frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 24 June 2025
DOI 10.3389/fevo.2025.1533703

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A mammoth task: stable isotope analyses as a tool to prevent illegal trade of elephant ivory

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RECEIVED 24 November 2024
ACCEPTED 30 April 2025
PUBLISHED 24 June 2025

CITATION
Santos MEA, Toropov P, Agarwal P, Frichot PAJ, Tilley HB, Wan Zhongyue W, Chan J and Baker DM (2025) A mammoth task: stable isotope analyses as a tool to prevent illegal trade of elephant ivory. *Front. Ecol. Evol.* 13:1533703. doi: 10.3389/fevo.2025.1533703

Although mammoth ivory was claimed as a substitute to elephant ivory, there are several issues with the current methods to differentiate the two ivory, which provided a loophole to laundering and illegal trade. To contribute to developing efficient tools to distinguish ivory samples, we applied a relatively cheap and fast protocol using stable isotope ratios of carbon ($\delta^{13}C$), hydrogen ($\delta^{2}H$), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$), and sulfur ($\delta^{34}S$). We compared the isotope ratios of the two ivory types and found statistically significant (p-value<0.01) differences in the Wilcoxon tests for $\delta^{2}H$, $\delta^{18}O$, $\delta^{13}C$ and $\delta^{34}S$, but no significant difference for $\delta^{15}N$. There was no overlap between $\delta^{2}H$ and a small overlap for $\delta^{18}O$, while $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ of most mammoth samples were within the larger isotopic range values of the elephant samples. The PCA also pointed to a higher contribution of $\delta^{2}H$ (96.9%) followed by $\delta^{18}O$ (2.7%) to differentiate the ivory types. Our results showed SIA as an efficient tool to distinguish elephant and mammoth ivory, and we recommend using a multi-elements SIA approach focusing on $\delta^{2}H$ and $\delta^{18}O$. While it is essential to address the social issues related to the ivory trade, including reducing human-elephant conflict and increasing financial support to Siberian carver communities, alternatives for natural ivory should also be sought, combined with strict policy changes to combat illegal trade and protect the African and Asian elephant populations.

KEYWORDS

conservation forensics, illegal trade, laundering, mammoth, stable isotope analyses, permafrost, trafficking, tusk

Introduction

Illegal or unsustainable wildlife trade (IUWT) is a major threat to biodiversity conservation worldwide, making it crucial to find effective solutions to control trade activities (Cardoso et al., 2021). Wildlife-related crimes, consisting of poaching, smuggling, breeding, and trapping, are often linked to the trafficking of drugs, weapons and people (Doody et al., 2021). The combat of IUWT is hampered by several factors, including that the wildlife collection mostly happens in isolated locations, with insufficient amounts of biological or physical evidence for accurate sample identification. However, recent efforts to advance laboratory techniques used to identify and confirm the origin of the specimens, combined with the creation of collaboration networks between countries, have improved conservation strategies (Woodcock et al., 2023). Thus, it is essential to consolidate feasible tools to support law enforcement (Kanthaswamy, 2024).

The poaching of elephants is a complex IUWT case, as the ivory trade occurs between multiple countries with different environmental and socio-economic impacts. The ivory tusks of species in the family Elephantidae are teeth-like structures that serve a variety of purposes including defense, digging, lifting objects, and gathering food (Steenkamp et al., 2007; Bielert et al., 2018). For millennia, ivory pieces have been used by human populations across the world as carving objects (Chaiklin, 2010; Lane, 2015; Steguweit, 2015) and a traditional art form (Gao and Clark, 2014), but in modern days become a main threat to the survival of elephant populations. All three extant elephant species are listed on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species as either ‘endangered’ (*Loxodonta africana* and *Elephas maximus*) or ‘critically endangered’ (*L. cyclotis*). Ivory poachers target mainly African elephants (*L. africana* and *L. cyclotis*), which had a population decline of over 80% in the past century. Elephants are often fatally shot by poachers so that ivory can be easily removed from carcasses, however, even if the elephants survive an instance of poaching, their tusks do not regrow (Raubenheimer, 2000; Gobush et al., 2021). Asian elephant ivory (*E. maximus*) is targeted on a smaller scale, as unlike their African cousins, usually only males possess tusks (Chelliah and Sukumar, 2013). Still, Asian elephants also face other challenges including poaching for their skin (Sampson et al., 2018; Menon and Tiwari, 2019), human-elephant conflict in their natural ranges (Doyle et al., 2010; Jarungrattanapong and Olewiler, 2024), and exploitation with a third of the global population residing in captivity (Sukumar, 2006; Hankinson and Nijman, 2020).

Elephants were first added to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendix list in 1989, but still allowing domestic trade (UNEP et al., 2013). In 2018, China, one of the central ivory markets (Sosnowski et al., 2019), imposed a comprehensive ban of elephant ivory for commercial trade (Chen et al., 2023). Hong Kong SAR, a main trade hub between China and other countries, banned the elephant ivory trade in 2021. One of the main ivory alternatives are from mammoths (*Mammuthus* spp.). Although these elephantids went extinct during the last Ice Age over 4,000 years ago (Haynes, 1991), the remains of millions of individuals, including their tusks, are preserved underground in high latitude regions and mostly exploited from the Siberian tundra in Russia. Harvesting of the woolly mammoth (*M. primigenius*) is a potential substitute to elephant ivory, though this activity is also associated with ecosystemic and economic issues (Potravny et al., 2024).

The exploitation of mammoths could decrease the pressure suffered by elephant populations, still, there are several issues with the current methods available to distinguish the two ivory types. Therefore, instead of acting as a substitute for the demand for elephant ivory, mammoth ivory provided loopholes for elephant ivory dealers (Chen et al., 2023; Cox and Hauser, 2023). Illegal ivory can be sold under the guise of legal mammoth ivory (Shepherd et al., 2024), incentivizing poachers to continue the killing of elephants (Yu et al., 2017). For instance, although the angle of specific marks in the ivory is one straightforward morphological method (Trapani and Fisher, 2003), called Schreger lines, these marks are often not visible in pieces that have been polished or carved (Ngatia et al., 2019). It is also possible to discriminate mammoth and elephant ivory using spectrometry, but the intensity ratios are dependent upon the environmental condition to which the ivory specimens have been exposed (Parungao et al., 2024). The most effective methods in ivory identifications are radiocarbon dating (Cerling et al., 2018; Quarta et al., 2019) and genetic analyses (Ewart et al., 2020; Hale et al., 2021; Cox and Hauser, 2023). However, these tools are expensive and a long time is needed to receive results (weeks to months) with large amounts of ivory required (often more than 100 mg) for the testing process.

