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Sodium constraints on megaherbivore communities in Africa

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Sodium (Na) is an essential nutrient for animals, but not for most plants. Consequently, herbivores may confront a mismatch between forage availability and metabolic requirement. Recent work suggests that larger-bodied mammals may be particularly susceptible to Na deficits, yet it is unknown whether Na availability constrains the density or distribution of large herbivores at broad scales. Here we show that plant-Na availability varies >1,000-fold across sub-Saharan Africa and helps explain continent-scale patterns of large-herbivore abundance. We combined field data with machine-learning approaches to generate high-resolution maps of plant Na, which revealed multi-scale gradients arising from sea-salt deposition, hydrology, soil chemistry and plant traits. Faecal Na concentration was positively correlated with modelled dietary Na, supporting the prediction that variation in plant Na is a major determinant of herbivore Na intake. Incorporating plant-Na availability improved model predictions of large-herbivore population density, especially for megaherbivore species, which are depressed in very-low-Na regions (<100 mg kg^{-1}), consistent with Na limitation. Our study offers an explanation for the scarcity of megaherbivores in parts of Central and West Africa, which has major ecological ramifications given the strong influence of large herbivores on ecosystem functioning and the profound human-induced changes to Na availability in Africa and beyond.

Animals require over 25 elements to survive and reproduce, some in large quantities and others in trace amounts[1]. Too little (deficiency) or too much (toxicity) of specific elements can cause physiological stress with consequences for animal health and population dynamics[2]. Sodium (Na), for example, is increasingly recognized for its important role in ecosystem functioning[3]. Na is essential for many homeostatic, metabolic, neural and muscular processes in animals[1,4,5] but is non-essential for most plants. While trace amounts of Na are harmless or mildly beneficial to many plants, high concentrations can be osmotically stressful and toxic[6,7]. Yet, because Na is energetically expensive for plants to expel, it tends to accumulate passively in tissues. As a result, foliar Na concentrations generally reflect local conditions, spanning orders of magnitude across plant species and locations[8–10]. Animals that obtain the majority of their Na from plants[11] (that is, herbivores) may thus struggle to meet dietary requirements in low-Na environments or face toxic effects in high-Na environments[4,10].

Although herbivores show physiological and behavioural adaptations for obtaining, conserving and excreting electrolytes, Kaspari[3] recently outlined four mechanisms by which Na shortfall might limit herbivore survival and reproduction: (1) insufficient Na relative to potassium (K), leading to disabled Na–K pumps and ionic imbalance; (2) reduced capacity to effectively use nitrogen (N) and phosphorus (P); (3) increased exposure of the intestinal tract to toxic effects of plant secondary compounds such as tannins; and (4) starvation of symbiotic gut microorganisms that rely on Na–P co-transporters to obtain phosphate. Consistent with these and other possible mechanisms, previous studies have documented effects of Na availability on the behaviour, growth and ecological impacts of animals. For example, experimental Na addition in salt-poor tropical forests and temperate grasslands

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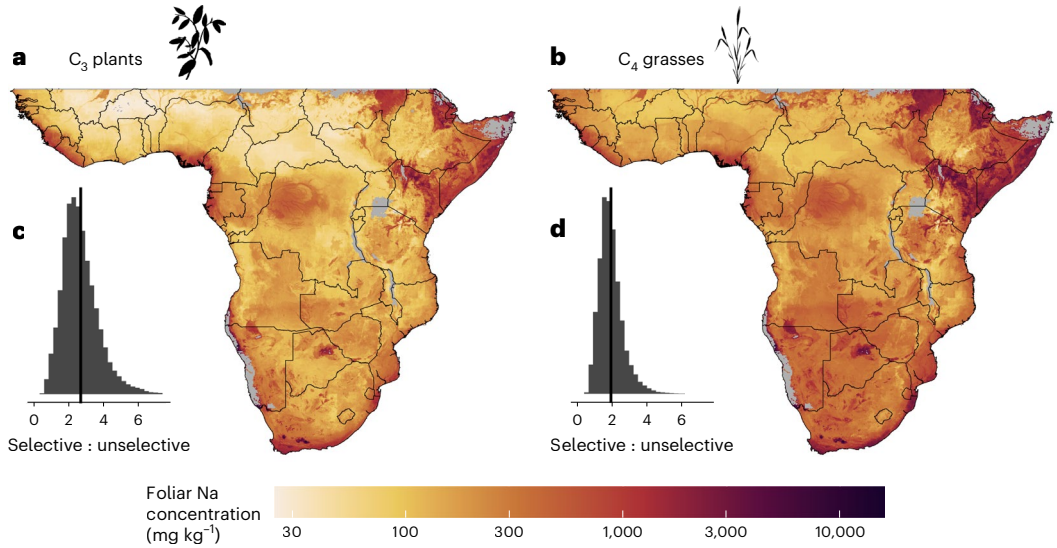


Fig. 1 | Spatial mapping of plant foliar Na concentration for C_3 and C_4 plant functional groups across sub-Saharan Africa. a,**b**, These 0.1° resolution maps are representative of C_3 plant (**a**) and C_4 grass (**b**) Na availability to herbivores under an unselective foraging scenario (that is, not specifically targeting plants with higher Na concentration). For maps of selective foraging (that is, 95th percentile foliar Na), see Extended Data Fig. 3. To better visualize geographic patterns, concentrations have been plotted on a $\log_{10}$ scale. Across the region, C_4 plants have twofold higher Na concentration than C_3 plants. **c**,**d**, Inset histograms show the relative increase of plant Na concentration in the selective foraging scenario compared with the unselective scenario for C_3 (**c**) and C_4 (**d**) plant functional groups. Silhouettes from PhyloPic under a Creative Commons license CC0 1.0: plant, T. Michael Keesey; grass, Mason McNair; map elements created with Natural Earth (https://www.naturalearthdata.com).

