Science of the Total Environment 1012 (2026) 181193

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Soil ingestion: An important contamination pathway for toxic element exposure in wild herbivores

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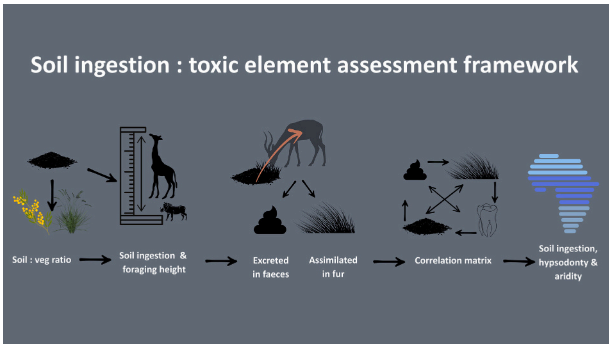
HIGHLIGHTS

- Human activities have increased toxic metal bioavailability in soils across the globe.
- Wild herbivores that feed close to the ground ingest more soil during foraging.
- Soil ingestion in low-grazing and fossorial wildlife accounts for >20–60 % of toxic element intake.
- Hypsodonty can be used to identify species vulnerable to toxic-element intake from soil ingestion.
- We provide a non-invasive framework for conservation practitioners to identify vulnerable species.

GRAPHICAL ABSTRACT

Soil ingestion: overview of the framework used to assess toxic element intake



ARTICLE INFO

Keywords:
Foraging height
Diet
Hypsodonty
Wildlife communities
Wildlife biomonitoring
Environmental risk assessment
Rehabilitation
Restoration
Rewilding

ABSTRACT

Human activities have increased pollution and toxic element concentrations in soils across the Earth's surface. These activities could have profound implications for wildlife that directly or incidentally ingest soil during foraging, and for humans that consume animals as a primary source of protein. To date, levels of soil ingestion in large herbivores and species-specific vulnerability to toxic element exposure via this pathway have not yet been assessed. Here, we tested the hypothesis that animals feeding closer to the ground ingest more soil than their browsing counterparts. Across a community of 16 African herbivore species, we found that soil ingestion was highest in grazing (blue wildebeest, white rhino and buffalo) and fossorial (warthog and porcupine) animals. This translated to 20–60 % higher total element intake for chromium, cobalt, tin, lead, vanadium and arsenic in these groups. Faecal and fur concentrations were similarly elevated in these species, highlighting that the toxic elements ingested from soil are assimilated into body tissues with potential repercussions for animal and human health. In ungulates, soil ingestion rates align with species-level hypsodonty (height of the tooth crown). We propose that hypsodonty can be used as a proxy for identifying species-specific vulnerability to toxic-element

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https://doi.org/10.1016/j.scitotenv.2025.181193
Received 30 July 2025; Received in revised form 9 December 2025; Accepted 9 December 2025

exposure at broad scales. The non-invasive framework developed here, may be applied to monitoring wild herbivore exposure to toxic elements and may be particularly relevant for ongoing conservation and rewilding efforts in areas with high levels of anthropogenic pollution.

1. Introduction

Environmental pollution and unmanaged waste are inextricably linked to biodiversity loss and climate change. The reliance on heavily extractive and fossil fuel industries in the absence of adequate regulation, particularly in developing countries, have led to toxic element pollution reaching unprecedented levels (Ding et al., 2022). For example, waste products and transport activities from coal mining operations increase chromium, nickel, copper, zinc, cadmium and lead availability in surface soils that far exceed natural background concentrations (Hou et al., 2025). While some elements are essential for the maintenance of physiological processes in plants and animals, the alteration of natural mineral concentrations influences soil health, biodiversity and food security, causing morbidity and economic loss as well as impacting reproductive success in wildlife communities (Martinez-Morata et al., 2023; Hou et al., 2025).

Although all elements occur naturally in the environment, differences in underlying geology, element abundance in the Earth's crust, rates of weathering, leaching and anthropogenic activities influence geochemical profiles at local, regional and global scales (Alloway, 2013). Soils provide a range of essential ecosystem services, but are also a major sink for accumulated contaminants, which can pose risks to environmental, animal and human health (Alloway, 2013; Ding et al., 2022). Complex interactions between soils (e.g. element speciation, pH, exchange capacity) and root morphology, mycorrhizal exchange and transpiration rates influence the bioavailability of toxic elements for uptake by plants (Schück and Greger, 2019; Ding et al., 2022), which are then ingested by plant-eating animals, including humans. Over time, these toxins can accumulate and are biomagnified in the body tissues of higher trophic levels through various food web interactions (World Health Organisation/United Nations Environment Programme (WHO/UNEP), 2012). Wild animals interact with their environments in different ways, consequently individual vulnerability and community level exposure to contaminants are also highly variable (van der Merwe et al., 2018; Spurgeon et al., 2020). Even at low levels exposure to toxic elements, particularly in utero or during other critical windows of development, can impair the development and biological function in living organisms (World Health Organisation/United Nations Environment Programme (WHO/UNEP), 2012).

While previous research has focussed on the ingestion of toxic elements via water and forage (van der Merwe et al., 2018; Nasi and Fa, 2015), few studies have quantified toxic element exposure in wildlife through direct soil ingestion - geophagy - or incidental soil ingestion during foraging. Geophagy in domestic and wild animals is widespread and thought to serve multiple purposes including the acquisition of micronutrients to allay nutrient deficiency (Abrahams, 2012). Although certain clays have the capacity to neutralize mycotoxins and secondary organic plant compounds in the gut, when contaminated soils are ingested, animals are exposed to the inherent risks of toxicity (Abrahams, 2012; van der Merwe et al., 2018; Ding et al., 2022). For many animals, incidental soil ingestion during foraging and grooming may form a considerable proportion of overall soil, dust or grit intake but is typically overlooked in nutritional studies (Thornton and Abrahams, 1983; Beyer et al., 1994; Hummel et al., 2011). Animals that ingest large amounts of soil have evolved a number of morphological and physiological adaptations. For example, the associated grinding action of exogenous grit has immediate effects on tooth wear and levels of soil ingestion have been suggested to correlate with hypsodonty (a measure of relative tooth height: width/length). Grazing species such as blue wildebeest (*Connochaetes taurinus*) have more hypsodont teeth than browsing animals (Janis, 2008), while animals such as porcupines (*Hystrix africaeaustralis)*, that live a more fossorial lifestyle, have hypselodont (rootless continuously growing) teeth (Van Aarde, 1985). These differences may be explained by higher abrasive silica content in grasses and the consumption of soil covered food items obtained when foraging close to the ground (Damuth and Janis, 2011; Hummel et al., 2011; Kaiser et al., 2013).

Once soil is ingested, cell membranes in the gut and designated high-affinity ligands and organic acids bind toxic elements to mitigate long-term effects and prevent interference with cellular processes (Valerio et al., 2022; Hall, 2002). However, some ingested toxins from soil may still be assimilated into body tissues. When this is the case, the liver, kidneys, bile and gut play an important role in their excretion via urine, milk, nails, faeces and fur. Additionally, specific tissues (e.g. nails, hair, adipose tissue and bone) act as less harmful storage locations in the body (Hall, 2002). Ingested toxins can therefore be quantified in these matrices (Martinez-Morata et al., 2023). Faecal concentrations align with gut passage time, reflect resource utilisation and are closely linked to intake, making faeces a useful indicator of toxic element exposure over the short-term (24–48 h). Although fur morphology can influence metal absorption (Squadrone et al., 2022), it has a high binding affinity for toxic metals and can be used as a bioindicator of toxic element exposure and bioavailability, providing a more integrated profile of total exposure over the medium to long term (van der Merwe et al., 2018; Squadrone et al., 2022; Sach et al., 2022).

