c does not include plant tissues that were very rare (e.g., bark, husk, pod, seed), and that only sites with coordinates known within 50 km are shown in frame d.

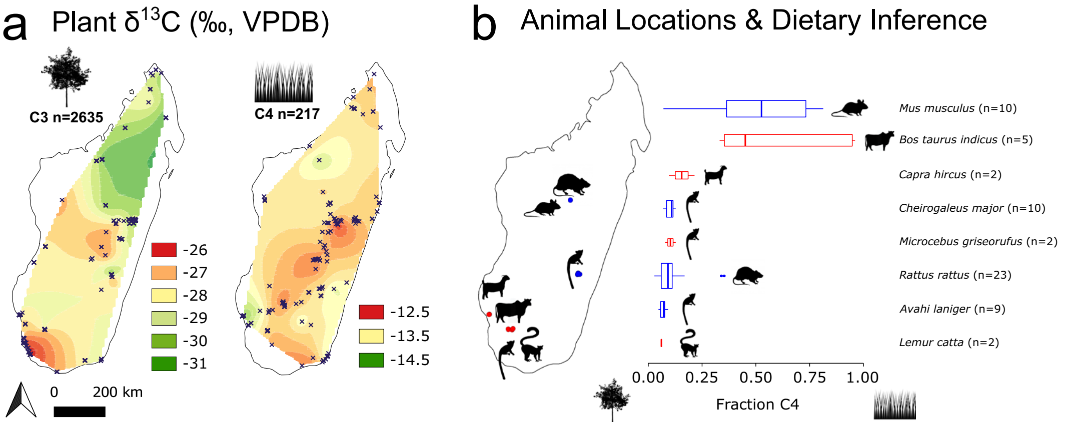

Fig. 3 Maps of Madagascar showing interpolated C_3 and C_4 plant $\delta^{13}C$ values based on data from the marked collection sites (**a**), locations of selected mammals with bone collagen $\delta^{13}C$ data, and the inferred contribution of carbon from C_4 plant protein in the diet of each group (**b**). Frame a includes $\delta^{13}C$ values only from plants with known collection times (including specimens collected since 1880) and sites identified to within 50 km. Dietary contributions in frame b were estimated using ReSources, as described in the main text. Box plots have widths scaled to sample size; boxes illustrate interquartile ranges and whiskers extend to minimum/maximum points that fall with 1.5 times the interquartile ranges. Boxes are colored according to region, with blue = Central Highlands and red = southwest Madagascar.

availability as well as physiological differences among plants growing in the different regions[33]. In contrast, there is comparatively little geographic variability in C_4 plant $\delta^{13}C$ values, which is consistent with studies elsewhere[34–36].

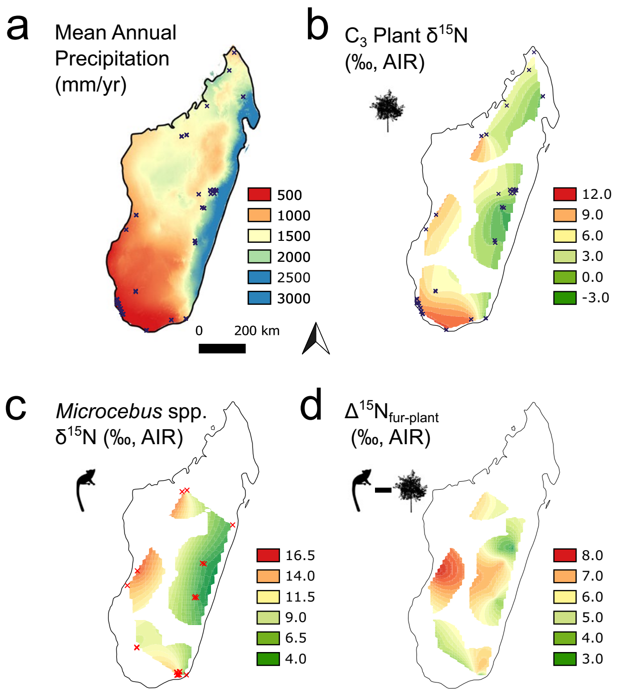

Fig. 4 Interpolated surfaces of mean annual precipitation (MAP) (**a**), δ^{15}N values for terrestrial C_3 plant tissues not belonging to members of Fabaceae (n = 2,441) (**b**), δ^{15}N values for *Microcebus* spp. fur (n = 1,246) (**c**), and differences between *Microcebus* spp. fur and C_3 plant tissue δ^{15}N values ($\Delta^{15}N_{\text{fur-plant}}$) from the same regions (**d**). MAP data are taken from WorldClim 2.1[24]. Collection site was known to within 50 km for plant and lemur data entries. The δ^{15}N surfaces are masked to within 150 km of each collection site (marked with an "x" in frames a-c) and were generated using a Bayesian approach with constant interpolation in AverageR and OperatoR.