increased insect abundance, herbivory and litter decomposition[3,12,13], while insects feeding on Na-rich plants developed larger bodies, brains and physiological capacity[14]. Mammalian herbivores, which face the additional demands of gestation and lactation, also respond positively to Na supply. Ad libitum provision of NaCl-enriched water increased offspring production in captive meadow voles by 40–60% relative to those given distilled water[15]. Na supplementation is also common in livestock husbandry and has been shown to increase weight gain (for example, by up to 65% in sheep and 48% in cattle[16]). Mammals frequent natural salt licks worldwide[5], and hotspots of Na availability have been linked to habitat selection in Serengeti ungulates[17] and African elephants[18,19], although this effect appears reduced at higher elephant densities[20]. In high-Na environments, however, animals may experience significant physiological stress due to Na toxicity (for example, hypertension), especially where water availability is also limited[2].

Recent studies[5,21] have suggested that, due to discrepancies between allometric scaling relationships of Na requirement and dietary Na intake, larger-bodied herbivores may be particularly vulnerable to Na limitation (Supplementary Fig. 1). This hypothesis is thought to explain the more common Na-seeking behaviours of large herbivores in the wild[5,11,22,23]. However, there is scant evidence that Na actually limits the population growth, density or distribution of large mammalian herbivores (>2 kg) at any scale. Established predictors of abundance in large herbivores include primary productivity and its climatic and edaphic determinants, forage quality (that is, protein and energy content, digestibility and related quantities), water requirements and top-down forces (for example, predation, disease)[24–26]. Previous research has shown that interactions among these factors and species' traits such as body mass, diet and habitat preference can explain considerable variation in community structure at continental to global scales[24–31]. However, the extent to which mineral nutrients contribute to these effects remains undetermined.

Here we quantify Na availability and its effects on large-herbivore density across sub-Saharan Africa (<15° N), which supports the world's most diverse communities of large herbivores. We developed high-resolution maps of foliar Na concentration by collating an extensive dataset of foliar Na measurements and using an ensemble of machine-learning techniques. By combining these maps with continentally distributed data on herbivore faecal Na concentration and population densities, we tested the predictions that (1) large-herbivore Na intake reflects patterns of foliar Na concentration and (2) dietary Na availability constrains large-herbivore densities at the continental scale.

Results

Patterns of foliar sodium across sub-Saharan Africa

We generated 0.1° maps of foliar Na concentration for C_3- and C_4-photosynthesizing plant groups using 4,258 continentally distributed field measurements of foliar Na concentration from 289 locations (Supplementary Text 1 and Extended Data Fig. 1) and an ensemble of machine-learning approaches trained on 11 predictor variables (Supplementary Tables 1 and 2 and Supplementary Fig 3). This allowed us to estimate dietary differences in Na uptake across the continuum—from grazers that specialize on C_4 grasses to browsers that specialize on C_3 eudicots[32]. As it is unknown to what degree different herbivores concentrate their foraging on the most Na-rich plants in a community[10], we calculated the median and 95th percentile foliar concentrations for each grid cell to represent two different foraging behaviour scenarios (hereafter 'unselective' and 'selective' foraging scenarios, respectively). As the data were right skewed, we trained models on $\log_{10}$(foliar Na concentration). The ensemble model was consistently the best-performing model with robust prediction accuracy ($R^2 > 0.35$; root mean squared error (RMSE) < 0.4 $\log_{10}$ units) although model performance decreased with distance from training points across all models tested (Extended Data Fig. 2). Nonetheless, we found that foliar Na varied by a factor >1,000 across the continent, and that spatial patterns were similar for selective and unselective foraging scenarios (Fig. 1 and Extended Data Fig. 3). At any given location, C_4 grasses had twofold higher median Na concentrations than C_3 plants (1.4-fold higher at the 95th percentile), congruent with the fact that many of the most widespread and abundant African grasses are among the C_4 taxa known to uptake Na (for example, *Cynodon*, *Chloris*, *Panicum* spp.)[7]. The selective foraging scenario increased estimates of Na availability by a mean factor of 1.9 (for strict C_4 grazers) to 2.7

Table 1 | The percentage area of sub-Saharan Africa that is below foliar Na concentration thresholds where large-herbivore density may become constrained by Na

	Threshold concentration (mg Na kg^{-1})	Area of sub-Saharan Africa (%)			
		C_3 plants		C_4 grasses	
		Median	95th percentile	Median	95th percentile
Considered optimal for livestock production	>500	10.0	30.3	19.4	45.2
Potentially limiting Na concentrations	<500	90.0	69.7	80.6	54.8
	<100	33.2	4.3	6.3	0.4
	<50	11.3	0.0	0.1	0.0

It is generally considered that foliar Na concentrations >500 mg kg^{-1} are optimal for livestock production[4,48]. Area percentage values are provided for median (unselective foraging scenario) and 95th percentile (selective foraging scenario) concentrations in C_3 plants and C_4 grasses.

(for strict C_3 browsers) relative to the unselective scenario across the region (Fig. 1, Table 1 and Extended Data Fig. 3).