A much cheaper and faster testing alternative to distinguishing between elephant and mammoth ivory is using stable isotope analyses (SIA). Species living in environments with different isotope ratios of elements will absorb those isotopes, resulting in distinctive isotope signatures. Thus, measuring the isotopes ratios in the tissue or bone of animals allows, for example, the identification of their geographic source location (Hobson, 1999; Sung et al., 2021), and status as captive or wild animals (Andersson et al., 2021). SIA has contributed to the combat of IUWT for several species (Meier-Augenstein, 2019; Prigge et al., 2024), including wood turtles (*Glyptemys insculpta;* Hopkins et al., 2022), African grey parrots (*Psittacus erithacus*; Alexander et al., 2019), and yellow-crested cockatoos (*Cacatua sulphure*; Andersson et al., 2021). Although SIA has been used to estimate the country of origin of elephant ivory (van der Merwe et al., 1990; Codron et al., 2012; 2016; Hale et al., 2021), comparisons between elephant and mammoth ivory are scarce. A recent World Wide Fund for Nature (WWF) report letter showed distinct hydrogen (δ^2H) and oxygen (δ^{18}O) isotopic signatures between these ivory (Ziegler, 2021). This is due to their very distinct habitats; elephants are found in tropical and subtropical areas, while woolly mammoths used to live in colder and drier high latitudes environments (Ziegler, 2021), indicating that SIA is a promising tool to ivory conservation forensics.

In this study, we optimized and applied a multi-elements approach with isotope ratios of carbon (δ^{13}C), hydrogen (δ^2H), nitrogen (δ^{15}N), oxygen (δ^{18}O), and sulfur (δ^{34}S) to ivory samples. Our goal is to highlight the isotopic differences and provide a protocol to differentiate between elephant and mammoth ivory. As SIA is a powerful tool to prevent illegal trade in several species (Alexander et al., 2018; Meier-Augenstein, 2019), we here expand the reference database and provide an essential foundation to further developing a framework to certify the origin of ivory objects.

Materials and methods

Ivory samples

In total, we analyzed 79 ivory objects (Supplementary Table 1), identified as elephant (44) or mammoth (35) by seizure agencies and sellers. Elephant ivory objects were acquired in seizures between 2007 to 2023 by the Agriculture, Fisheries and Conservation Department of the Hong Kong government (AFCD) in illegal imports to Hong Kong from African countries (Ethiopia, Gabon, Ghana, Ivory Coast, Nigeria, South Africa, and Zimbabwe), China, Thailand, and the United States of America. We acquired unworked mammoth ivory fragments from Siberian carvers, and additional mammoth ivory objects purchased between 2022 to 2024 in markets in China (Shanghai) and Hong Kong (Supplementary Table 1), mostly by donations of WWF-Hong Kong. Unfortunately, the exact geographical origin and species identification is unknown. Samples were drilled between January and August of 2024, and stored in a dry-cabinet before isotope measurements.

Stable isotope analyses and statistics

We developed a protocol adapted from the literature to analyze ivory powder (Ziegler et al., 2016) with four main steps described below: 1) drilling, 2) cleaning, 3) weighting, and 4) measuring δ^{13}C, δ^{2}H, δ^{15}N, δ^{18}O, and δ^{34}S. These steps were designed to optimize time and costs, with a minimum ivory powder amount required of 5 mg using the Continuous Flow-Isotope Isotope Ratio Mass Spectrometer (CF-IRMS) at the Stable Isotope Laboratory, University of Hong Kong (SIRMS-HKU).

1. Drilling: For each sample, we drilled between 5–50 mg using a drilling Dremel® 4250. We held the objects with a plier or tweezer while drilling and to avoid losing ivory material, we molded a 20–50 cm piece of aluminum foil into a funnel shape, according to the size of the object. We used rounded drill shanks, as among the different shanks available, these produced more ivory powder more quickly. We then discarded the aluminum foil. Between samples, the shanks were cleaned by scrubbing with a metallic brush, followed by thoroughly washing it with a sponge and detergent under running water, and then dried. This step required ~ 5–15 min, depending on the size of the sample.
2. Cleaning: We added 1–5 ml of dichloromethane to each of the falcon tubes to extract apolar substances from the samples for five hours followed by air-drying the samples within an oven at 50-60°C overnight. Samples were then stored in a desiccator to avoid humidification.
3. Weighting: Using a highly sensitive precision microbalance, for each sample, a subsample of 1 mg (+-0.5 mg) was weighed and packed into silver capsules (3.3×5mm) to obtain measurements of δ^{2}H, δ^{18}O, %H, and %O, with another subsample of 4 mg (+-0.5 mg) weighted and packed into tin capsules (4×6mm) to obtain measurements of δ^{13}C, δ^{15}N, δ^{34}S, %C, %N, and %S. This step takes approximately 5 min/sample.
4. Isotope measurements: We used certified international standards (Benzoic Acid and USGS40) to track precision and normalize data between analytical runs. The isotope ratios within their silver capsule and tin capsule samples were analyzed with the Elemental Analyzer (EA) CF-IRMS. Stable H, O, C, N, and S isotope compositions were expressed as isotope-delta (δ) values with the conventional unit per mil (‰) and relative to the international standards Vienna Pee Dee Belemnite and atmospheric N2. The precision of the standard was better than 0.2‰ and there were no high peaks for blanks for all isotopic values, with exception of O. The results of the EA-OH pyrolysis showed a high O peak for blank after running samples, and it is possible that the samples cannot be fully pyrolyzed. It could be that the high mineral content of the ivory occupies the reaction surfaces of the glassy carbon and graphite in the reactor. As such, we recommend smaller batches (<30 samples) in between maintenance of the reactor to improve this issue.