The assessment of toxic element exposure pathways and species-specific vulnerability are essential for identifying contaminants that cause disruption of functional ecosystem roles and morbidity in wildlife as well as humans that rely on game meat as a source of primary protein (Nasi and Fa, 2015). Here, we define toxic elements as transition metals (e.g. chromium, cobalt, mercury, lead and vanadium), metalloids (e.g. arsenic, boron) and post transition metals (e.g. tin and lead) that can have harmful effects on individual health when present at high concentrations in the body (World Health Organisation/United Nations Environment Programme (WHO/UNEP), 2012). We hypothesize that soil ingestion is likely to be a key pathway for toxic element intake in free-ranging wildlife, particularly for grazing and fossorial species. We quantified a suite of 20 elements in paired soil and vegetation samples across our semi-arid study site and calculated the soil to vegetation ratio for each element to identify which elements are disproportionately concentrated in soil compared to vegetation. Using faecal Al concentrations as a marker for soil ingestion, we assessed soil ingestion levels across a community of African herbivores. We then assessed the proportion of toxic element intake across species and elements and validated whether toxic elements ingested (detected in faeces) are also being assimilated (detected in fur). We hypothesize that hypsodonty can be used as a broad proxy for soil ingestion. To investigate this, we constructed a correlation matrix that directly compares toxic element concentrations in biomarkers (faeces and fur) against soil ingestion and hypsodonty index. Finally, we integrated toxic element data with hypsodonty across species assessed at our study site and expand these results across feeding groups for a continental overview. We then overlay the location of mined sites in sub-Saharan Africa to identify geographic patterns of high impact in which large herbivore communities may be most vulnerable to toxic element intake.

2. Materials and methods

2.1. Study site

The study was conducted at Tswalu Kalahari Reserve (Tswalu), an ~110,000 ha fenced reserve (S27°13′30″ and E22°28′30″) situated in the semi-arid savannah of the Northern Cape Province, South Africa (Fig. 1). The reserve falls within the Kalahari Deciduous Acacia Bushland and Woodland Grassland of the Kalahari-Highveld Transition Zone and Southern Kalahari Salt Pan vegetation type. The property receives highly variable rainfall (mean annual rainfall of ~325 mm) between October and May. Historical mean temperatures range from 24 to 35+ °C in the wet summer months and from <7 to 21 °C in dry winter months (Mucina and Rutherford, 2006). In 1995, land previously utilized for domestic livestock farming was converted into a single wildlife reserve for restoration of Kalahari habitat. The reserve currently supports historically endemic and marginal mammalian herbivores and carnivores, as well as a variety of birds, reptiles and insects. Surrounding anthropogenic activity includes the generation of thermal and solar power and intensive historical and current farming of cattle and sheep. Additionally, Tswalu is situated in the most intensively mined manganese area on the continent (Webster et al., 2020).

2.2. Quantification of elements in vegetation and soils

To understand which elements are disproportionately concentrated in soils relative to plants, we collected paired sediment and vegetation samples from around waterpoints at 25 geographically independent sites across the reserve between April and July 2019 (Fig. 1). Sediment was collected approximately 30 cm from the waterline at a depth of 3–5 cm. Leaves from commonly grazed C_4 grass genera (*Digitaria* spp. and *Eragrostis* spp.) and browsed C_3 woody species (*Grevia flava*; de Candolle), *Boscia albitrunca* (Burch.) Gilg & Gilg-Ben, *Vachellia erioloba* (E. Mey) and *Ziziphus mucronata* (Willd.) were collected within 20 m of sediment samples and frozen at −20 °C. Individual soil and plant samples were lyophilized at −50 °C for 4–7 days and milled for 5 min at 90 rpm using a Retsch® agate ball mill to homogenize. Individual dry mass sediment (~0.1 g) and vegetation (~0.3 g) samples were acid-digested in 6 ml (65 %) HNO_3: 2 ml (30 %) HCl and 6.5 ml (65 %) HNO_3: 0.5 ml (30 %) HCl respectively. Post-digestion, de-ionised water was added to make 30 ml final volume of each sample (USEPA, 2007) and elements (aluminium, antimony, arsenic, barium, boron, cadmium, chromium,

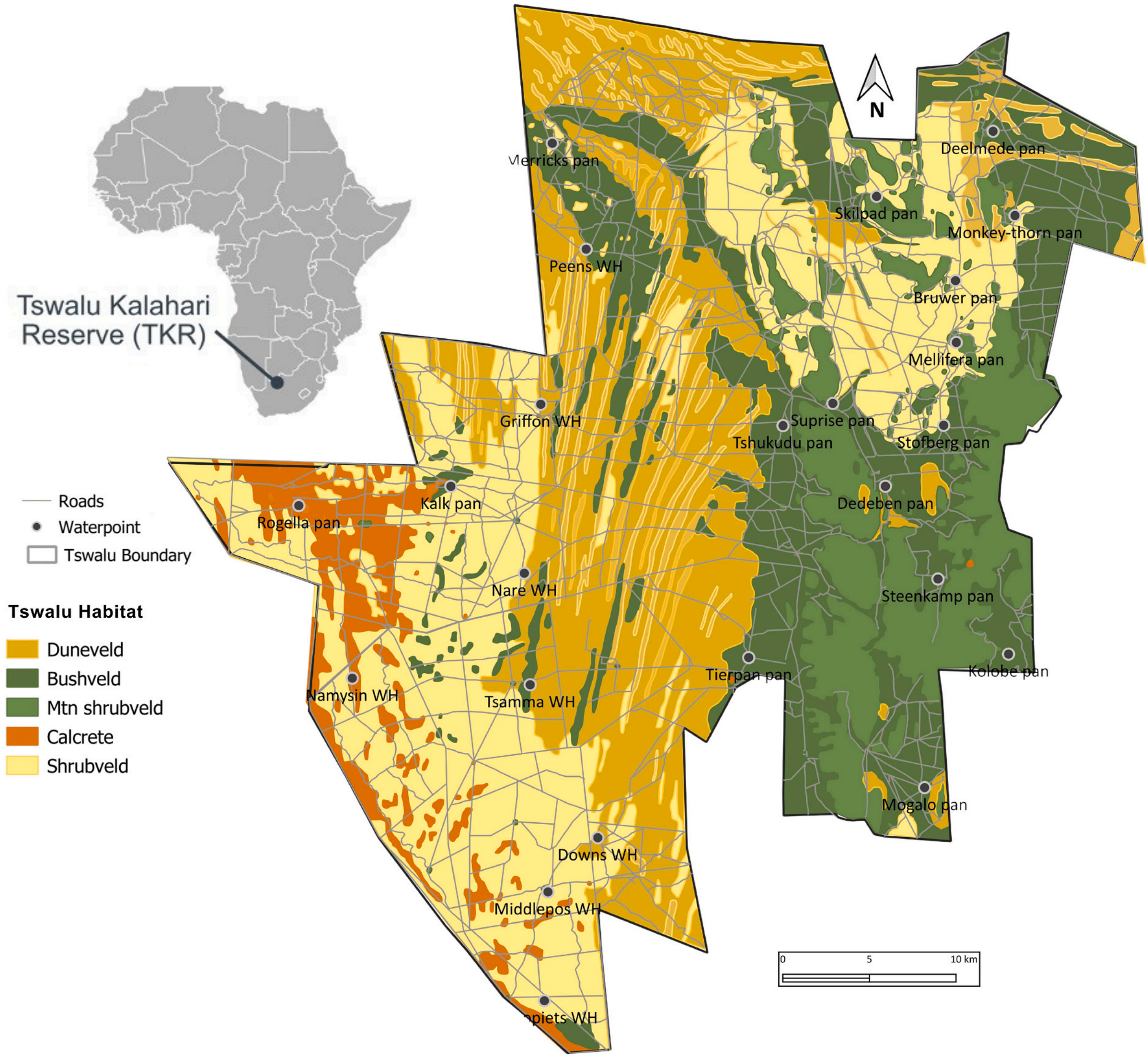

Fig. 1. Continental orientation map of Tswalu Kalahari Reserve, Northern Cape Province, South Africa. The property boundary, internal road network, waterpoints (location of 25 paired soil and vegetation sampled sites) and broad vegetation communities are highlighted. Biological samples (n = 691) from 16 herbivore species were collected across the entire property; scale bar indicates 5 km.

cobalt, copper, mercury, iron, lead, manganese, molybdenum, nickel, selenium, strontium, tin, vanadium and zinc) were quantified in both matrices using ICP-MS and reported in μg/kg dry weight (Webster et al., 2020, 2021). The range, median and standard deviation (σ) for toxic elements in soil and vegetation are provided in Table S1. Detailed parameters for method validation, element quantification and range adjustments are outlined in Webster et al. (2020). The specific instrument and methodological limits of quantification (LOQ) for all elements and matrices can be found in Table S2.