As in North[3] and South America[13], variation in plant Na across sub-Saharan Africa is strongly correlated with environmental gradients. Variable importance calculations indicate that sea-salt aerosol deposition is the strongest and most consistent predictor of foliar Na concentration (Supplementary Fig. 4), with conspicuous signatures of prevailing wind direction (Fig. 1 and Supplementary Fig. 2). Exchangeable soil Na and rock Na weathering rate were positively associated with foliar Na, while soil K and net primary productivity showed negative relationships (Extended Data Fig. 4). Aridity was among the most important predictors of both median and 95th percentile values, but its relationship with foliar Na was variable and nonlinear, suggesting that its effects are context dependent (Extended Data Fig. 4). Alluvial input was also positively related (and height above the nearest drainage negatively related) to foliar Na, especially in determining the 95th percentile; alluvial inputs are patchy and cover a small fraction of the continent (Supplementary Fig. 2), such that this variable did not have high relative importance at the continental scale, but its localized effects at inland locations are dramatic. Consequently, our maps show the highest foliar Na concentrations in windward coastal regions (for example, Somalia and eastern Kenya, southern Mozambique and South Africa) and/or low-lying wetlands, drainage basins and pans (for example, Niger and Okavango deltas; Turkana, Congo and Cuvelai-Etosha basins; Makgadikgadi and Kafue flats), many of which are arid or semi-arid. Conversely, foliar Na is low in inland and upland regions, many of which are comparatively well watered and productive (for example, Ethiopian and East African highlands and much of central Africa) (Fig. 1 and Extended Data Fig. 3).

Our study provides a detailed multifactorial analysis of spatial patterns in foliar Na at the continental scale, revealing major variation that cannot be explained by simple proxies such as distance from coastline[8,9,33] (Extended Data Fig. 2). While sea-salt deposition is indeed a primary source of Na, we find that local and regional geology (for example, watercourses, Na-rich geological substrates[34]) and climate also have important roles.

Herbivore sodium intake as a function of plant Na gradients

Animals cannot store Na in the body in the long term and so must continuously consume it to maintain Na homeostasis[35]. To evaluate the extent to which geographic patterns of plant-Na availability influence Na intake by large herbivores, we compared the concentration of Na in the faeces of wild mammalian herbivores (n = 1,356 samples from 28 species in 20 protected areas) with the modelled average of Na concentration in their diet from sites distributed across eastern and southern Africa (ranging ~75-fold in foliar Na availability; Supplementary Table 3 and Supplementary Fig. 7). Dietary Na concentration was calculated using species-specific data on diet composition (relative percentage of C_4 and C_3 plants in the diet; Supplementary Table 4) and local foliar Na concentrations from our maps. Mammals have a high absorption capacity of Na (on the order of ~90% (ref. 36)). Once in the bloodstream, Na is mostly excreted through urine with a variable amount lost through sweat and saliva or resecreted back into the digestive system[35]. However, several studies have shown that faecal Na concentration correlates positively with Na intake[35–40]. Consequently, a strong, positive relationship between our modelled plant Na concentration and faecal Na concentration represents compelling evidence that geographic variations in plant Na are the primary determinant of herbivore intake and are not masked by alternative sources of Na (for example, geophagy, omnivory).

Indeed, we found strong positive relationships between large-herbivore dietary Na concentration and faecal Na for both unselective (conditional R^2 = 0.50; marginal R^2 = 0.38; F value = 38.2; P value < 0.001; Extended Data Fig. 5) and selective (conditional R^2 = 0.56; marginal R^2 = 0.41; F value = 44.6; P value < 0.001; Fig. 2a) foraging scenarios, indicating that gradients of foliar Na concentration primarily constrain herbivore Na intake. Interestingly, this effect appeared to level off at ~1,000–3,000 mg kg^{-1}. In addition, we found that across 12 wildlife reserves where faecal Na measurements were available for both grazers (C_4-dominated diets) and browsers (C_3-dominated diets), grazers showed 1.35× (s.d. = 0.22) higher faecal Na concentrations (Fig. 2b), a result that aligns with our finding that Na concentration is 1.3–2.0-fold higher in C_4 than C_3 plants (Fig. 1).

Evidence that sodium constrains megaherbivore densities

While large-herbivore Na intake appears regulated by plant-Na availability (Fig. 2), this does not necessarily result in Na availability constraining herbivore abundance in low- or high-Na environments. Rather, Na constraints will occur only when Na intake falls below minimum herbivore Na requirements or exceeds toxic levels[3]. A recent study[5] attempted to estimate minimum daily Na requirements in mammals, finding that larger herbivores are more vulnerable to Na deficiencies. However, while the overall conclusions of this study appear robust (that is, even lower uncertainty bounds of Na requirement were found to scale with body mass at a factor higher than Na intake from food and water), accurately predicting Na requirements from this study remains difficult owing to a low sample size and restriction to domesticated animals[5]. Similarly, exact levels of Na toxicity are difficult to pinpoint owing to species- and environment-specific idiosyncracies[2]. We therefore chose not to a priori specify minimum and toxic Na thresholds in our study but use an alternative macro-ecological approach to examine whether patterns of plant-Na availability improve our capacity to predict natural large-herbivore density across sub-Saharan Africa. Which species, if any, are most affected and in which places?

We collated 1,170 density observations for 64 terrestrial large-herbivore species (body mass: 2–4,100 kg) from 123 protected areas across sub-Saharan Africa[27] (Supplementary Fig. 8) and based on the framework of Santini et al.[24] used generalized additive mixed models (GAMMs) to predict density from relevant environmental, anthropogenic and functional-trait covariates (Supplementary Tables 4 and 5). On the basis of identified nonlinear relationships in the