Samples had a non-normal distribution and we tested for significant differences in the stable isotopic signatures with the Wilcoxon test and Principal Component Analyses (PCA) in RStudio 1.3.1093 (R Team, 2020).

Results

Ivory samples

Among the carved ivory objects acquired in illegal seizures and observed in Chinese and Hong Kong markets, we found a variety of samples, including bracelets, combs, chopsticks, earrings, neckless, and seals (Figure 1; Supplementary Table 1). Two main types of mammoth ivory carved artefacts were being sold (staff of the Chinese market, personal communication): "bai jian (摆件)", which are large items that can be displayed standing up, such as plates or a single carved tusk, and "accessories (饰 品)", such as bracelets, pendants, earrings. We also observed that the markets in China and Hong Kong further classified mammoth ivory objects in four subjective categories related to the color and aspect of the ivory:

FIGURE 1
Carved elephant [**(A, B)**; in red] and mammoth [**(C, D)**; in blue] and unworked **(E, F)** ivory samples.

(1) highest quality with shiny illustrious white ivory, with an oily sheen and not visible or delicate lines with narrow spaces; (2) milky white, oily sheen, lines rather delicate with narrow spaces; (3) yellowish white, waxy sheen, lines quite coarse with wide spaces; and (4) “coffee”, when the color is dull/dark yellow with earthy sheen, lines are coarse, with wide spaces.

Isotopic signatures of ivory

Stable isotope data revealed statistically significant differences in the Wilcoxon tests for δ^2H and δ^{18}O of the elephant and mammoth samples (p-values = $3x10–^{14}$ and $3.5x10^{-12}$, respectively). Although there was no overlap between the δ^2H values of the two ivory types, the δ^{18}O data of two elephant samples were within the value range of mammoth samples (Supplementary Table 1; Figure 2). We also observed significant differences in the Wilcoxon tests between elephant and mammoth ivory samples for δ^{13}C and δ^{34}S, while no significant difference was reported for δ^{15}N (p-values = $8x10^{-2}$, $1.5x10^{-8}$, and 0.64, respectively). Nevertheless, these three isotopes had overlapping values between elephant and mammoth samples. The δ^{13}C and δ^{15}N data of all mammoth samples were within the range values of elephant samples, while δ^{34}S data of 67 mammoth samples were within the range of elephant samples (Supplementary Table 1; Figure 3). The first two principal components of the PCA explained over 99% of the total variance (Figure 4). The individual

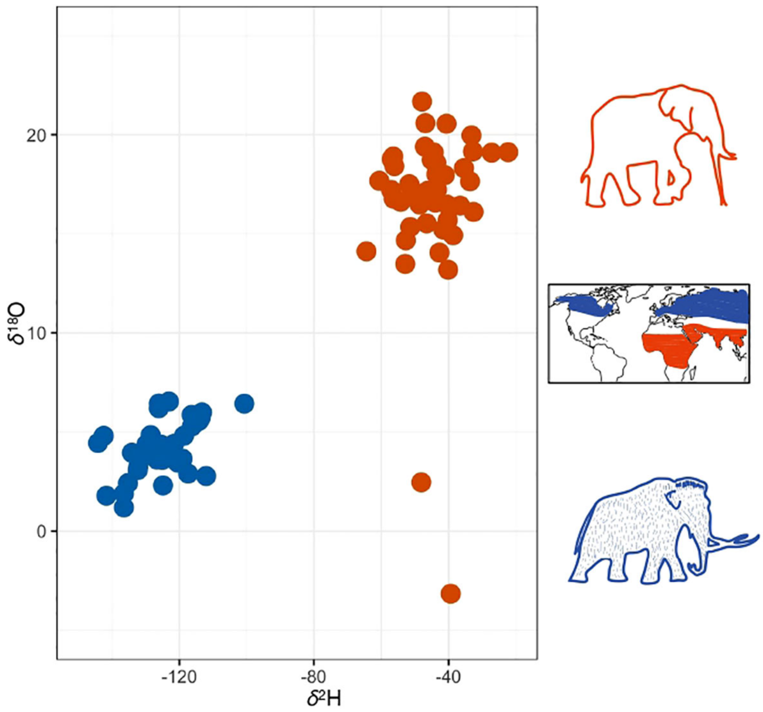

FIGURE 2
Biplot of isotope ratios of hydrogen (δ^2H) and oxygen ($\delta^{18}O$) of the elephant and mammoth ivory samples (red and blue, respectively).

contributions to these eigenvalues were 96.9% for δ^2H, 2.7% for $\delta^{18}O$, 0.23% for $\delta^{34}S$, 0.07% $\delta^{13}C$, and 0.003% for $\delta^{15}N$.

Discussion

Potential of SIA to ivory conservation forensics

Our results showed that δ^2H is the most efficient element to distinguish elephant and mammoth ivory, as there were no overlapping values between the two sample types. (Supplementary Table 1; Figure 2). Additionally $\delta^{18}O$ values were distinct between most elephant/mammoth samples. Thus, we recommend using a multi-elements SIA approach focusing on δ^2H and $\delta^{18}O$ to distinguish the two ivory types. Although our analysis omitted the extraction of collagen to optimize the protocol time, the isotopic values are potentially still comparable with elephant reference databases (e.g., www.ivoryid.org) using offsets discussed in the literature (Ziegler et al., 2016), and stable isotope ranges were similar as previously reported in the literature for elephants (van der Merwe et al., 1990; Codron et al., 2012; Ziegler et al., 2016; Ziegler, 2021) and mammoths (Bocherens et al., 1996; Ziegler, 2021). Due to their natural range, elephants consume water from tropical regions, and therefore have heavier δ^2H and $\delta^{18}O$ isotopic signatures compared to mammoths that ingested water from temperate environments of higher latitudes (Ziegler, 2021). On the other hand, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ are associated with animals' diet and trophic niche (Peterson and Fry, 1987; McCutchan et al., 2003; Boecklen et al., 2011; Jackson et al., 2011). The larger variation of these isotopes for elephant samples could be related to a more generalist feeding strategy (Codron et al., 2012) compared to mammoths, and/or a higher baseline variation of the food sources, as our sampling likely included elephant samples from across Africa and Asia. Thus, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ are less useful when the focus is simply distinguishing between mammoth and elephant ivory, compared to δ^2H and $\delta^{18}O$. Further work targeting samples of specific elephantid populations, and including SIA of their food sources such as grass, woody material, and fruits (Tchamba and Seme, 1993), will shed light on comparisons on the trophic niche of these megaherbivore species.