Using Eq. 1, we calculated the soil-to-vegetation ratio for all measured elements and ranked elements from highest to lowest.

$$\text{Soil : vegatation ratio} = \frac{\text{soil concentration}}{\text{vegetation concentration}} \tag{1}$$

We then used the median soil:vegetation ratio to identify elements through which incidental soil ingestion may represent an important pathway of toxic element exposure. We considered only elements that were >10 times higher in soils compared to vegetation as potentially important for the soil ingestion pathway.

2.3. Soil ingestion and feeding height across herbivore species

To quantify soil ingestion levels across different herbivore species we used faecal aluminium (Al) concentrations as a proxy. As a ubiquitous element in the Earth's crust, aluminium (Al) occurs mainly as non-toxic Al-silicates and oxides and is not considered essential for physiological plant processes and occurs at very low concentrations in plant tissues (Buchanan et al., 2015). In contrast, Al concentrations are often several orders of magnitude higher in soil (Schmitt et al., 2016). As Al assimilation through the digestive tract of animals is negligible, high faecal Al concentrations are considered to originate primarily from soil ingestion, which has been widely used to quantify rates of soil ingestion in domestic livestock (Abrahams, 2012) and humans (Clausing et al., 1987). Following Thorton and Abrahams (1983), we calculated species-specific soil ingestion rates using Eq. 2:

$$\text{Soil ingestion (\%)} = \frac{(1-D)^{*}Al_f}{Al_s - (D^{*}Al_f)}{}^{*}100 \tag{2}$$

where D is forage dry matter digestibility, Al_f is aluminium concentration in faeces and Al_s is aluminium concentration in soil. Dry matter digestibility was set at 0.65 for all species (Clauss et al., 2013).

Fresh faecal samples (n = 638) from 17 herbivore species were collected over multiple seasons from April 2019 to September 2024 (Table S3). To avoid contamination from substrate, subsamples were collected from the centre of all faecal deposits and immediately frozen at −20 °C to minimize microbial degradation post-defaecation (Webster et al., 2020). Faecal samples were lyophilized at −50 °C for 4–5 days, pulverised and (~0.3 g) dry mass was microwave digested in 6.5 ml (65 %) HNO_3:0.5 ml (30 %) HCl (Webster et al., 2022). Elements listed above were quantified using ICP-MS and reported in μg/kg dry weight. As soil Al concentrations are geographically varied and our study site is large (~1200 km^2), we estimated soil Al concentrations for each faecal sample individually. For this, we used a Bruker Tracer 5i X-ray Fluorescence (pXRF) and measured surface soil (1–3 cm deep) Al concentrations at 233 geographically distinct locations across our study site in Oct–Nov 2022 (Abraham et al., 2023). We then interpolated these point-based soil Al measurements using the "density.app" function in the "spatstat" package in R (Baddeley and Turner, 2005). This revealed a distinctive east to west spatial gradient across the reserve with values ranging between 2000 and 43,000 mg/kg (Fig. S1). The large herbivores considered in our study have a gut passage time of ~30–56 h, meaning soil may have been ingested away from where faecal samples were deposited (Abraham et al., 2021). For each faecal sample, we therefore estimated a circular buffer (Fig. S2), the specific size of which was estimated using the 95th percentile kernel distance from a published dung dispersal model (Pires et al., 2018) that integrates species-specific parameters of daily movement distances and gut passage time (Abraham et al., 2021). Mean soil Al concentrations from within each buffer sample was then used to estimate soil ingestion (%) for each individual faecal sample.

Steenbok (*Raphicerus campestris*) were excluded from soil ingestion analysis given the practice of burying their faeces, which contaminated samples. Plains (*Equus quagga*) and mountain (*Equus zebra*) zebra faecal data was combined as it was not always possible to distinguish between species. To ensure that extreme outliers did not interfere with our analysis, we performed outlier analysis on faecal Al concentrations for each species individually and used a z-score (>3) to remove 12 additional samples. This left a final sample size of 594 faecal samples from 16 species. To identify species-specific soil ingestion values, we calculated the median and interquartile soil ingestion range for each species. Based on visual inspection, and broad categorisation according to diet, we ranked species according to their median soil ingestion level (Low: <2 %, Medium: 2–4 %, High: 4–6 % and Very High: >6 %).

We broadly categorised each herbivore species according to feeding height (high-browser, low-browser, mixed feeder, high-grazer, low-grazer and fossorial) using behavioural characteristics (Table S3) and the literature (Arsenault and Owen-Smith, 2008). To test our hypothesis that feeding height influences levels of soil ingestion we fit a linear model. To avoid pseudo-replication between species with different samples sizes, we fitted the model using the median soil ingestion quantified for each species. Model diagnostics including normality, autocorrelation, heteroscedasticity and residuals were assessed using the 'performance' package in R and in all cases our model was robust (Table S4).

2.4. Toxic element ingestion across herbivore species

To compare how much soil ingestion contributes to total toxic element intake across herbivore species and elements, we calculated total elemental intake from dietary foraging and incidental soil ingestion. Forage intake was estimated using species-specific dry matter intake (g/day; Abraham et al., 2023) and the median elemental concentrations in vegetation calculated in Section 2.2. Soil ingestion intake was estimated using species-specific median soil ingestion in g/day (Section 2.3) and soil elemental concentrations determined in Section 2.2. We calculated the proportion (%) that soil ingestion contributes for each element across species using Eq. 3:

$$\text{Soil proportion (\%)} = \frac{\text{Soil intake}}{\text{Forage intake} + \text{Soil intake}}{}^{*}100 \tag{3}$$

2.5. Toxic element excretion across herbivore species

We used a subset of faecal samples (n = 108) collated to estimate soil ingestion as these samples had accurate measurements for aluminium, vanadium, lead, chromium, tin, cobalt and arsenic; the toxic elements identified in Section 2.2. We undertook principal component analysis (PCA) on these elemental concentrations using the 'FactoMineR' package (Lê et al., 2008), although Al was removed as this was used to calculated soil ingestion. Six outliers were identified using Mahalanobis Distance of PCA scores with an outlier cutoff at 99 % quantile of Chi-squared. On the remaining 102 samples, we checked correlation between PCA variables (R^2 between 0.3 and 0.9) and robustness of sample size using Kaiser-Meye-Olkin test (measure of sampling adequacy = 0.86; values >0.7 are considered adequate) (Fig. S3). A final PCA plot was constructed with faecal samples assigned to low, medium, high and very high soil ingestion groups identified in Section 2.3. Patterns of increased elemental concentrations in faeces for high soil ingestion groups would indicate a positive relationship between soil ingestion and exposure across a suite of toxins.

2.6. Toxic element assimilation across herbivore species

To assess whether toxic elements from soil ingestion are assimilated into herbivore body tissues, we measured elemental concentrations in herbivore fur samples. Fur was collected opportunistically from herbivore carcass remains at predator kill sites ($n = 53$). Due to the difficulty of locating smaller prey items and associated risks of working with large carnivores, fur samples were harder to collect for smaller antelope (consumed quickly) and porcupine (nocturnal). Given the potential influence of fur morphology on trace element analysis (Squadrone et al., 2022), fur was consistently collected from the rump area, washed in ultra-pure water for 15 min, double-washed in 10 ml methanol in an ultra-sonic water bath for 25mins and dried overnight at 70 °C in a drying oven. Individual fur samples (~0.3 gDM) were microwave digested in 4 ml (65 %) HNO_3:2 ml (30 %) H_2O_2. Post-digestion, 0.5 % HCl was added to make 30 ml final volume of each sample and all elements were quantified using ICP-MS (USEPA, 1994) and reported in μg/kg dry weight. We followed the approach described above to construct a PCA for fur, including Al as there were no issues of circularity. We identified six outliers which resulted in a final dataset of $n = 47$. Again, we checked correlation between PCA variables (R^2 between 0.35 and 0.75) and sample size using Kaiser-Meye-Olkin test (measure of sampling adequacy = 0.75) (Fig. S4). Additionally, we assessed the relationship between element concentrations in faeces and fur for high intake elements (Fig. S5). Patterns of increased elemental concentrations in fur for high soil ingestion groups would indicate a positive relationship between soil ingestion and assimilation across a suite of toxins.