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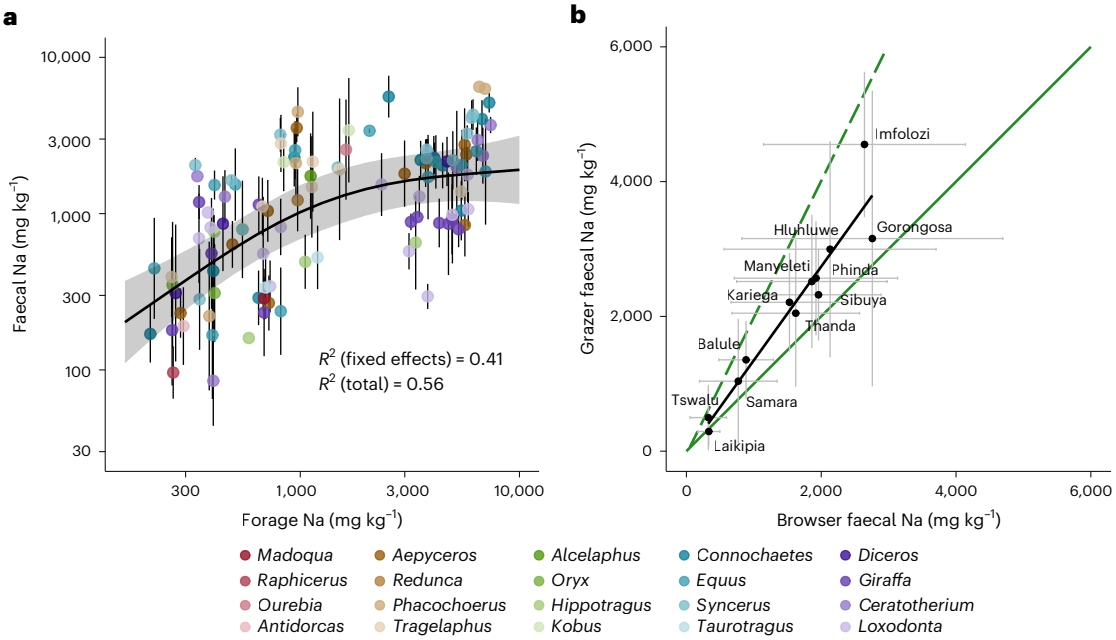


Fig. 2 | Herbivore Na intake as a function of plant Na gradients. a, Relationship between modelled dietary forage Na concentration and field-measured herbivore faecal Na concentration (here, using the selective foraging scenario; see Extended Data Fig. 5 for qualitatively equivalent results based on the unselective scenario). Points and vertical error bars represent the mean ± 1 s.d. faecal Na concentration per genus per protected area. The total number of independent points is n = 111 from 20 genera across 20 protected areas. Note that axes are on $\log_{10}$ scales to highlight low Na values. The black line represents the fit of a generalized additive mixed-effects model with genus included as a random effect. The marginal R^2 (fixed effects) denotes the proportion of variance explained by dietary Na. **b**, Relationship between mean browser and grazer faecal Na concentrations at 12 wildlife reserves in eastern and southern Africa. Species are categorized as grazers if their diet consists of >50% C_4 and browsers otherwise. Points and vertical error bars represent the mean ± 1 s.d. The solid green line shows a proportional (1:1) relationship between grazers and browsers. All means fall above this line, denoting higher faecal Na in grazers relative to browsers. The dashed line shows a slope of 2, in which grazers show faecal Na concentrations twice those of browsers. Overall, grazers had 1.35-fold (s.d. = 0.22) higher faecal Na concentration than browsers (solid black line).

literature, we also included interactive effects between body mass and selected covariates (for example, forage seasonality[41] and hunting pressure[42]). We first built a base GAMM without the inclusion of Na availability. To ensure the absence of spatial autocorrelation and check model performance of this base model, we calculated Moran's *I* statistic and undertook spatial-block, taxonomic-block and random-block cross-validation (see Supplementary Table 6, Supplementary Figs. 9 and 10, and Supplementary Text 2 for analysis and discussion of model robustness). We then separately included dietary Na concentrations from the unselective and selective foraging scenarios as an additional predictor and observed whether model performance improved based on marginal R^2 and Akaike information criterion corrected for small sample sizes (AICc). As larger animals may be more vulnerable to Na deficiencies[5,21], we also considered model variants with the inclusion of Na availability as an interactive effect with body mass.

The best-fitting GAMM included dietary Na from the selective scenario as an interactive term with body mass (Table 2), supporting the hypothesis of Na constraints for sub-Saharan African herbivores that are non-uniform across body sizes[5]. This model explained ~1.5% more of the variation in fixed effects than the base model, accounting for 38% of the total variation (conditional R^2), with fixed effects explaining 16% (marginal R^2) (see Extended Data Fig. 6 and Supplementary Table 7 for full model results). Body mass accounted for the largest proportion of the variance explained by fixed effects (14.6%), with environmental factors (forage seasonality (12.2%), forage quality (9.9%) and distance to water (8.4%)) ranking as the second, fourth and fifth most important variables, respectively. The human development index was the highest ranked anthropogenic factor (third; 11.4%), with hunting pressure ranked sixth (7.2%). Diet Na concentration was the eighth most important variable explaining 5.3% of the variance by fixed effects (Fig. 3a).

Inspection of partial dependence plots revealed logical outcomes that aligned with previous efforts to model large-herbivore densities[24,26]. For example, large-herbivore density decreased with lower forage availability, lower forage quality, lower habitat preference, increased seasonality (particularly for herbivores within the body mass range of 50–500 kg) and increased distance from water sources (Extended Data Fig. 6). The partial dependence plot for dietary Na availability revealed that large-herbivore density decreases in very-high-Na environments across all body sizes, and also in low-Na environments for large-herbivore species >1,000 kg (megaherbivores; Fig. 3c). Interestingly, the highest density for smaller-bodied herbivores occurred in low-Na environments in which megaherbivore density was reduced, possibly indicating second-order effects mediated by competition with megaherbivores.