Social aspects of the ivory trade

Although there are integrated approaches to understanding and mitigating human-elephant conflict (HEC) in Africa and Asia, HEC is a main issue for conservation strategies for all three elephant species (Dublin and Hoare, 2004; Gross et al., 2022; Saha and Soren, 2024). The most prominent human-elephant conflict usually arises over crop raiding incidents (Walpole and Linkie, 2007). There are many different approaches which are used to deter elephants, focusing on sensory deterrents, such as chili/beehive fences or loud noises (Chang'a et al., 2016; King et al., 2011; Enukwa, 2017). However, elephants are highly intelligent animals that often find ways around the obstacles, resulting in extensive HEC (Mumby and Plotnik, 2018). Therefore, farmers often support or are not opposed to poaching for ivory (Kiffner et al., 2021). To

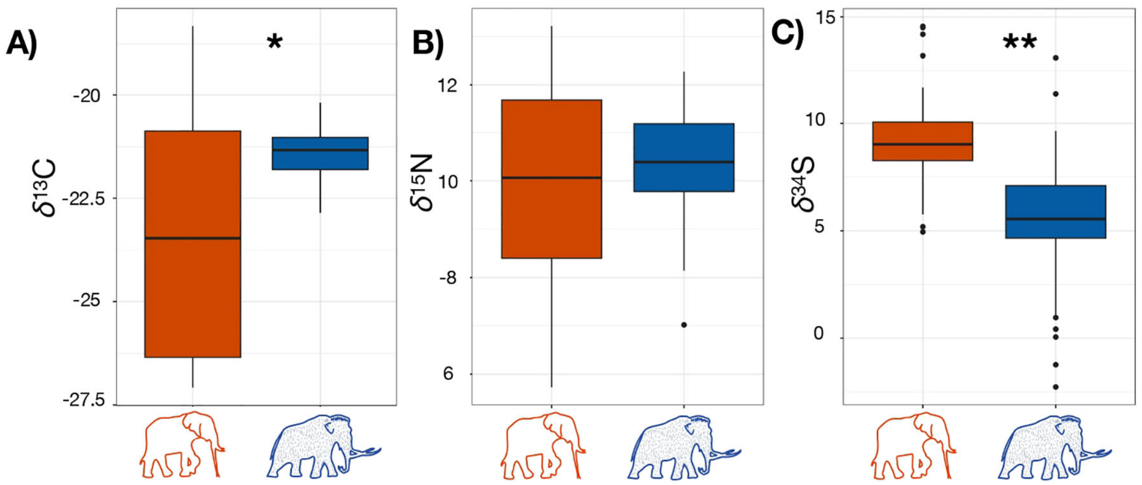

FIGURE 3
Boxplots of the isotope ratios of carbon [$\delta^{13}C$; **(A)**], nitrogen [$\delta^{15}N$; **(B)**], and sulfur [$\delta^{34}S$; **(C)**] of the elephant and mammoth ivory samples (left and right, respectively). The midpoints indicate the mean and whiskers show the 95% confidence intervals. Significance levels indicated as "*" for p<0.01 and "**" for p<0.001.

overcome this issue, recent popular programs targeting community attitudes and social change are currently in place to change the attitude paramount and alleviate the conflict (e.g.,Williams et al., 2024). Along with these initiatives, forensics tools, including SIA, could contribute to law enforcement and reducing poaching.

The trade ban in China and Hong Kong lead to an increasing market demand for harvesting mammoth material. Russia is the main export country of mammoth ivory, with more than 140 tons legally exported in 2023, most of which were destined to China, but also to Hong Kong and Netherlands (Potravny et al., 2024). The volume of illegal, and semi-legal exported ivory is thought to be three times more than that of legal ivory (Toropov, 2021). Siberian miners collect mammoths' tusks and other carving material during summer when the permafrost, the ice layer below the topsoil, starts to melt. Due to current difficult economic conditions in the region, some ivory miners engage in illegal practices of soil erosion using powerful water pumps (Vasileva, 2022). Although this activity has considerable environmental impacts, carvers argue that the damage is not comparable to that of gas and oil mining activities (Toropov, 2021). Carvers also reported that mammoth ivory has a low market value because it often has a yellowish color and a negative perception associated with the product as it is from extinct animals (Toropov, 2021). Nevertheless, harvesting it has become one of the few sources of income available to these communities.