2.7. Hypsodonty as a proxy for toxic element ingestion

It has been suggested that soil ingestion levels are linked to height of the tooth crown in ungulates (Eronen et al., 2010; Hummel et al., 2011; Kaiser et al., 2013). Accordingly, the presence of hypsodont (high crowned) teeth may be a useful proxy for identifying species-vulnerability to toxic element intake via soil ingestion. To examine if there is a relationship between hypsodonty and soil ingestion at our study site, we sourced hypsodonty index scores for each species from Janis (1988) published database. The index estimates tooth volume based on the ratio of tooth crown height to its length/width; a higher index indicates pronounced hypsodonty (common in grazing animals that consume abrasive forage) while a lower index is associated with other less abrasive dietary intake (e.g. browsing). We ran a linear regression model between hypsodonty and median soil ingestion values estimated in Section 2.2. Model diagnostics (normality, autocorrelation, heteroscedasticity and residuals) were evaluated as above and found to be robust in all cases (Table S4). To directly link soil ingestion and hypsodonty to toxic element ingestion and assimilation, we created a correlation matrix between median soil ingestion for each herbivore species and median faecal and fur concentrations for each element separately. As the data was not normally distributed for some elements, we implemented a Spearman correlation. Strong positive relationships indicate that soil ingestion, or hypsodonty as a proxy, drives toxic element exposure.

2.8. Identifying at-risk species and ecosystems vulnerable to toxic element exposure through soil ingestion for future application

Previous research has linked hypsodonty levels with precipitation (Damuth and Janis, 2011; Eronen et al., 2010) suggesting that hypsodonty is more pronounced in arid-adapted ungulates (Kaiser et al., 2013). Based on the results of Section 2.3, we assessed how this relationship differs between species feeding at different heights, potentially due to differences in soil ingestion between groups. Hypsodonty scores (index estimates based on the ratio of tooth crown height: width/length; Janis, 1988) were estimated for ungulates across Africa. All species were then categorised as either browsers, mixed feeders, grazers/fossorial (Hempson et al., 2015) and the mean aridity was calculated for each species using the Global aridity index (Zomer and Trabucco, 2019) and their historical ranges (present-natural) obtained from Phylacine (https://megapast2future.github.io/PHYLACINE_1.2/). To determine where species with higher hypsodonty occur, we assessed the relationship between aridity and hypsodonty at the continental scale. We ran linear regression models for each group (browsers, mixed feeders, grazers/fossorial) individually. Again, all models were checked to be sufficiently robust (checked model fit Table S3). As it is known that mining activities elevate toxins in surface soils (Hou et al., 2025) we also mapped mine locations across sub-Saharan Africa. Together, these datasets can help identify at-risk species and ecosystems based on animal feeding behaviour, precipitation gradients and anthropogenic toxic element disturbance.

3. Results

3.1. Soil to vegetation ratios

Soil to vegetation ratios were calculated for 16 of the 20 elements assessed (Fig. 2). Elements with a median ratio > 10 times that of vegetation were considered to be significantly elevated in soils. Median soil to vegetation ratios were below 0.1 for boron and strontium, below 1 for cadmium, selenium, zinc, molybdenum and barium and above 1 for copper and nickel. By contrast, median ratios for vanadium, aluminium, lead, chromium, tin, cobalt and arsenic were >10–100 times higher in soils than vegetation and are therefore considered as potentially important elements associated with incidental soil ingestion in herbivores.

3.2. Soil ingestion and feeding height across herbivore species

Across 594 faecal samples measured for soil ingestion, median soil ingestion levels were lowest (<2 %) for strictly browsing giraffe, kudu (*Tragelaphus strepsiceros*) and black rhino (*Diceros bicornis*) and showed little variation (1–3 %) within and between species (Fig. 3a). Mixed feeding species that predominantly graze in the wet season and switch to browse in the dry season had medium (2–4 %) soil ingestion levels but much greater variability within and between species. For example, impala (*Aepyceros melampus*) and springbok (*Antidorcas marsupialis*), displayed high variation in soil ingestion (0.5–9.8 % and 1–18 %) respectively. Short grass grazing gemsbok; *Oryx gazella;* (median = 2.3 %: range = 0.4 %–9.7 %), blue wildebeest (median = 3.4 %; range = 0.4–30.8 %) or white rhino (median = 3.8 %; range = 0.2–18.5 %), buffalo (median = 4.5 %; range = 1.0–10.6 %) and warthog (median = 4.8 %; range = 1.8–11.6 %) had high median soil ingestion levels (4–6 %) and also showed substantial variation within species' range. The highest soil ingestion levels (>6 %) were evident in burrowing, strictly fossorial porcupine (median = 6.7 %; range = 3.9 %–28.3 %). Using a linear model, we found that median soil ingestion had a significantly negative relationship ($R^2 = 0.42$, $p = 0.004$) with foraging height across herbivore species (Fig. 3b).

3.3. Toxic element intake

Soil ingestion contributes variably (<1–60 %) to total element intake across species (Fig. 4a), highlighting that soil ingestion can be an important pathway for toxic element intake for some elements and some species. For high-browsing species (giraffe, kudu, eland; *Taurotragus oryx*), soil ingestion is <20 % of total intake, even for elements disproportionately concentrated in soils such as vanadium, aluminium, and lead. Similarly, for elements that do not concentrate disproportionately in soils (e.g., boron, strontium, cadmium, selenium, zinc, molybdenum and barium), soil ingestion is a relatively minor (<10 %) contamination pathway for all foraging height groups. However, for low browsing to

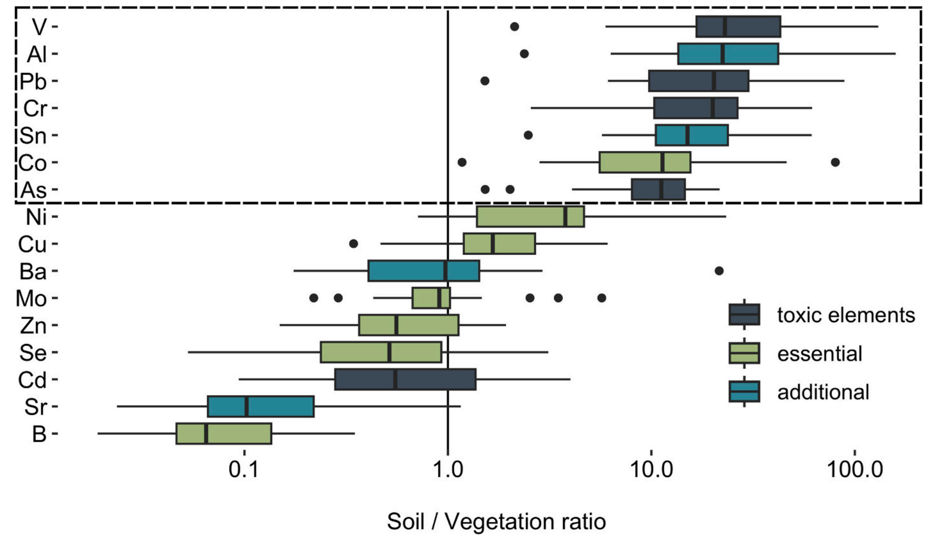

Fig. 2. Soil-to-vegetation ratios identify key elements (dotted black box) of relevance for soil ingestion. Paired soil and vegetation samples collected from 25 independent sites across Tswalu Kalahari Reserve, Northern Cape Province, South Africa illustrate toxic (grey), essential (lime) and additional (dark green) elements highly concentrated in soil compared to vegetation. The ratio for each element is visualized as horizontal box plots. Solid black line within each box represents median values, edges of the box represent lower (1st) and upper (3rd) quartiles and whiskers extending left and right depict minimum and maximum ratio values respectively. Black dots represent outliers.