To ensure that the result of Na constraints on megaherbivores was robust, we repeated the above analysis using density observations for megaherbivores only. The best megaherbivore-only model included dietary Na from the unselective scenario (Table 2), potentially reflecting their less selective feeding habits[43], and explained 50% of the variation (conditional R^2), with fixed effects explaining 28% (marginal R^2) (see Extended Data Fig. 7 and Supplementary Table 8 for full model results). Total forage availability was the most important fixed-effect variable (49.2%) with dietary Na availability second (13.9%), aligning with results assessing drivers of insect abundance in North America[44]. The dietary Na partial dependence plot for the megaherbivore-only model confirmed the result of the all-herbivore model, indicating that lower megaherbivore densities are associated with threshold diet Na concentration values < 100 mg kg^{-1} and >1,000 mg kg^{-1} (Fig. 3d).

To examine where low concentrations of plant Na may constrain natural megaherbivore densities, we spatially mapped where dietary Na concentration falls <100 mg kg^{-1} for elephants (*Loxodonta* spp.),

Table 2 | Comparison of model performance for GAMMs predicting large-herbivore density across Africa

Dataset	Model framework	Conditional R^2	Marginal R^2	Model AICc
All herbivores (n=1,170)	Base GAMM	0.370	0.143	2,616.2
	Base GAMM+s(Diet_Na_unselective)	0.373	0.137	2,613.1
	Base GAMM+s(Diet_Na_selective)	0.373	0.150	2,611.9
	Base GAMM+te(Diet_Na_unselective, body mass)	0.374	0.144	2,610.4
	Base GAMM+te(Diet_Na_selective, body mass)	**0.376**	**0.156**	**2,604.4**
Megaherbivores only (n=135)	Base GAMM	0.488	0.241	292.9
	Base GAMM+s(Diet_Na_unselective)	**0.501**	**0.276**	**289.6**
	Base GAMM+s(Diet_Na_selective)	0.494	0.251	292.6

We first generated a base model using all covariates listed in Supplementary Table 5, and then determined whether the inclusion of unselective or selective dietary sodium availability improved model performance based on marginal R^2 and AICc. Following ref. 81, we considered an improvement if δ AICc was >2. As larger animals may be more vulnerable to sodium deficiencies[5], we also considered model variants with the inclusion of sodium availability as a tensor product with body mass. To confirm our result that Na constrains megaherbivore density, we repeated the above analysis but for megaherbivore species only (elephant, giraffe, black rhino and white rhino). The best models in each case are in bold.

giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*) and white rhino (*Ceratotherium simum*) across their historical (pre-colonial) range[45]. We found that Na limitation appears to primarily constrain megaherbivores through the northern parts of Central and West Africa (Fig. 4). Notably, this area has been identified as having scarce or 'missing' megaherbivores, with populations of elephants, giraffe and black rhino occurring at lower densities than expected based on available primary productivity[46,47].

Discussion

Sub-Saharan Africa is characterized by extreme gradients of Na availability, with empirical measurements of plant Na concentration spanning four orders of magnitude (10–85,000 mg kg^{-1}). In general, we found that Na availability is low for wild herbivores compared with values considered optimal for domestic livestock production[4,48] (>500 mg kg^{-1}), with 55–90% of the land area showing foliar concentrations <500 mg kg^{-1}, depending on the functional group and feeding scenario considered (Table 1). However, low Na availability does not appear to substantially limit the abundance of most herbivore species weighing <1,000 kg (Fig. 3c). These populations either (1) are not Na deficient, (2) are able to compensate for any deficits by using alternative Na sources (for example, geophagy[23]) or (3) are predominately limited by other factors (for example, predation, competition[26,27,31,46]). Instead, our results are congruent with the hypothesis[5] that the largest-bodied herbivores (for example, elephants, rhino, giraffe) are most vulnerable to Na deficits in low-Na environments (Supplementary Fig. 1). Na limitation is probably to be most pronounced for pregnant or lactating females, as their Na requirements increase by >2× during gestation and lactation[5]. In the absence of sufficient Na intake, physiological consequences, such as impaired protein and energy metabolism[4], may lead to reduced survival, reproduction and population growth[3,15]. Our results also indicate that large herbivores of all body sizes may be limited in very-high-Na environments (>3,000 mg Na kg^{-1}), such as near coastal areas or arid environments (Figs. 1 and 3c). In these landscapes, chronically high Na intake, potentially combined with reduced water availability, may cause physiological stress (for example, hypertension) and premature death[21,35].

We found that Na constraints on megaherbivore densities were greatest in parts of Central and West Africa, which showed some of the lowest plant Na concentrations (30–100 mg kg^{-1}; Fig. 1), owing to low Na input rates and high levels of leaching (Supplementary Fig. 2). We hypothesize that Na limitation is an additional mechanism contributing to scarce or 'missing' megaherbivores in this region, which has previously been ascribed to overhunting and/or infertile soils[27,46,49]. Similarly, our results potentially help explain the curious absence of perissodactyls (odd-toed ungulates) from the same region[47] (Fig. 4). There are no records of zebras or hipparions (an extinct genus of horse) in West Africa, while black rhino density is particularly sparse. Na limitation offers a plausible explanation; equids use Na-costly sweating to thermoregulate more than other ungulates[50], while black rhino have unusually high endogenous faecal losses of Na[39]. Disproportionately high Na requirements (megaherbivores) and losses (perissodactyls) could result in substantial Na deficits, thereby constraining their geographical distribution and density. Although low-Na availability is probably not singularly responsible for the scarcity of megaherbivores and perissodactyls in West Africa, it may work in conjunction with other previously considered anthropogenic or environmental stressors: Na shortage may predispose these species to low abundance, making populations more susceptible to extirpation from factors such as hunting or landscape fragmentation that impede herbivore movement towards sites of high mineral resources (for example, salt licks[11,23]).