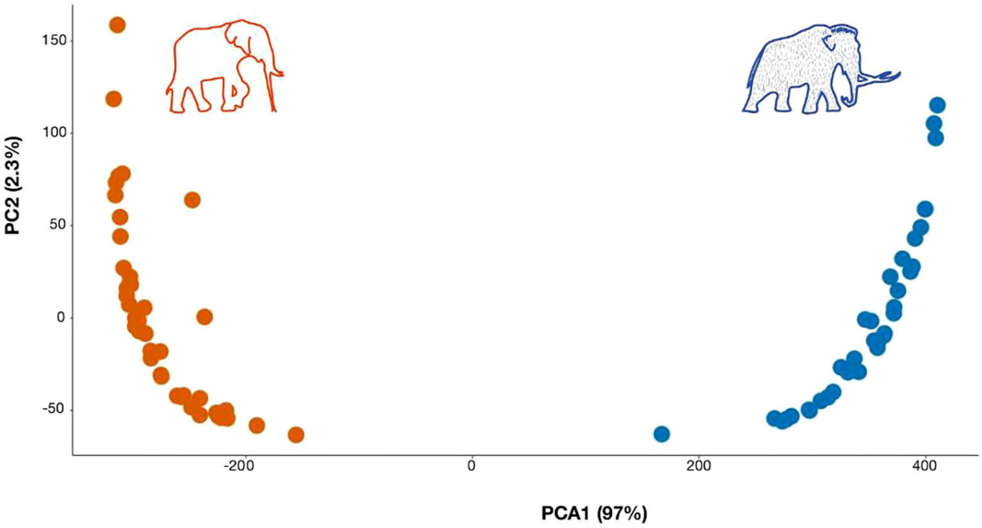

FIGURE 4
Principal Component Analyses (PCA) of isotope ratios of carbon ($\delta^{13}C$), hydrogen ($\delta^{2}H$), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$), and sulfur ($\delta^{34}S$) of the elephant and mammoth ivory samples (red and blue, respectively).

The trade of ivory flows across country borders, each of which have distinct social and economic environments. Conservation efforts for elephants are hampered by the current levels of governmental and localized corruption that makes it difficult to prevent the laundering of illegal ivory into legal markets (Bennett, 2015), including in the online trade (Venturini and Roberts, 2020). We suggest that the SIA approach described here is applied to distinguish between mammoth and elephant ivory, as the protocol is a relatively fast and economical tool (CF-IRMS measurements <USD25/sample). We highlight that although SIA will be facilitative in law enforcement, it is not suitable for presentation in court. In a potential framework to identify the ivory source, a batch of samples would be screened using SIA by an accredited laboratory. Fewer random objects, or any ivory samples with ambiguous results, could then be tested with more expensive and time consuming methods (e.g., genetics analyses and radiocarbon dating) to validate the results. In this way, governmental agencies would be able to analyze a higher volume of samples for a lower price and waiting time. We expect that a SIA database will be progressively constructed for this task, based on reports and publications. Besides individual government budgets, support to such a framework could be acquired from international multilateral foundations, United Nations programs, and non-governmental organizations, which have already financed ranger, customs and criminal justice functions to combat IUWT in several countries across Africa and Asia (UNODC, 2024).

While it is imperative to address the social issues related with the ivory trade, including reducing HEC (Jarungrattanapong and Olewiler, 2024; von Hagen et al., 2024; Williams et al., 2024) and offering financial support to Siberian carver communities (Potravny et al., 2024), alternatives for natural ivory should be a prioritized option in the markets, such as utilizing polished cattle bones (Sims et al., 2011) or developing materials for 3D printing with optical imitation of natural ivory (Rath et al., 2021). It is key to combine the investment in law enforcement with measures that address corruption and poverty (Hauenstein et al., 2019) and public engagement, such as education on the importance of elephants as key species to ecosystem health (van de Water et al., 2022; Williams et al., 2024), and on the Siberian permafrost to the ecosystem carbon balance (Bouchard et al., 2018).

Future steps of the SIA ivory research field

Further studies will clarify how the isotopic signatures of elephant and mammoth ivory are influenced by biological factors, for instance, the animal's age or the tusk portion analyzed (Codron et al., 2012) that could partly explain variations in some of the isotopes observed here. SIA applications in the field should also focus in estimating their isotopic niche (Jackson et al., 2011; Schwartz-Narbonne et al., 2019), a proxy of the trophic niche. Comparing the amount of isotopic niche overlap (Jackson et al., 2011) between different elephant populations, as well as mammoth populations, will contribute to revealing the resource partition and diet preferences of elephantids. Such analyses could also provide insights on the isotopic niche changes between wild and captive elephants. Compound specific isotopes analyses (CSIA), including amino acids and fatty acids, should also be used for a detailed comparison of their diets (McMahon and McCarthy, 2016). Although CSIA has a higher cost and is more time-consuming compared to SIA, such analyses could also be used to distinguish the two ivory types, when bulk isotope values are ambiguous. Lastly, it will be vital to facilitate networks between different countries' institutes to combat illegal ivory trade.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Ethics statement

Ethical approval was not required for the studies on animals in accordance with the local legislation and institutional requirements because only commercially available established cell lines were used.

Author contributions

MEAS: Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. PT: Funding acquisition, Writing – review & editing. PA: Investigation, Writing – review & editing. PAJF: Investigation, Writing – review & editing. HBT: Writing – review & editing. WWZ: Funding acquisition, Writing – review & editing. JC: Writing – review & editing. DMB: Funding acquisition, Supervision, Writing – review & editing.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This project was funded by the Environment and Conservation Fund project 118/2022.

Acknowledgments

The comments of three reviewers and the editor greatly improved this manuscript. We thank Kit Sum Leung (SIRMS-HKU) for advice and assistance with SIA. We are also grateful for the suggestions and support from Baker Lab members (HKU), Tracey-Leigh Prigge (HKU), Chloe Hatten (HKU), Oscar So Wing Wa (HKU), Noor Azleen Mohd Kulaimi (Department of Wildlife and National Parks, Malaysia), Jessica Bell Rizzolo (Kerulos

Center), and Renato Yudi. Chan Chi-Wai and his colleagues at the Agriculture, Fisheries and Conservation Department of Hong Kong, and the World Wide Fund for Nature - Hong Kong are thanked for their kind support with sample donations.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1533703/full#supplementary-material

SUPPLEMENTARY TABLE 1
List and description of the ivory samples.

References

Alexander, J., Downs, C. T., Butler, M., Woodborne, S., and Symes, C. T. (2019). Stable isotope analyses as a forensic tool to monitor illegally traded African grey parrots. *Anim. Conserv.* 22, 134–143. doi: 10.1111/acv.12445

Andersson, A. A., Gibson, L., Baker, D. M., Cybulski, J. D., Wang, S., Leung, B., et al. (2021). Stable isotope analysis as a tool to detect illegal trade in critically endangered cockatoos. *Anim. Conserv.* 24, 1021–1031. doi: 10.1111/acv.12705

Bennett, E. L. (2015). Legal ivory trade in a corrupt world and its impact on African elephant populations. *Conserv. Biol.* 29, 54–60. doi: 10.1111/cobi.12377

Bielert, C., Costo, N., and Gallup, A. (2018). Tuskedness in African elephants – an anatomical investigation of laterality. *J. Zool.* 304, 169–174. doi: 10.1111/jzo.12511

Bocherens, H., Pacaud, G., Lazarev, P. A., and Mariotti, A. (1996). "Stable isotope abundances (^{13}C, ^{15}N) in collagen and soft tissues from Pleistocene mammals from Yakutia: Implications for the palaeobiology of the Mammoth Steppe," in *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 126. .