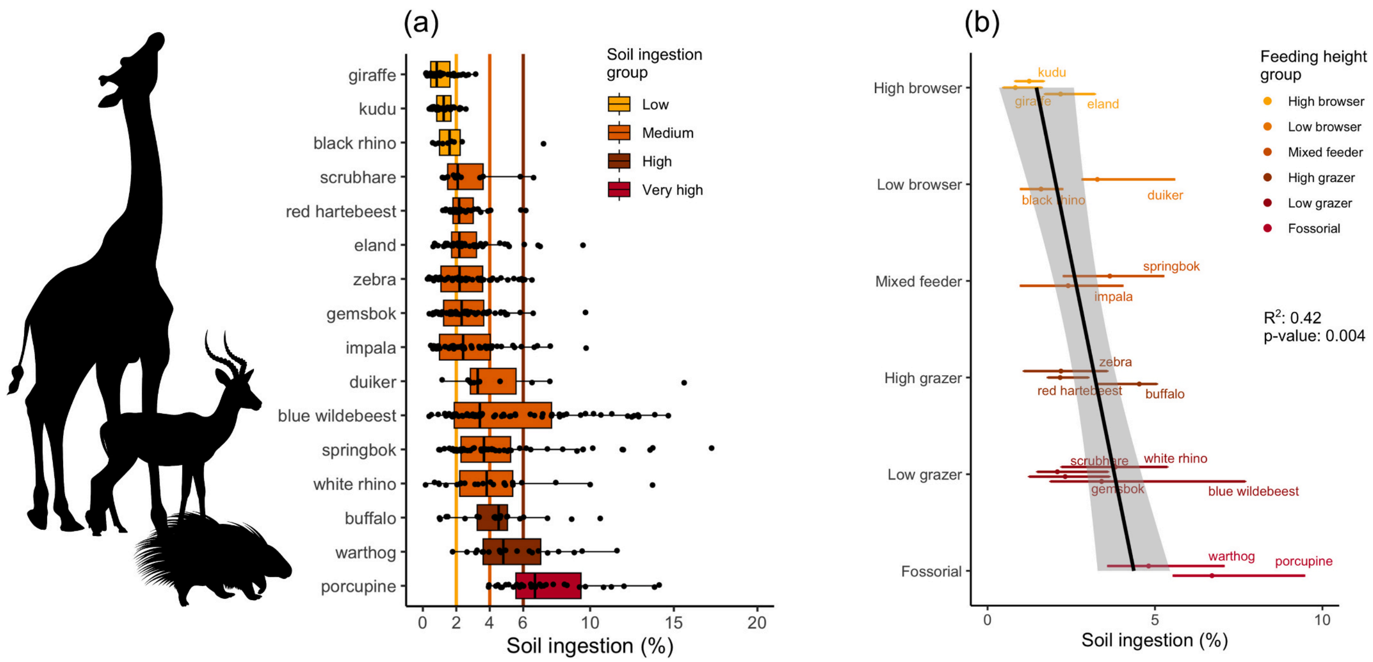

Fig. 3. Species-specific soil ingestion levels (%) are influenced by feeding height. Panel 3a uses soil and faecal Al concentrations to determine soil ingestion expressed as percentage (x-axis) across species (y-axis). Vertical yellow (<2 %), orange (2–4 %), brown (4–6 %) and red (>6 %) lines show soil ingestion thresholds low, medium, high and very high soil ingestion groups. The solid black line within horizontal boxes represents median values, edges of the box reflect lower (1st) and upper (3rd) quartiles and whiskers extending left and right depict minimum and maximum values. Black dots represent individual samples showing soil ingestion variation within species. Note: the x-axis scale limit is set to 20 % for visualisation, which omits some extreme outliers. Panel 3b reflects the negative relationship between feeding height (y-axis) and soil ingestion expressed as % (x-axis). The shaded area around the slope indicates a 95 % confidence interval. Named, colour coded points represent median soil ingestion (%) and correspond to feeding height. Horizontal (error) bars for each point reflect variability for each species.

fossorial species, soil ingestion may represent a considerable proportion of total toxic elements ingestion for vanadium, aluminium, lead, chromium, tin, cobalt and arsenic (20–60 %), which are highly concentrated in soils (Fig. 2). For some low grazing and fossorial species, soil ingestion is likely to be the predominant pathway of toxic element ingestion (Fig. 4a).

3.4. *Toxic element excretion*

In the herbivore faecal dataset, the first two principal components explained 85.4 % (Dim1 = 68 %; Dim2 = 17 %) of the total variance (Fig. 4b). The PCA confirms our calculations that toxic element ingestion is related to levels of soil ingestion. All toxic elements except Cr were strongly aligned with Dim1. High browsers (the lowest soil ingestion