Our results extend previous research assessing how broad-scale variation in Na availability influences animal populations, much of which has relied on simple proxies of Na availability (for example, sea-salt deposition[8,33]) and concentrated on invertebrates (for example, refs. 12–14,33). Previous studies in mammals have only examined localized impacts (for example, altered movement patterns[17,18,23]). The plant Na concentration maps generated here show that inland hotspots of Na associated with hydrology, soil chemistry and climatic factors are found to be critically important sources of animal mineral nutrition. Contrary to some previous results[10], we also found a local effect of plant photosynthetic pathway (C_3 versus C_4) on gradients of foliar Na concentration. Our extensive faecal data further show that variations of plant-Na availability shape herbivore Na intake, and that diet type (C_4 grazer versus C_3 browser) modifies Na intake by up to a factor of two. Our finding that Na deficits are strong enough to influence herbivore community structure at the continental scale, with particularly strong constraints on megaherbivore abundance, provides empirical support for recent theoretical predictions[5], while also identifying Na-poor areas where such effects appear most influential.

Our methodological approach did, however, incur a number of limitations. For example, there are large areas of sub-Saharan Africa (41%) that are >500 km from the nearest observation in our training data used to generate our foliar Na predictions (Extended Data Fig. 2 and Supplementary Fig. 7a). Similarly, our field data span several decades and are derived from various field campaigns and analysed using different laboratories, while the time span of covariates used to predict foliar Na and herbivore density did not always perfectly align with when observations were collected. Partial dependence plots across models are found to be generally consistent with logical expectations; nevertheless, future mapping efforts will benefit from the addition of new and higher-resolution data that represent a broader area, while assessment of intra- and interannual variations may reveal the effects of CO_2-induced nurient dilution on foliar Na concentrations[51].

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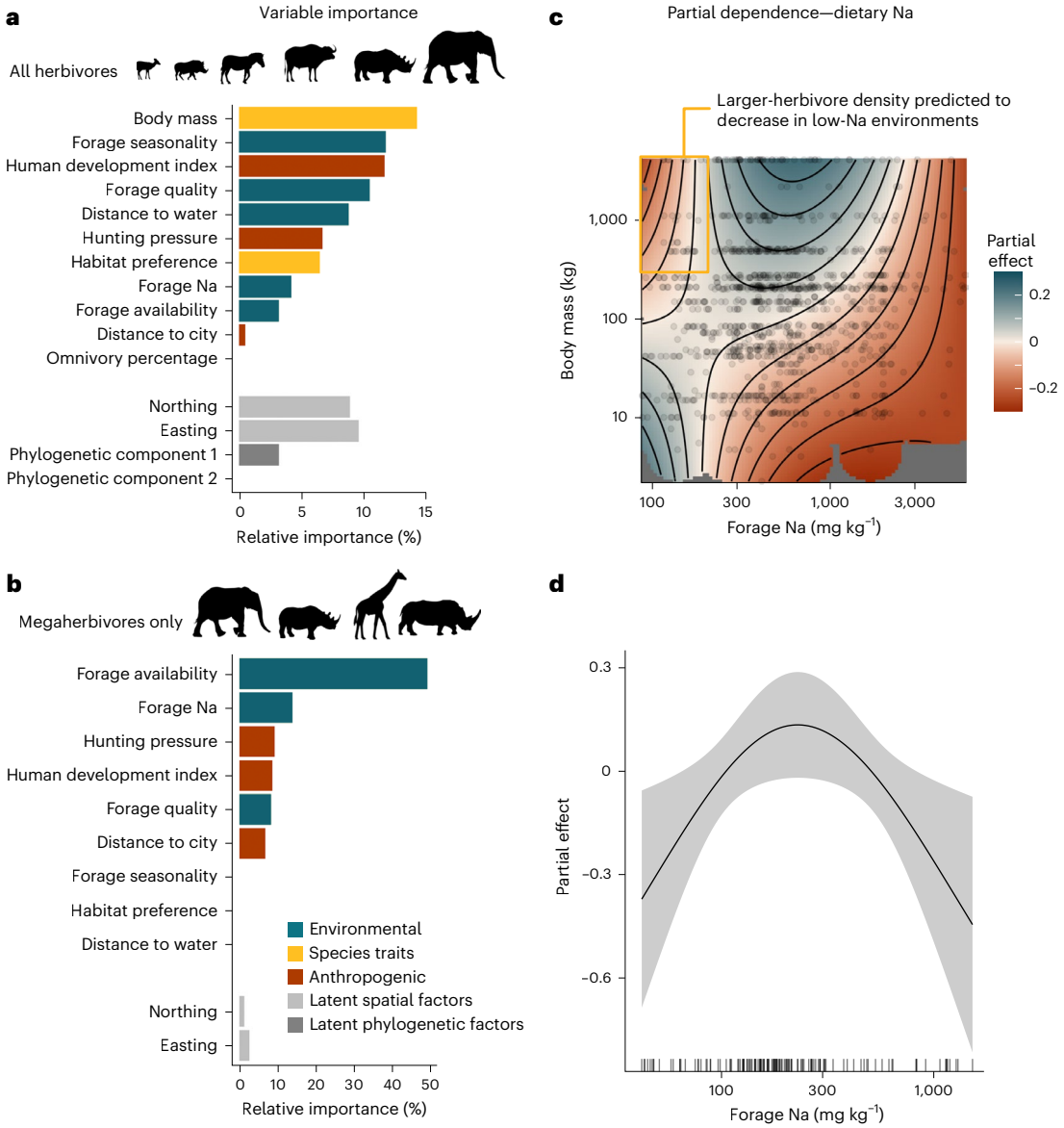