Boecklen, W. J., Yarnes, C. T., Cook, B. A., and James, A. C. (2011). Use of stable isotopes in foraging ecology and food web analysis. *Annu. Rev. Ecol. Evol. Syst.* 42, 411–440. doi: 10.1146/annurev-ecolsys-102209-144726

Bouchard, F., Sansoulet, J., Fritz, M., Malenfant-Lepage, J., Nieuwendam, A., Paquette, M., et al. (2018). Frozen-Ground Cartoons: Permafrost comics as an innovative tool for polar outreach, education, and engagement. *Polar Record* 54, 366–372. doi: 10.1017/S0032247418000633

Cardoso, P., Amponsah-Mensah, K., Barreiros, J. P., Bouhuys, J., Cheung, H., Davies, A., et al. (2021). Scientists' warning to humanity on illegal or unsustainable wildlife trade. *Biol. Conserv.* 263. doi: 10.1016/j.biocon.2021.109341

Cerling, T. E., Andanje, S. A., Gakuya, F., Kariuki, J. M., Kariuki, L., Kingoo, J. W., et al. (2018). Stable isotope ecology of black rhinos (*Diceros bicornis*) in Kenya. *Oecologia* 187, 1095–1105. doi: 10.1007/s00442-018-4185-4

Chaiklin, M. (2010). Ivory in world history – Early modern trade in context. *History Compass* 8, 530–542. doi: 10.1111/j.1478-0542.2010.00680.x

Chang'a, A., Souza de, N., Muya, J., Keyyu, J., Mwakatobe, A., Malugu, L., et al. (2016). Scaling-up the use of chili fences for reducing human-elephant conflict across landscapes in Tanzania. *Trop. Conserv. Sci.* 9, 921–930. doi: 10.1177/194008291600900220

Chelliah, K., and Sukumar, R. (2013). The role of tusks, musth and body size in male–male competition among Asian elephants, *Elephas maximus*. *Anim. Behav.* 86, 1207–1214. doi: 10.1016/j.anbehav.2013.09.022

Chen, Y., Wang, Y., and Mumby, H. S. (2023). Five years of the ivory ban in China: Developments, limitations, and potential for improvement. *Biol. Conserv.* 284, 110177. doi: 10.1016/j.biocon.2023.110177

Codron, J., Codron, D., Sponheimer, M., Kirkman, K., Duffy, K. J., Raubenheimer, E. J., et al. (2012). Stable isotope series from elephant ivory reveal lifetime histories of a true dietary generalist. *Proc. R. Soc. B: Biol. Sci.* 279, 2433–2441. doi: 10.1098/rspb.2011.2472

Cox, C., and Hauser, L. (2023). Ice Ivory to White Gold: Links between the illegal ivory trade and the trade in geocultural artifacts. *J. Int. Wildl. Law Policy* 26, 22–46. doi: 10.1080/13880292.2023.2217615

Doody, J. S., Reid, J. A., Bilali, K., Diaz, J., and Mattheus, N. (2021). In the post-COVID-19 era, is the illegal wildlife trade the most serious form of trafficking? *Crime Sci.* 10, 1–12. doi: 10.1186/s40163-021-00154-9

Doyle, S., Groo, M., Sampson, C., Songer, M., Jones, M., and Leimgruber, P. (2010). Human-elephant conflict – What can we learn from the news. *Gajah* 32, 14–20.

Dublin, H. T., and Hoare, R. E. (2004). Searching for solutions: the evolution of an integrated approach to understanding and mitigating human–elephant conflict in Africa. *Hum. Dimens. Wildl.* 9, 271–278. doi: 10.1080/10871200490505701

Enukwa, E. H. (2017). Human-Elephant conflict mitigation methods: A review of effectiveness and sustainability. *J. Wildl. Biodivers.* 1, 69–78.

Ewart, K. M., Lightson, A. L., Sitam, F. T., Rovie-Ryan, J. J., Mather, N., and McEwing, R. (2020). Expediting the sampling, decalcification, and forensic DNA analysis of large elephant ivory seizures to aid investigations and prosecutions. *Forensic Sci. International: Genet.* 44. doi: 10.1016/j.fsigen.2019.102187

Gao, Y., and Clark, S. G. (2014). Elephant ivory trade in China: Trends and drivers. *Biol. Conserv.* 180, 23–30. doi: 10.1016/j.biocon.2014.09.020

Gobush, K. S., Edwards, C. T. T., Maisels, F., Wittemyer, G., Balfour, D., and Taylor, R. D. (2021). "*Loxodonta cyclotis* (errata version published in 2021)," in *The IUCN Red List of Threatened Species 2021: e.T181007989A204404464*. doi: 10.2305/IUCN.UK.2021-1.RLTS.T181007989A204404464.en

Gross, E. M., Pereira, J. G., Shaba, T., Bilério, S., Kumchedwa, B., and Lienenlüke, S. (2022). Exploring routes to coexistence: Developing and testing a Human–Elephant Conflict-management framework for African elephant-range countries. *Diversity* 14, 2–28. doi: 10.3390/d14070525

Hale, C., Ogden, R., Ciavaglia, S. A., Cook, G. T., Clarke, G., Ogle, S., et al. (2021). "Investigating the origins of ivory recovered in the United Kingdom," in *Forensic Science International: Animals and Environments*, vol. 1. . doi: 10.1016/j.fsiae.2021.100027

Hankinson, E., and Nijman, V. (2020). "Asian elephants: 15 years of research and conservation," in *Journal of Physics: Conference Series*, vol. 1460. (IOP Publishing), 012055.