We used the Bayesian mixing model called ReSources[37], an updated version of a previously published mixing model called FRUITS[38], to infer the fraction of carbon from C_4 plants in the diet of introduced murid rodents and bovids, as well as endemic lemurs collected from sites in the Central Highlands and relatively arid Southwest. We worked exclusively with bone collagen and used the locations of where bones were collected (Fig. 3b) to extract local estimates of C_3 and C_4 plant δ^{13}C values (Fig. 3a). Estimated contribution of C_3 and C_4 plants to the diet of each species, summarized in Fig. 3b, were derived by independently modeling the proportion of carbon from C_4 plants in the diet of each individual. We assumed that collagen carbon is derived only from dietary protein C and accounted for the offset in δ^{13}C values between consumer collagen and dietary protein through an estimated constant correction of 5.8 ± 1.0‰ (based on a controlled feeding experiment with *Rattus* sp.[39]). Each consumer δ^{13}C value was also assumed to have an associated uncertainty of 0.5‰. Consistent with previous work on Madagascar[4,7,20,40], modeled data suggest that all four lemur species primarily consume C_3 foods while introduced mice (*Mus musculus*) and cows (*Bos taurus indicus*) consume a fair amount of C_4 plants. Introduced goats (*Capra hircus*) and murid *Rattus* tend to get more of their food from C_3 plants, which likely indicates foraging on forest-derived foods rather than grassy biomes. This supports the concern that introduced animals may negatively impact endemic forest-dwelling animals through competition and possibly predation[7,41].

Example 2. Additional inference regarding consumer diet is possible based on the nitrogen isotope content of consumer tissue. Geographic variation in plant δ^{15}N values complicates the interpretation of consumer δ^{15}N values from different ecoregions[42,43] but also gives opportunities to learn about the microhabitat use of particular taxa[4,17]. Based on reviews of plant δ^{15}N data[44–47] and previous work on Madagascar[40], we expect that soil moisture availability, and related variables like mean annual precipitation (MAP), explain the majority of the spatial variation in plant δ^{15}N values across the island. Indeed, as generally expected, application of the Bayesian spatial smoothed model AverageR[48] to the IsoMad compilation (including samples from a variety of years and seasons) illustrates how increasing MAP is associated with lower C_3 plant δ^{15}N values (Fig. 4a,b).

Based on a past study of spatial variation in mouse lemur (*Microcebus* spp.) fur δ^{15}N values[40], we expect isotopic variability in the fur of these C_3 plant consumers (Fig. 3b) to closely match that of C_3 plant δ^{15}N values. Indeed, geographic differences in δ^{15}N values are similar for plants and fur (Fig. 4b-c). However, apparent differences between fur and plant δ^{15}N values ($\Delta^{15}N_{\text{fur-plant}}$) are quite variable and range from ~3 to 8‰ across the interpolated surfaces of δ^{15}N values (Fig. 4d). A relatively consistent and positive $\Delta^{15}N_{\text{fur-plant}}$ is expected[49] given that mouse lemurs consume a mix of plant and animal matter, primarily fruit and arthropods[50]. Some species or populations of mouse lemurs might eat relatively more animal matter than others, and this could impact estimated $\Delta^{15}N_{\text{fur-plant}}$ values by up to ~3‰[51,52]. Variation in $\Delta^{15}N_{\text{fur-plant}}$ values can also be explained by different collection times for fur and plant samples, as well as interpolation of plant values across diverse environments.