Fig. 3 | Evidence that Na constrains megaherbivore densities. a,**b**, Relative importance of fixed-effect variables included in GAMMs predicting large-herbivore densities across sub-Saharan Africa using all herbivore density observations (**a**) and observations for megaherbivore species only (**b**). The best all-herbivore model included dietary Na concentration (selective foraging scenario) as an interactive effect with body mass, while the best megaherbivore-only model included dietary Na concentration (unselective foraging scenario). **c**, The partial dependence plot of dietary Na in the all-herbivore model revealed that large-herbivore density decreased (brown areas) in high-Na environments across all body sizes, and also in low-Na environments for herbivore species >1,000 kg (megaherbivores). **d**, The megaherbivore-only model confirmed this result, indicating that lower megaherbivore densities are associated with threshold diet Na concentration values < 100 mg kg^{-1} and >1,000 mg kg^{-1}. The shaded area in **d** represents the 95% CI. Silhouettes from PhyloPic under a Creative Commons license CC0 1.0: duiker, Robert Hering; wart-hog, black rhino and elephant, Steven Traver; hartebeest, Lisa Nicvert; buffalo and giraffe, Jody Taylor; white rhino, Christophe Mallet; map elements created with Natural Earth (https://www.naturalearthdata.com).

Our faecal data were positively correlated with forage Na availability, yet even in low-Na environments, some faecal samples showed high Na values (>1,000 mg kg^{-1}) suggestive of alternative Na sources for large herbivores (for example, geophagy, osteophagy, omnivory[23,52,53]). Our modelled estimates of herbivore density do not include the availability of these alternative Na sources as spatial and chemical information was not available across sites, but see Supplementary Text 3 for further discussion on how this may influence results. Furthermore, we do not include species-specific differences in Na requirement as they are essentially unknown. Body mass is one known covariate[5], with the estimated Na requirement scaling to the power of 0.91, but there is considerable variation in this relationship (95% confidence interval (CI) of the scaling exponent: 0.80–1.00) some of which is undoubtedly explained by other physiological factors (for example, high sweating rates in equids[50]) that influence Na needs and conservation. Adding these factors, as well as others (for example, wildlife management histories, species-specific hunting pressure; Supplementary Text 2), may help improve the relationships between dietary Na and both faecal Na concentration and large-herbivore density.

Given the enormous influence of large animals on ecological processes[54,55], the constraints imposed by Na availability on megaherbivore density shown here are likely to have wide-ranging ecological ramifications[54,55]. Megaherbivores have unique functional roles in ecosystems arising from biomass consumption, ecosystem engineering (for example, soil compaction, tree toppling, fire dynamics) and long-distance dispersal of seeds and nutrients[56,57], including Na[8]. While our results suggest that meso-herbivores occur at higher densities in areas where megaherbivores are Na limited, meso-herbivores

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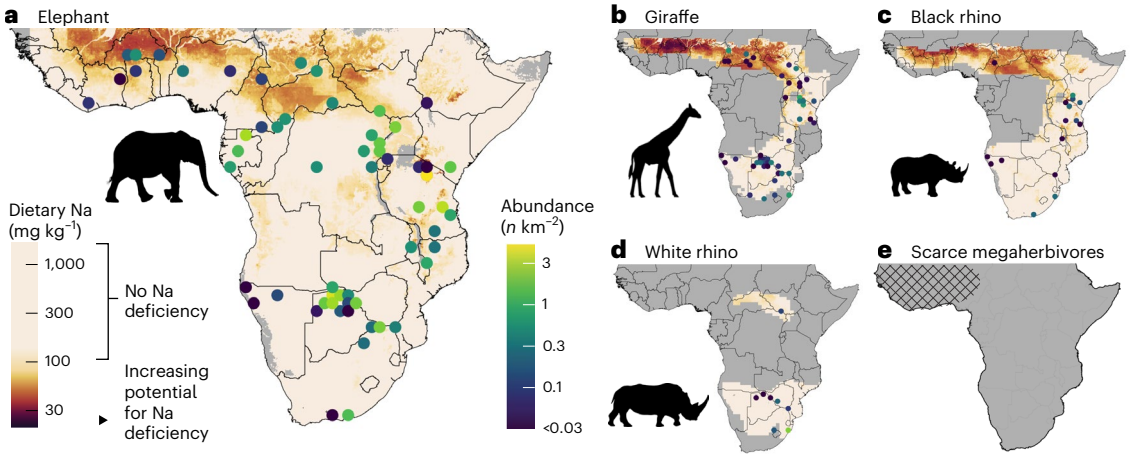


Fig. 4 | Na as a constraint on megaherbivore density across sub-Saharan Africa. **a**–**d**, Spatial mapping of areas where dietary Na concentrations fall below the threshold of 100 mg kg^{-1} for megaherbivore species: elephants (**a**), giraffe (**b**), black rhino (**c**) and white rhino (**d**) across their pre-colonial era range[45]. Below this threshold value, colours are increasingly darkened to reflect the increasing potential of Na acting as a constraint on megaherbivore density. Overlain are megaherbivore densities obtained from census measurements[27]. Note: both the dietary Na concentrations (mg kg^{-1}) and megaherbivore density (n km^{-2}) legends are plotted on a $\log_{10}$ scale to highlight regions where low plant Na constrains megaherbivore abundance. **e**, Geographical region of scarce or 'missing' megaherbivores as denoted by refs. 46,47. Silhouettes from PhyloPic under a Creative Commons license CC0 1.0: black rhino and elephant, Steven Traver; giraffe, Jody Taylor; white rhino, Christophe Mallet; map elements created with Natural Earth (https://www.naturalearthdata.com).

generally do not compensate for lost ecological functions[55]. Given the extinction and ongoing decline of many megaherbivore species over the last 50,000 years[55], our results indicate that the geography of Na may have had a central role in shaping large-herbivore populations and ecosystems of the past[8].