Hauenstein, S., Kshatriya, M., Blanc, J., Dormann, C. F., and Beale, C. M. (2019). African elephant poaching rates correlate with local poverty, national corruption and global ivory price. *Nat. Commun.* 10, 1–9. doi: 10.1038/s41467-019-09993-2

Haynes, G. (1991). *Mammoths, mastodonts, and elephants: biology, behavior and the fossil record* (Cambridge University Press), 3–7.

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* 120, 314–326. doi: 10.1007/s004420050865

Hopkins, J. B., Frederick, C. A., Yorks, D., Pollock, E., and Chatfield, M. W. H. (2022). Forensic application of stable isotopes to distinguish between wild and captive turtles. *Biology* 11. doi: 10.3390/biology11121728

Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80, 595–602. doi: 10.1111/j.1365-2656.2011.01806.x

Jarungrattanapong, R., and Olewiler, N. (2024). Ecosystem management to reduce human–elephant conflict in Thailand. *Environ. Dev. Sustainabil.* doi: 10.1007/s10668-024-04485-w

Kanthaswamy, S. (2024). "Review: Wildlife forensic genetics—Biological evidence, DNA markers, analytical approaches, and challenges," in *Animal Genetics*, vol. 55. (John Wiley and Sons Inc), 177–192. doi: 10.1111/age.13390

Kiffner, C., Schaal, I., Cass, L., Peirce, K., Sussman, O., Grueser, A., et al. (2021). Perceptions and realities of elephant crop raiding and mitigation methods. *Conserv. Sci. Pract.* 3. doi: 10.1111/csp2.372

King, L. E., Douglas-Hamilton, I., and Vollrath, F. (2011). Beehive fences as effective deterrents for crop-raiding elephants: field trials in northern Kenya. *Afr. J. Ecol.* 49, 431–439. doi: 10.1111/j.1365-2028.2011.01275.x

Lane, P. J. (2015). "Introduction: archaeological ivories in a global perspective," in *World Archaeology*, vol. 47. (Routledge), 317–332. doi: 10.1080/00438243.2015.1046252

McCutchan, J. H., Lewis, W. M., Kendall, C., and McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102, 378–390. doi: 10.1034/j.1600-0706.2003.12098.x

McMahon, K. W., and McCarthy, M. D. (2016). "Embracing variability in amino acid δ^{15}N fractionation: Mechanisms, implications, and applications for trophic ecology," in *Ecosphere*, vol. 7. (Ecological Society of America). doi: 10.1002/ecs2.1511

Meier-Augenstein, W. (2019). "From stable isotope ecology to forensic isotope ecology — Isotopes' tales," in *Forensic Science International*, vol. 300. (Elsevier Ireland Ltd), 89–98. doi: 10.1016/j.forsciint.2019.04.023

Menon, V., and Tiwari, S. K. R. (2019). Population status of Asian elephants *Elephas maximus* and key threats. *International Zoo Yearbook* 53 (1), 17–30. doi: 10.1111/izy.12247

Mumby, H. S., and Plotnik, J. M. (2018). Taking the elephants' perspective: Remembering elephant behavior, cognition and ecology in human-elephant conflict mitigation. *Front. Ecol. Evol.* 6, 122. doi: 10.3389/fevo.2018.00122

Ngatia, J. N., Lan, T. M., Ma, Y., Dinh, T. D., Wang, Z., Dahmer, T. D., et al. (2019). Distinguishing extant elephants ivory from mammoth ivory using a short sequence of cytochrome b gene. *Sci. Rep.* 9. doi: 10.1038/s41598-019-55094-x

Parungao, D., Candeias, A., Lopes, J. A., and Miguel, C. (2024). On the use of *in-situ* spectroscopic techniques for the study of the provenance of historic ivories. *J. Cultural Heritage* 68, 205–215. doi: 10.1016/j.culher.2024.05.018

Peterson, B., and Fry, B. (1987). Stable Isotopes in ecosystems studies. *Annu. Rev.* 18, 293–320. doi: 10.1146/annurev.es.18.110187.001453

Potravny, I., Apulu, O. G., and Chindina, A. (2024). Will mining mammoth tusks in the Russian arctic help preserve African elephants? *Jpn. J. Res.* 5, 048.

Prigge, T. L., Andersson, A. A., Hatten, C. E. R., Leung, E. Y. M., Baker, D. M., Bonebrake, T. C., et al. (2024). Wildlife trade investigations benefit from multivariate stable isotope analyses. *Biological Reviews*. doi: 10.1111/brv.13175

Quarta, G., D'Elia, M., Braione, E., and Calcagnile, L. (2019). Radiocarbon dating of ivory: Potentialities and limitations in forensics. *Forensic Sci. Int.* 299, 114–118. doi: 10.1016/j.forsciint.2019.03.042

R Team. (2020). RStudio: Integrated development envi- ronment for R. *RStudio, PBC*.

Rath, T., Martl, O., Steyrer, B., Seidler, K., Addison, R., Holzhausen, E., et al. (2021). Developing an ivory-like material for stereolithography-based additive manufacturing. *Appl. Mater. Today* 23. doi: 10.1016/j.apmt.2021.101016

Raubenheimer, E. (2000). Development of the tush and tusk and tusklessness in African elephant *(Loxodonta africana*). *Koedoe* 43(2), 57–64. doi: 10.4102/koedoe.v43i2.199

Saha, S., and Soren, R. (2024). "Human-elephant conflict: Understanding multidimensional perspectives through a systematic review," in *Journal for Nature Conservation*, vol. 79. (Elsevier GmbH). doi: 10.1016/j.jnc.2024.126586

Sampson, C., McEvoy, J., Oo, Z. M., Chit, A. M., Chan, A. N., Tonkyn, D., et al. (2018). New elephant crisis in Asia—Early warning signs from Myanmar. *PloS One* 13, e0194113. doi: 10.1371/journal.pone.0194113