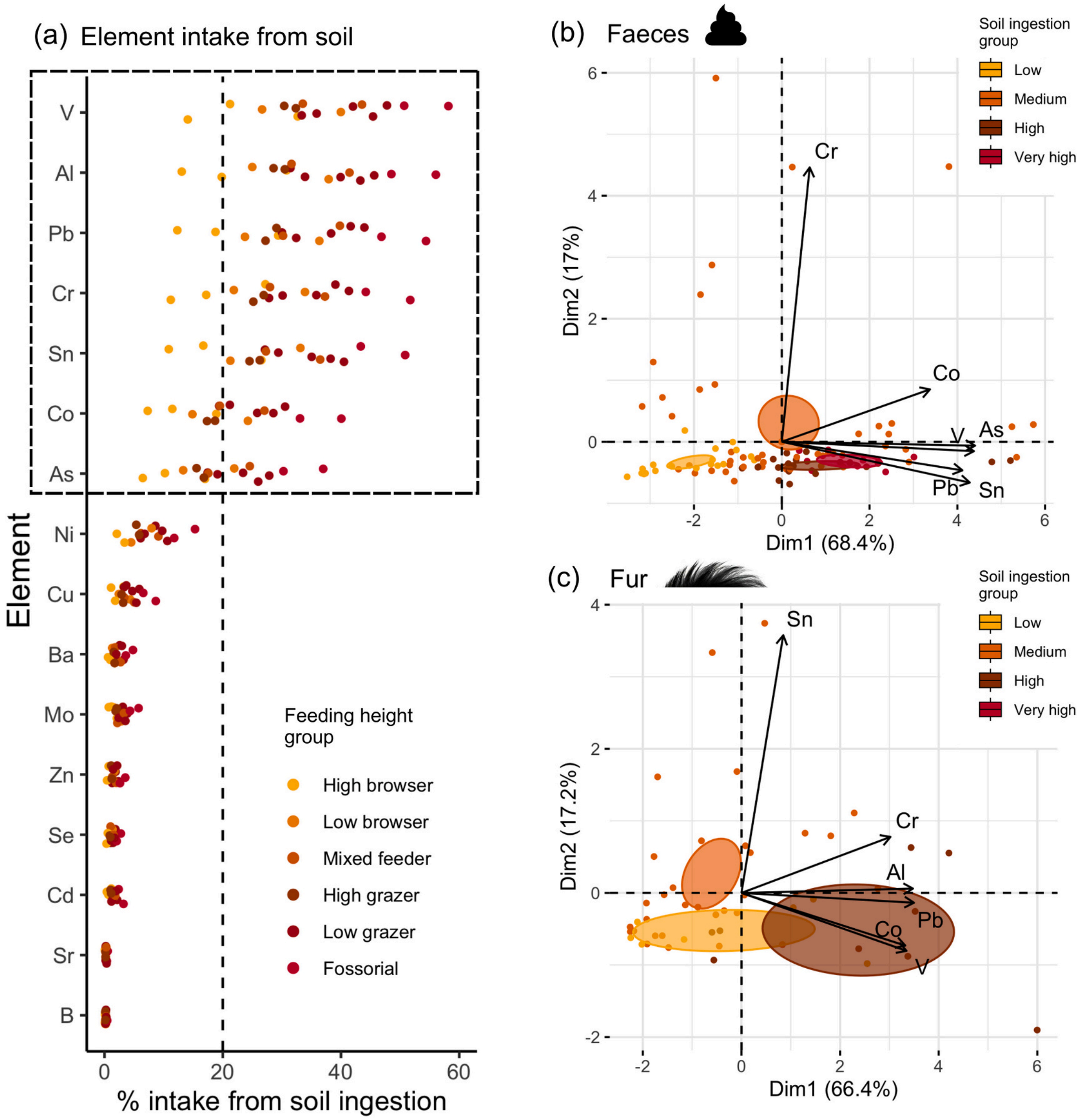

Fig. 4. Soil ingestion is a key pathway for toxic element intake, excretion and assimilation. Panel 4a shows elements assessed (y-axis) against the % intake of each element via soil ingestion in animals feeding at different heights (coloured dots). The vertical dotted line (20 % threshold) and dotted black box distinguish elements and feeding groups where soil ingestion is a major contamination pathway. Panel 4b reflects response loadings (black arrow) in μg/kg dry weight for each element (symbols) assessed in faeces. Variation in the dataset is explained by horizontal (Dim1), and vertical (Dim2) dimensions (%) on each axis. Panel 4c reflects response loadings (black arrow) in μg/kg dry weight for each element (symbols) assessed in fur. Colours in PCA plots correspond to low (<2 %), medium (2–4 %), high (4–6 %) and very high (>6 %) soil ingestion levels.

group) were clustered along the negative side of Dim1, which aligned with the low toxic element concentrations in their faeces. Greater variability and higher concentrations of excreted toxic elements, specifically chromium (Cr range; 1991–10,847 μg/kg) are seen in the medium soil ingestion group (clustered along Dim2). In contrast the highest excreted concentrations of (Co range; 458–2206 μg/kg), arsenic (As range; 9–529 μg/kg), tin (Sn range; 50–221 μg/kg), lead (Pb range; 512–2072 μg/kg) and vanadium (V range; 2528–11,145 μg/kg) are seen in the high and very high soil ingestion groups (grazing and fossorial species) with high positive loading on Dim1. Faecal Al was excluded from analysis as it was used to estimate soil ingestion.

3.5. *Toxic element assimilation*

PCA analysis in the fur dataset, confirmed that toxic elements ingested are assimilated into body tissues. Here, 83.6 % of the total variance is explained by the first two principal components (Dim1 = 66.4 %; Dim2 = 17.2 %) (Fig. 4c). All toxic elements except tin (Sn range; 31–299 μg/kg), were strongly associated with Dim1. This PCA highlights a similar overall pattern to that reflected by faeces, where species with higher soil ingestion levels also assimilate higher levels of toxic elements in fur. Across the suite of toxic elements, lower concentrations are generally associated with lower concentrations in fur. Grazers, with high soil ingestion, consistently had higher levels of cobalt (Co range; 136–2372 μg/kg), lead (Pb range; 174–1475 μg/kg), chromium (Cr range; 877–6203 μg/kg) and vanadium (V range; 877–6203 μg/kg) in fur. As circularity was not a concern for fur samples, aluminium was included in this analysis and also showed increased concentrations in the high soil ingestion group (Al range; 426–3982 μg/kg). We did not include samples from the highest soil ingestion group (porcupine) due to differences in toxic element uptake associated with quill morphology.

3.6. *Comparison of toxic element excretion and assimilation*

Across faecal and fur matrices, the relationship between excreted (faeces) and assimilated (fur) concentrations showed a strong positive correlation (R2 > 0.4) for toxic elements, vanadium, lead, selenium and aluminium. No correlation was found for cobalt and zinc and no or negative correlation was found for remaining elements (Fig. S5).

3.7. *Correlation matrix for soil ingestion, hypsodonty and biological matrices*

For the elements disproportionately concentrated in soils (aluminium, arsenic, chromium, lead and vanadium), we generally found a positive relationship between soil ingestion or hypsodonty (as a proxy for soil ingestion) and toxic element concentrations quantified in faeces or fur (Fig. 5). With the exception of Sn concentrations in fur, the Spearman's correlation coefficient was typically >0.4 for these elements. Toxic elements in faeces typically had stronger relationships with soil ingestion than hypsodonty; by contrast, toxic elements in fur were more closely related to hypsodonty. For all other elements, relationships were variable across matrices. For elements disproportionately concentrated in plants (boron, strontium, cadmium, selenium), the Spearman's correlation coefficient was often strongly negative representing an inverse relationship between soil ingestion or hypsodonty with elemental intake (faeces) and assimilation (fur).

3.8. *Hypsodonty and aridity as a framework for toxic metal intake*

There was a non-significant, weak positive correlation ($R^2 = 0.11$; $p = 0.149$) between soil ingestion (%) and hypsodonty index at the local scale using data from our Tswalu study site (Fig. 6a). Buffalo, white rhino and warthog (all grazers) appear to be outliers with greater soil ingestion relative to their hypsodonty index. At a continental scale, browsers did not show a significant relationship of hypsodonty index with aridity (Table S4; $R^2 = 0.10$; $p = 0.099$); by contrast, mixed feeders ($R^2 = 0.35$; $p = 0.011$) and grazers/fossorial species ($R^2 = 0.30$; $p = 0.01$) displayed significant, strong relationships with aridity (Fig. 6b; Table S4).

4. Discussion

Understanding toxic element dynamics, the transfer pathways and species-specific vulnerabilities in wildlife, is crucial for developing management strategies for biodiversity conservation and mitigating the effects of anthropogenic pollution (Penrose et al., 2019). While placental transfer, exposure to contaminated forage and water have been