Co-occurring plants can have variable $\delta^{15}N$ values due to a variety of factors[10,40], and there can be considerable variability in plant $\delta^{15}N$ values among adjacent microhabitats[10,40,53]. We used BMSC, a Bayesian regression model selection algorithm[54], to identify the relative influence of MAP, coastal proximity, and plant part on plant $\delta^{15}N$ values (Supplementary Information – Usage Notes S1, Fig. S2). This example highlights areas for finer-scale investigation as well as some of the complexity associated with interpreting consumer $\delta^{15}N$ values.

Code availability

The statistical analysis and modeling employed for examples given in the Usage Notes was done using R packages developed within the Pandora & IsoMemo initiatives[38,48,54]. The source code for all of these is available for download on GitHub: AverageR (https://github.com/Pandora-IsoMemo/DSSM), BMSC (https://github.com/Pandora-IsoMemo/bmsc), and ReSources (https://github.com/Pandora-IsoMemo/resources). These can be run online or locally (https://github.com/Pandora-IsoMemo/drat) as Shiny apps[55]. For modeling reproducibility, a full description of model options is available through the IsoMad data community (https://pandoradata.earth/organization/isomad-isotopic-data-of-madagascar), which is stored on the Pandora data platform. This platform is based on the CKAN open source data management system (https://ckan.org/) and is hosted by the Max Planck Computing and Data Facility.