Schwartz-Narbonne, R., Longstaffe, F. J., Kardynal, K. J., Druckenmiller, P., Hobson, K. A., Jass, C. N., et al. (2019). "Reframing the mammoth steppe: Insights from analysis of isotopic niches," in *Quaternary Science Reviews*, vol. 215. (Elsevier Ltd), 1–21. doi: 10.1016/j.quascirev.2019.04.025

Shepherd, R. F., Lister, A. M., Roberts, A. M., Taylor, A. M., and Kerns, J. G. (2024). Discrimination of ivory from extant and extinct elephant species using Raman spectroscopy: A potential non-destructive technique for combating illegal wildlife trade. *PloS One* 19. doi: 10.1371/journal.pone.0299689

Sims, M. E., Baker, B. W., and Hoesch, R. M. (2011). Tusk or bone? An example of ivory substitute in the wildlife trade. *Letters* 2, 40–44. doi: 10.14237/ebl.2.2011.27

Sosnowski, M. C., Knowles, T. G., Takahashi, T., and Rooney, N. J. (2019). Global ivory market prices since the 1989 CITES ban. *Biol. Conserv.* 237, 392–399. doi: 10.1016/j.biocon.2019.07.020

Steenkamp, G., Ferreira, S. M., and Bester, M. N. (2007). Tusklessness and tusk fractures in free-ranging African savanna elephants (*Loxodonta africana*). *J. South Afr. Vet. Assoc.* 78, 75–80. doi: 10.4102/jsava.v78i2.294

Steguweit, L. (2015). Rotten ivory as raw material source in european upper palaeolithic. *Quaternary Int.* 361, 313–318. doi: 10.1016/j.quaint.2014.11.019

Sukumar, R. (2006). A brief review of the status, distribution and biology of wild Asian elephants *Elephas maximus*. *International Zoo Yearbook*. 40, 1–8. doi: 10.1111/j.1748-1090.2006.00001.x

Sung, Y. H., Liew, J. H., Chan, H. K., Lee, W. H., Wong, B. H.-F., Dingle, C., et al. (2021). Assessing the diet of the endangered Beale's eyed turtle (*Sacalia bealei*) using faecal content and stable isotope analyses: implications for conservation. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 31 (10), 2804–2813.

Tchamba, M. N., and Seme, P. M. (1993). Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *Afr. J. Ecol.* 31, 165–171. doi: 10.1111/j.1365-2028.1993.tb00529.x

Toropov, P. (2021). *China Mammoth ivory: curbs on the Siberian trade may be good news for elephants. China Dialogue*. Available online at: https://Chinadialogue.net/en/nature/mammoth-ivory-curbs-on-the-siberian-trade-may-be-good-news-for-elephants/ (Accessed February 13, 2024).

Trapani, J., and Fisher, D. C. (2003). Discriminating proboscidean taxa using features of the Schreger pattern in tusk dentin. *J. Archaeological Sci.* 30, 429–438. doi: 10.1006/jasc.2002.0852

United Nations Environment Programme (UNEP), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), International Union for Conservation of Nature (IUCN) and Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC) (2013). *Elephants in the Dust – The African Elephant Crisis. A Rapid Response Assessment*. Available online at: www.grida.no (Accessed July 19, 2024).

United Nations Office on Drugs and Crime (UNODC) (2024). "What works to decrease wildlife crime?," in *World Wildlife Crime Report -Trafficking in Protected Species* (United Nations), 135–153. doi: 10.18356/9789211064582

van der Merwe, N., Lee-Thorp, J., Thackeray, J., Hall-Martin, A., Kruger, F., Coetzee, H., et al. (1990). Source-area determination of elephant ivory by isotopic analysis. *Nature* 346, 744–746. doi: 10.1038/346744a0

van de Water, A., Henley, M., Bates, L., and Slotow, R. (2022). "The value of elephants: A pluralist approach," in *Ecosystem Services*, vol. 58. (Elsevier B.V). doi: 10.1016/j.ecoser.2022.101488

Vasileva, O. V. (2022). Is the extraction of fossil mammoth bone a form of traditional Nature management? *Arktika i Sever [Arctic North]* 46, 169–180. doi: 10.37482/issn2221-2698.2022.46.205

Venturini, S., and Roberts, D. L. (2020). Disguising elephant ivory as other materials in the online trade. *Trop. Conserv. Sci.* 13, 1–8. doi: 10.1177/1940082920974604

von Hagen, L., Schulte, B. A., Steury, T. D., Dunning, K., Githiru, M., Zohdy, S., et al. (2024). Lack of crucial information exacerbates barriers to mitigating human–elephant conflicts in rural Kenya. *Oryx*, 1–9. doi: 10.1017/s0030605323001795

Walpole, M., and Linkie, M. (2007). *Mitigating Human-Elephant Conflict: Case studies from Africa and Asia* (Fauna & Flora International).

Williams, H. F., Leneuiyia, K. L., Mwalavu, B., Serem, G., Sempeyo, V., Pope, F., et al. (2024). The Elephant Queen: Can a nature documentary help to increase tolerance towards elephants? *People Nat.* 6, 762–774. doi: 10.1002/pan3.10599

Woodcock, L., Gooch, J., Wolff, K., Daniel, B., and Frascione, N. (2023). "Fingermarks in wildlife forensics: A review," in *Forensic Science International*, vol. 350. (Elsevier Ireland Ltd). doi: 10.1016/j.forsciint.2023.111781

Yu, Y., Wetzler, A., Yang, X., Tang, R., and Zhang, L. (2017). Significant and timely ivory trade restrictions in both China and the United States are critical to save elephants. *Conserv. Lett.* 10, 596–601. doi: 10.1111/conl.12279

Ziegler, S. (2021). Distinguish mammoth and elephant ivory with stable water isotopes. *Academia Lett.* doi: 10.20935/al4314

Ziegler, S., Streit, B., and Jacob, D. E. (2016). "Assigning elephant ivory with stable isotopes," in *Isotopic Landscapes in Bioarchaeology* (Springer, Berlin Heidelberg), 213–220. doi: 10.1007/978-3-662-48339-8_12