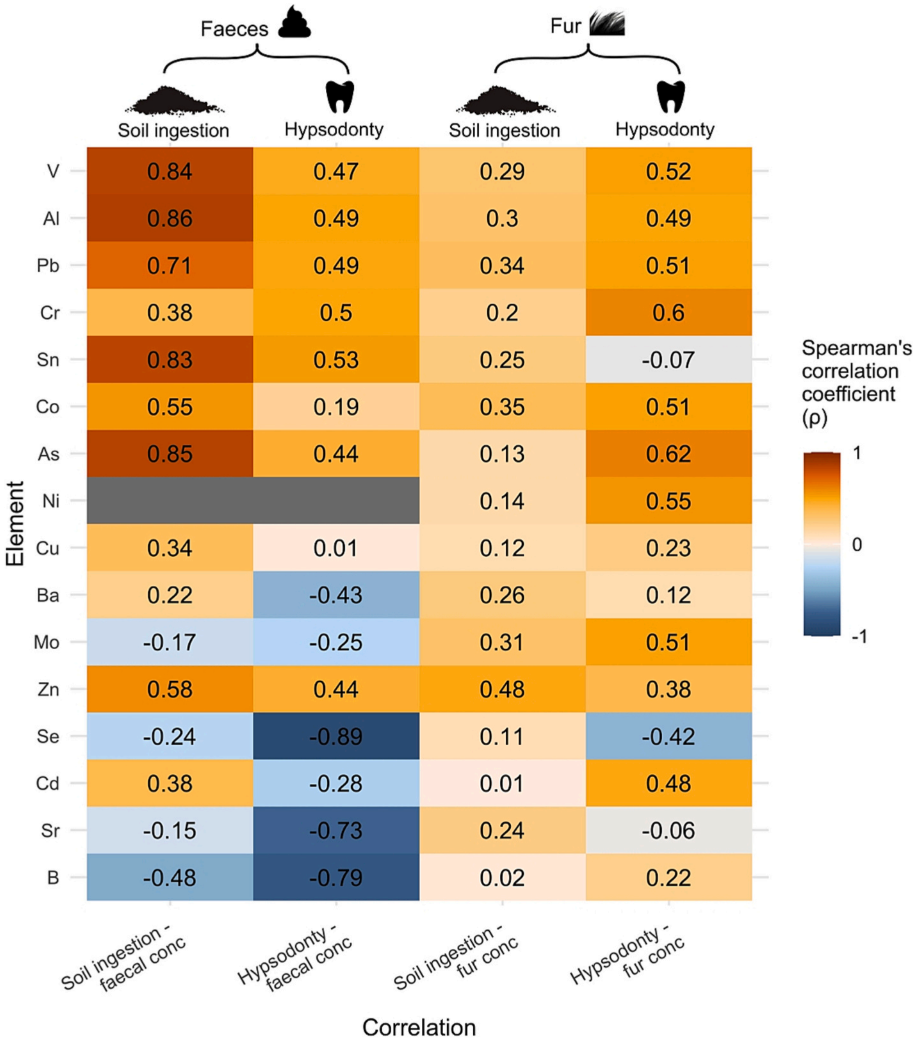

Fig. 5. Correlation matrix highlights the relationship between soil ingestion, hypsodonty in toxic elements in faeces and fur. Correlations between soil ingestion, faecal and fur concentrations (columns 1 and 3) and hypsodonty, faecal and fur concentrations (columns 2 and 4) are presented for all elements assessed (y-axis). Tile colour corresponds with positive (dark orange — $R^2 = 1$) or negative (dark blue — $R^2 = -1$) correlation for each element and each matrix. Grey tiles represent insufficient information.

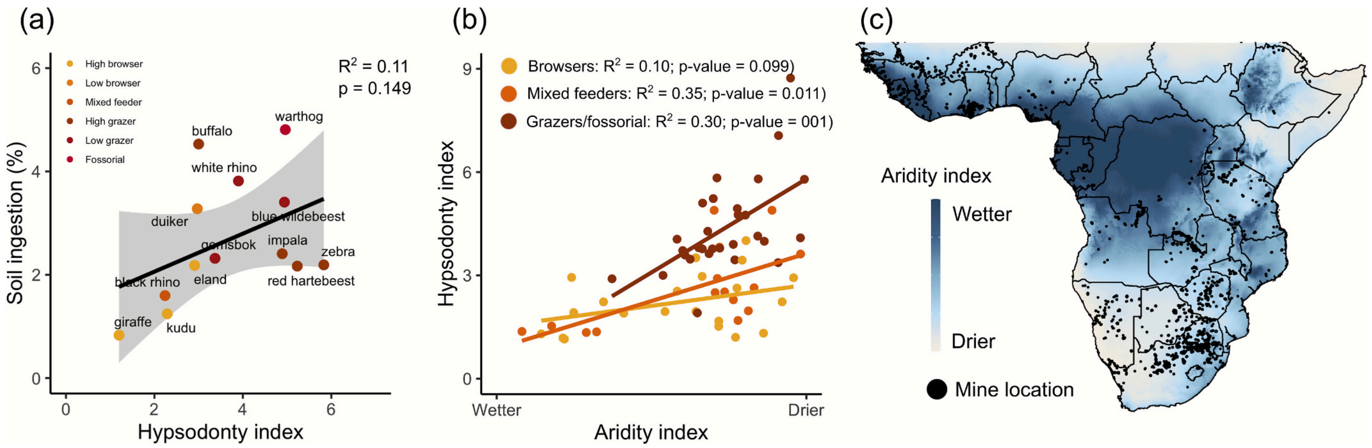

Fig. 6. The relationship between hypsodonty, soil ingestion and aridity at local and continental scales. Panel a shows the relationship between % soil ingestion (y-axis) and hypsodonty index (x-axis; estimate of tooth volume based on the ratio of tooth crown to its height/length) in herbivores at Tswalu. Panel b highlights the relationships between hypsodonty (y-axis) and aridity (x-axis) at continental scale for African ungulates. Panel c highlights increased mining activity (black dots = ~4500 mines) in arid regions (dry = grey; wet = blue) across sub-Saharan Africa, indicating greater potential for toxic element exposure through consumption of contaminated surface soils.

identified as primary pathways of contamination in wildlife (World Health Organisation/United Nations Environment Programme (WHO/UNEP), 2012), this research demonstrates species-specific vulnerability to toxic element exposure through soil ingestion. We confirmed our hypothesis that species foraging closer to the ground (i.e. grazing and fossorial species) ingest more soil than canopy feeding browsers. These differences in diet and foraging behaviour subsequently correspond to higher toxic element intake, excretion (faeces) and assimilation (fur) in the body. We also confirm that hypsodonty appears to align with toxic element exposure and soil ingestion and can therefore be used as a crude proxy to predict species-specific vulnerability to toxic-elements at broad scales. Together, these insights form a general framework to non-invasively identify and monitor toxic element exposure from soil ingestion in wild herbivores for application in global restoration, rewilding and conservation management efforts.

4.1. Soil as a major sink of toxic elements

Soils are a major sink of toxic elements (Alloway, 2013). Soils in the Kalahari are predominately sandy with low organic content and cation exchange capacity. The soils of the Kalahari are typically acidic, which influences toxic element solubility, mobility and spatial heterogeneity in the environment and can result in certain elements, (vanadium, aluminium, lead, chromium, tin, cobalt and arsenic) being highly concentrated in soils compared to vegetation (Wang et al., 2007; Ding et al., 2022). Underlying geology, environmental conditions and anthropogenic activity influence spatial variation in toxic element abundance. For example, within our study site, substantial differences were noted in soil aluminium concentrations (Fig. S1) across the reserve. This variability in background concentrations can influence toxic element consumption by wildlife given their mobility between areas of high and low concentration, as well as seasonal shifts in range to meet nutrient requirements.

While plant-specific characteristics have not been addressed in this study, we note that plant anatomy, morphology, biochemical and phenological characteristics determine how plants respond to toxic elements in the soil and that intraspecific variation and trait-environment relationships with respect to toxic element accumulation are fluid (Kattge et al., 2020). For example, some woody species (e.g. *Vachellia farnesiana* (L.)) and grasses (e.g. *Hyparrhenia hirta* (L.) Stapf) can tolerate high concentrations of certain toxic elements from surrounding soil. Grasses grazed early in the growing season or after fires, are able to absorb 100–1000 times the quantity of toxic elements in their roots and shift these quantities to above-ground shoots as they grow (Xu et al., 2020). Although grasses become less palatable later in the wet season, consumption of hyperaccumulating grass species such as these, in combination with high levels of toxic elements concentrated in soil, would contribute markedly to toxic element intake. Habitat, plant morphology and physical processes such as wind and disturbance by animals interact to influence soil particle re-suspension and variation of soil loading on plant surfaces for subsequent ingestion (Damuth and Janis, 2011). Forage quality and availability are closely linked to precipitation in the Kalahari and influences the regional, seasonal and sex-specific diet composition requirements of herbivore species during different times of the year (Staver and Hempson, 2020). As a consequence, species-specific vulnerability to toxic element intake via the soil ingestion pathway will also differ.

4.2. Drivers of soil ingestion in wild herbivores

Our results highlight that feeding height is a strong determinant of soil ingestion in wild herbivores (Fig. 3). Although the variation between browsers is low (Fig. 3a), soil ingestion levels reflect the foraging gradient at different regions of the browse canopy. Browsers select different plants and plant parts (buds, flowers, pods, leaves). However, browsers feeding at the top (e.g. giraffe and kudu) of the canopy have lower soil ingestion levels and less variability than those feeding lower down (e.g. black rhino, duiker; *Sylvicapra grimmia*), suggesting higher areas are less affected by soil/dust deposition or animal movement (Damuth and Janis, 2011). In this regard, high browser-soil substrate interactions are reduced, which in turn limits soil ingestion potential. In mixed feeders, median soil ingestion levels are higher and more variable within and between species. This pattern is likely influenced by access to the vegetation communities (duneveld, bushveld, salt pans) species preferentially occupy, the height at which they forage and the degree to which different species predominantly browse or graze in response to their physiological requirements and resource availability over the year (Owen-Smith, 1982; Staver and Hempson, 2020).