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References

1. Ralimanana, H. *et al*. Madagascar's extraordinary biodiversity: Threats and opportunities. *Science* **378**, eadf1466 (2022).
2. Winter, K. $\delta^{13}C$ values of some succulent plants from Madagascar. *Oecologia* **40**, 103–112 (1979).
3. Crowley, B. E., McGoogan, K. C. & Lehman, S. M. Edge effects on foliar stable isotope values in a Madagascan tropical dry forest. *PloS one* **7**, e44538 (2012).
4. Crowley, B. E. *et al*. Extinction and ecological retreat in a community of primates. *Proceedings of the Royal Society of London B: Biological Sciences* **279**, 3597–3605 (2012).
5. Crowley, B., Blanco, M., Arrigo-Nelson, S. & Irwin, M. Stable isotopes document resource partitioning and effects of forest disturbance on sympatric cheirogaleid lemurs. *Naturwissenschaften* **100**, 943–956 (2013).
6. Bamford, A. J., Razafindrajao, F., Robson, H., Woolaver, L. G. & de Roland, L. A. R. The status and ecology of the last wild population of Madagascar Pochard *Aythya innotata*. *Bird Conservation International* **25**, 97–110 (2015).
7. Dammhahn, M., Randriamoria, T. M. & Goodman, S. M. Broad and flexible stable isotope niches in invasive non-native *Rattus* spp. in anthropogenic and natural habitats of central eastern Madagascar. *BMC ecology* **17**, 1–13 (2017).
8. Hixon, S. W. *et al*. Dogs occupying grassy habitat near protected areas in eastern Madagascar rely on foods from forests. *Plants, People, Planet* (2022).
9. Crowley, B. E., Castro, I., Soarimalala, V. & Goodman, S. M. Isotopic evidence for niche partitioning and the influence of anthropogenic disturbance on endemic and introduced rodents in central Madagascar. *The Science of Nature* **105**, 1–13 (2018).
10. Rakotondranary, S. J., Struck, U., Knoblauch, C. & Ganzhorn, J. U. Regional, seasonal and interspecific variation in ^{15}N and ^{13}C in sympatric mouse lemurs. *Naturwissenschaften* **98**, 909–917 (2011).
11. Frédérich, B., Fabri, G., Lepoint, G., Vandewalle, P. & Parmentier, E. Trophic niches of thirteen damselfishes (Pomacentridae) at the Grand Récif of Toliara, Madagascar. *Ichthyological Research* **56**, 10–17 (2009).
12. Mortillaro, J.-M. *et al*. Trophic functioning of integrated rice-fish farming in Madagascar: Insights from stable isotopes ($\delta^{13}C$ & $\delta^{15}N$). *Aquaculture* **555**, 738240 (2022).
13. Dammhahn, M., Soarimalala, V. & Goodman, S. M. Trophic Niche Differentiation and Microhabitat Utilization in a Species-rich Montane Forest Small Mammal Community of Eastern Madagascar. *Biotropica* **45**, 111–118 (2013).
14. Dammhahn, M., Rakotondramanana, C. F. & Goodman, S. M. Coexistence of morphologically similar bats (Vespertilionidae) on Madagascar: stable isotopes reveal fine-grained niche differentiation among cryptic species. *Journal of Tropical Ecology* **31**, 153–164 (2015).
15. Mittelheiser, L., Lepoint, G., Gillet, A. & Frederich, B. Ecomorphology of six goatfish species (Mullidae) from Toliara Reef, Madagascar. *Environmental Biology of Fishes* **105**, 1015–1032 (2022).
16. Crowley, B. E. & Godfrey, L. R. Why all those spines?: Anachronistic defences in the Didiereoideae against now extinct lemurs. *South African Journal of Science* **109**, 1–7 (2013).
17. Hixon, S. W. *et al*. Nitrogen isotope ($\delta^{15}N$) patterns for amino acids in lemur bones are inconsistent with aridity driving megafaunal extinction in south-western Madagascar. *Journal of Quaternary Science* **33**, 958–968 (2018).
18. Tovondrafale, T., Razakamanana, T., Hiroko, K. & Rasoamiaramanan, A. Paleoecological analysis of elephant bird (Aepyornithidae) remains from the Late Pleistocene and Holocene formations of southern Madagascar. *Malagasy Nat* **8**, 1–13 (2014).
19. Godfrey, L. R. *et al*. What did *Hadropithecus* eat, and why should paleoanthropologists care? *American Journal of Primatology* **78**, 1098–1112 (2016).
20. Hixon, S. W. *et al*. Late Holocene spread of pastoralism coincides with endemic megafaunal extinction on Madagascar. *Proc. R. Soc. Lond. B* **288**, 20211204 (2021).
21. Hixon, S. *et al*. Ecological consequences of a millennium of introduced dogs on Madagascar. *Frontiers in Ecology and Evolution* **9**, 428 (2021).
22. Hansford, J. P. & Turvey, S. T. Dietary isotopes of Madagascar's extinct megafauna reveal holocene browsing and grazing guilds. *Biology Letters* **18**, 20220094 (2022).
23. Wilkinson, M. D. *et al*. The FAIR Guiding Principles for scientific data management and stewardship. *Scientific data* **3**, 1–9 (2016).
24. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315 (2017).
25. Randrianizahana, H. *et al*. Global Register of Introduced and Invasive Species - Madagascar (2020).
26. Hixon, S. *et al*. IsoMad Modern Biological Material. *Pandora*, https://doi.org/10.48493/wvsn-k463 (2024).
27. Pérez, P. A., Docmac, F. & Harrod, C. No evidence for effects of mill-grinding on δ13C, $\delta^{15}N$ and $\delta^{34}S$ values in different marine taxa. *Rapid Communications in Mass Spectrometry* **36**, e9336 (2022).
28. Paul, D., Skrzypek, G. & Fórizs, I. Normalization of measured stable isotopic compositions to isotope reference scales–a review. *Rapid Communications in Mass Spectrometry: An International Journal Devoted to the Rapid Dissemination of Up-to-the-Minute Research in Mass Spectrometry* **21**, 3006–3014 (2007).
29. Stichler, W. Interlaboratory comparison of new materials for carbon and oxygen isotope ratio measurements. *Reference and intercomparison materials for stable isotopes of light elements* **825**, 67–74 (1995).