The height at which grazing species preferentially forage reduces competition between species on one hand, and by reducing grass biomass, facilitates access to forage of a suitable height or quality for other species on the other (Arsenault and Owen-Smith, 2008). Many arid-adapted species (e.g. red hartebeest, gemsbok and eland) take advantage of short new growth after fires or during the wet season but are able to digest medium-long grasses of lower quality as well. In contrast, grazers such as white rhino, buffalo, plains zebra and blue wildebeest feed exclusively on short grass and grass parts that they select for maximum nutrient gain. As a result, their proximity to the substrate during foraging increases soil ingestion levels (Arsenault and Owen-Smith, 2008; Damuth and Janis, 2011). Median soil ingestion was however highest in substrate-level feeding warthog and the truly fossorial porcupine, which aligns with what we know about their diet of grass, geophytes, tubers, roots, bulbs and barkto which soil adheres. Additionally, their excavating and burrowing activities displace deeper-lying contaminants, creating new surface pathways for toxic element exposure (Penrose et al., 2019). Estimates from this study align with previous research on grazing wombats (*Vombatus ursinus*; Penrose et al., 2019) and bison (*Bison bison*; Beyer et al., 1994), but it is clear that soil ingestion and subsequent intake are influenced by complex interactions between toxic element specific characteristics, environmental factors and animal behaviour.

4.3. *Toxic element exposure via soil ingestion*

Assessing heavy metal exposure and estimating internal dose through biomarkers can be complex. The unique and shared sources of contamination, coupled with different routes of exposure, mean some elements share common absorption, transformation and elimination pathways, while others are metabolised and reflect as such in different biomarkers (Martinez-Morata et al., 2023). For example, Pb concentrations in whole blood represent (~2 %) recently absorbed concentrations, hair more accurately reflects total intake and the skeletal pool represents as much as 90 % of absorbed Pb under stable conditions (Squadrone et al., 2022). Our results show that highest egested (faeces) and assimilated (fur) total toxic element concentrations occur in grazing and fossorial species and to a lesser degree in some mixed feeders (Fig. 4). This provides a rough approximation of exposure and indicates potentially increased vulnerability in these species due to their diet and foraging behaviour. Our findings confirm that faecal concentrations, representative of short-term exposure, are a relatively reliable indicator of subsequent chronic exposure reflected in fur, although the timeframe of assimilation for all elements remains uncertain. When the relationship between soil ingestion, hypsodonty, and toxic element concentrations in faeces and fur were examined, an overall positive relationship was evident across variables (Fig. 5). Toxic elements in faeces typically had stronger relationships with soil ingestion than hypsodonty but in fur were more closely related to hypsodonty. The comparison of total element concentrations in fur and faeces cannot provide insights into total body burden, fractionation of elements in different tissues, or actual effects. However, our results substantiate the interpretation that both diet-related soil ingestion and hypsodonty have predictive value for assessing species-specific vulnerability in wildlife, supporting the broader functional link between foraging ecology and contaminant exposure. To better link exposure patterns more directly to wildlife impacts, our findings further highlight these toxic element thresholds, particularly in systems where elevated soil ingestion may increase contaminant exposure beyond limits that influence physiological and reproductive function.

4.4. *Hypsodonty as a proxy for toxic element exposure via soil ingestion*

Previous research has linked hypsodont teeth to ungulate feeding ecology and precipitation in species that occupy open, arid environments in which C_4 grasses with high abrasive content and soil/dust/grit loading are predominant in the diet (Eronen et al., 2010; Hummel et al., 2011; Kaiser et al., 2013). Based on this, we expected grazing species to have high levels of soil ingestion and higher hypsodonty in response to increased wear. Although the relationship was weak ($p = 0.15$), we did find a positive relationship between soil ingestion and hypsodonty. It is possible that these results are influenced by the small sample size, or a combination of environmental and behavioural factors (soil type, feeding site selection, mobility or seasonality) that influence actual soil ingestion independent of tooth morphology. However, for elements disproportionally concentrated in soils, we did find that hypsodonty displayed a strong positive correlation with toxic element concentrations in faeces and fur (Spearman's correlation coefficient > 0.5). These findings are consistent with ecological theory and confirm our hypothesis that hypsodonty can be used as a crude proxy for soil ingestion and potential toxic element exposure (Hummel et al., 2011; Damuth and Janis, 2011).

At a continental scale, we found that species hypsodonty was associated with aridity for mixed, grazing and fossorial species (Fig. 6b). These results indicate that when species within these groups occupy more arid regions, they are likely to be at greatest risk of toxic element exposure via the soil contamination pathway, particularly in areas of high anthropogenic activity. Mining is a major contributor to toxic element pollution in Africa and operations are concentrated in semi-arid/arid regions across sub-Saharan Africa, where grazing and fossorial species are dominant (Fig. 6c). Elevated exposure to toxic elements amplified by industrial contamination, could disproportionately affect these species. In these systems, land degradation is accelerated by mining activities which can push systems over the recovery threshold (Cymes and Krekeler, 2018). We suggest that combining datasets of hypsodonty, aridity and mining locations help target where local-scale studies should be prioritised for further investigation, incorporating seasonal soil, plant and animal datasets with specific toxic element thresholds.

4.5. *Future directions*

Moving forward, applying sound restoration initiatives, particularly in developing countries where data on toxic element distribution are deficient, is critical for climate change mitigation, biodiversity restoration and community health (Hou et al., 2025). Conservation and restoration initiatives should combine environmental contamination assessments with a range of biomarkers collected from management hunts or natural mortalities to evaluate organ-specific toxicity and subsequent effects of exposure. Future surveys should include non-target screening and account for historical and recent activities prior to phased species re-introductions. The assessment of toxic elements, their interactions and effects in free-ranging wildlife is inherently complex. However, the development of wildlife refugia and conservation areas around industrialized and mined sites is a core component of restoration efforts across the globe. While transformed, landscapes may have conservation value, their viability needs to be assessed over time at the community level, to determine the risks for wildlife associated with recolonisation and subsequent use of wildlife as protein for human consumption.

5. Conclusion

The framework developed here provides a tool for identifying sites impacted by toxic elements and species most at risk via the soil ingestion pathway. This may prove useful for guiding community-level species reintroductions that aim to re-establish ecological processes at rehabilitation, restoration and rewilding sites. Additionally, this framework can be used to broadly identify locations likely to have higher environmental toxic element concentrations and therefore, higher species vulnerability risk of toxicity via the soil ingestion pathway, ensuring identified high-risk ecosystems and animal groups can be targeted for further monitoring. When assessments are aligned with a One Health approach, toxic elements and other emerging contaminants of concern at specific sites can be quickly identified and monitored to assess the potential for adverse effects at both species and community levels, while simultaneously identifying contaminants of concern for human health.

CRediT authorship contribution statement

Andrea B. Webster: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Nigel C. Bennett:** Writing – review & editing, Supervision, Funding acquisition. **Marcus Clauss:** Writing – review & editing, Methodology, Conceptualization. **Andre Ganswindt:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Andrew J. Abraham:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Statement of ethics

This study and all data were collected with the approval of the University of Pretoria's Research and Animal Use and Care Committee (Reference EC043-18 and EC043-18-A1 and NAS028/2022) and the South African Department of Agriculture, Land Reform and Rural Development (Reference DAFF-18/02/2019 and 12/11/1/1/8 (2319JD).

Funding

ABW acknowledges funding from the Department of Science and Technology and National Research Foundation SARChI chair of Mammalian Behavioural Ecology and Physiology, South Africa (GUN number 64756), Additionally, the Tswalu Foundation and Oppenheimer Generations Conservation and Research are acknowledged for financial support for this project.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Andrea B. Webster reports financial support was provided by The Tswalu Foundation. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. All authors have approved this manuscript for publication. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank Tswalu Kalahari Reserve for facilitating the research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.181193.

Data availability

The datasets presented in this study are available at UPresearchdata.14675388. Data will be made available on request.

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