30. Pestle, W. J., Crowley, B. E. & Weirauch, M. T. Quantifying inter-laboratory variability in stable isotope analysis of ancient skeletal remains. *PloS one* **9**, e102844 (2014).
31. West, J. B., Bowen, G. J., Cerling, T. E. & Ehleringer, J. R. Stable isotopes as one of nature's ecological recorders. *Trends in Ecology & Evolution* **21**, 408–414 (2006).
32. Keeling, C. D. The Suess effect: 13Carbon-14Carbon interrelations. *Environment international* **2**, 229–300 (1979).
33. Farquhar, G., Hubick, K., Condon, A. & Richards, R. in *Stable isotopes in ecological research* 21-40 (Springer, 1989).
34. Luo, W. *et al*. Effects of plant intraspecific variation on the prediction of C3/C4 vegetation ratio from carbon isotope composition of topsoil organic matter across grasslands. *Journal of Plant Ecology* **14**, 628–637 (2021).
35. Ehleringer, J. R. & Cerling, T. E. C3 and C4 photosynthesis. *Encyclopedia of Global Environmental Change, The Earth system: biological and ecological dimensions of global environmental change* **2**, 186–190 (2002).
36. Swap, R., Aranibar, J., Dowty, P., Gilhooly, W. & Macko, S. A. Natural abundance of ^{13}C and ^{15}N in C3 and C4 vegetation of southern Africa: patterns and implications. *Global Change Biology* **10**, 350–358 (2004).
37. Sołtysiak, A. & Fernandes, R. Much ado about nothing: assessing the impact of the 4.2 kya event on human subsistence patterns in northern Mesopotamia using stable isotope analysis. *Antiquity* **95**, 1145–1160 (2021).
38. Fernandes, R., Millard, A. R., Brabec, M., Nadeau, M.-J. & Grootes, P. Food reconstruction using isotopic transferred signals (FRUITS): a Bayesian model for diet reconstruction. *PloS one* **9**, e87436 (2014).
39. Jim, S., Jones, V., Ambrose, S. H. & Evershed, R. P. Quantifying dietary macronutrient sources of carbon for bone collagen biosynthesis using natural abundance stable carbon isotope analysis. *British Journal of Nutrition* **95**, 1055–1062 (2006).
40. Crowley, B. E. *et al*. Explaining geographical variation in the isotope composition of mouse lemurs (*Microcebus*). *Journal of Biogeography* **38**, 2106–2121 (2011).
41. Goodman, S. M. Rattus on Madagascar and the dilemma of protecting the endemic rodent fauna. *Conservation Biology* **9**, 450–453 (1995).
42. Casey, M. M. & Post, D. M. The problem of isotopic baseline: reconstructing the diet and trophic position of fossil animals. *Earth-Science Reviews* **106**, 131–148 (2011).
43. Woodcock, P. *et al*. Assessing trophic position from nitrogen isotope ratios: effective calibration against spatially varying baselines. *Naturwissenschaften* **99**, 275–283 (2012).
44. Amundson, R. *et al*. Global patterns of the isotopic composition of soil and plant nitrogen. *Global biogeochemical cycles* **17** (2003).
45. Handley, L. *et al*. The ^{15}N natural abundance (δ^{15}N) of ecosystem samples reflects measures of water availability. *Functional Plant Biology* **26**, 185–199 (1999).
46. Craine, J. M. *et al*. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist* **183**, 980–992 (2009).
47. Austin, A. T. & Vitousek, P. Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia* **113**, 519–529 (1998).
48. Cubas, M. *et al*. Latitudinal gradient in dairy production with the introduction of farming in Atlantic Europe. *Nature Communications* **11**, 1–9 (2020).
49. Kelly, J. F. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian journal of zoology* **78**, 1–27 (2000).
50. Mittermeier, R. A., Nash, S. D. & International, C. *Lemurs of Madagascar*. (Conservation International, 2010).
51. Sponheimer, M. *et al*. Nitrogen isotopes in mammalian herbivores: hair δ^{15}N values from a controlled feeding study. *International Journal of Osteoarchaeology* **13**, 80–87 (2003).
52. Adams, T. S. & Sterner, R. W. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. *Limnology and Oceanography* **45**, 601–607 (2000).
53. Crowley, B. E., Rasoazanabary, E. & Godfrey, L. R. Stable isotopes complement focal individual observations and confirm dietary variability in reddish–gray mouse lemurs (*Microcebus griseorufus*) from southwestern Madagascar. *American Journal of Physical Anthropology* **155**, 77–90 (2014).
54. Fernandes, R., Geeven, G., Soetens, S. & Klontza-Jaklova, V. Deletion/Substitution/Addition (DSA) model selection algorithm applied to the study of archaeological settlement patterning. *Journal of Archaeological Science* **38**, 2293–2300 (2011).
55. Chang, W., Cheng, J., Allaire, J., Xie, Y. & McPherson, J. Shiny: web application framework for R. *R package version* **1**, 2017 (2017).

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Author contributions

Sean Hixon and Brooke Crowley compiled the data and designed the metadata structure. Sean Hixon wrote the manuscript and performed the modeling. Ricardo Fernandes supervised data collection and modeling and co-wrote the manuscript. All remaining authors contributed data and assisted with revising the manuscript.

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Additional information

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