Today, humans have substantially shifted the natural patterns of Na availability through the anthropogenic salt cycle[58], which may similarly affect ecosystem processes at broad scales through influence on herbivore populations. For example, the direct supply of Na to ecosystems through boreholes[18], artificial salt licks[11], road salting[13], mining and other industrial activities[59] may enable higher herbivore population densities in certain Na-poor areas with unintended consequences for ecosystem integrity[11]. By contrast, the erection of barriers (for example, fences) may limit access to Na resources and thus amplify Na constraints on large herbivores. Because sea-salt aerosol deposition was an important predictor of foliar Na concentration (Supplementary Fig. 4), impacts of climate change, which are altering wind and rainfall patterns globally, may also modify Na ecosystem inputs[60], alleviating deficiencies in some places and creating toxicity in others. Likewise, increasing global temperatures may alter herbivore Na requirements (via heat stress and thermoregulatory costs[4]), while loss of large herbivores may lead to losses of allochthonous Na inputs[8] or diluted foliar concentrations due to a greater accumulation of uneaten vegetation biomass[51]. Such changes may have critical knock-on effects for large-herbivore movement patterns, ecosystem impacts and human–wildlife conflict. In the context of global change, past and present, the relationship between large herbivores and salt warrants much more attention.

Methods

Foliar sodium concentration data

We collated data on foliar Na concentration from available literature sources by systematically reviewing relevant papers in Web of Science and Google Scholar using combinations of the following keywords: [sodium, Na, concentration, plant, foliar, Africa] through June 2021 (n = 596 observations from 16 studies). We also collated unpublished data from field collections (n = 4,023 observations from 18 field campaigns; https://figshare.com/s/166a498424860b2fbd8a?file=53037215). All measurements were categorized as belonging to either the C_3 or C_4 plant functional group based on ref. 61. In most cases, we obtained the raw data (that is, one measurement per observation). However, in some circumstances (24 out of 289 locations), the data had already been pooled and only a mean value was available. As we wanted to maximize data inclusion and incorporate sites from across as much of the environmental space in sub-Saharan Africa as possible, in these instances, we randomly generated plant Na concentration values using the mean value obtained and the associated number of observations (see Supplementary Text 1 for details). Our final dataset comprised 4,258 measurements of foliar Na concentration. Of these, 2,768 observations (65%) were raw data, 1,490 observations (35%) were from simulated data, 2,857 (67%) observations were from plants using the C_4 photosynthetic pathway and 1,401 (33%) observations were from plants using the C_3 photosynthetic pathway. We then grouped measurements for each photosynthetic pathway group into 0.1° grid cells (~121 km^2), which resulted in 289 geographically distinct pooled grid-cell measurements (119 C_3 and 170 C_4). We recognize that our 0.1° groupings do not capture fine-scale foliar Na concentration gradients[3] and may contain phylogenetic[10,62] and seasonal[37,63–65] and interannual signals, reflecting an inevitable trade-off between spatial and temporal extent and grain in macro-ecological studies. Nevertheless, we believe that the exceptional scale and depth of this dataset make it a robust basis for assessing continental-scale spatial patterns of foliar Na.

Modelling foliar sodium concentration patterns

To estimate median (unselective foraging) and 95th percentile (selective foraging) foliar Na concentrations across sub-Saharan Africa, we used an ensemble of predictive machine-learning techniques commonly used for mapping nutrient concentrations across large scales[66,67]. For each of our 289 distinct geographical locations, we extracted the mean values of 11 predictor variables that have been suggested to impact foliar Na concentration at 0.1° resolution: sea-salt aerosol deposition, rock Na weathering rate, percentage of alluvial soil, height above nearest drainage, aridity, percentage of clay soil, soil cation exchange capacity, soil Na concentration, soil K concentration, soil pH and net primary productivity[3,6,8,10]. Supplementary Table 1 summarizes the datasets used, and Supplementary Text 1 provides details on how we generated three predictors (sea-salt aerosol deposition, Na rock weathering and net primary productivity), specifically for this study.

Using R statistical software version 4.3.1, we built five separate machine-learning models using the 'caret' package[68]: gradient boosting[69] ('gbm'), random forest[70] ('rf'), neural network[71] ('nnet'), support vector machine[72] ('svmRadial') and cubist[68] ('cubist'). To account for varying degrees of confidence in our calculation of the median and 95th percentile foliar Na concentration for each grid cell (the total number of foliar samples collated within grid cells ranged from 1 to 785), individual training points were weighted using $\log_{10}+1$ of the total number of samples collected within that grid cell (that is, cells in which we are more confident of the median and 95th percentile foliar Na concentration due to greater sample size were weighted more strongly in the model). To optimize each machine-learning model, we defined a hyper-parameter grid (see Supplementary Table 2 for the range of parameters). The parameter set that generated the lowest RMSE from a tenfold repeated cross-validation was selected as the final ('best') model for each machine-learning technique. We also trained a generalized linear model on the outputs of the five separate machine-learning models using the functions 'caretList' and 'caretStack' within the 'caret' package to build an ensemble model.

Ploton et al.[73] highlighted that the predictive capacity of some large-scale ecological mapping efforts has been exaggerated owing to spatial autocorrelation between the training and test datasets. We therefore performed a buffered leave-one-out cross-validation (BLOOCV; that is, we removed training points proximate to the test observation and re-ran models) to assess the performance of our five machine-learning models and ensemble model with sequentially increasing buffer sizes. As previous studies have used distance from the coast as a proxy for Na input[8,52], we also included a simple linear model using this predictor and a purely spatial model based on a kernel smooth between geographical points to assess if the machine-learning models presented here are better than current practice. Supplementary Fig. 3 provides the workflow for how we implemented our BLOOCV. Selecting the predictive model with the lowest RMSE from our BLOOCV, we then predicted median and 95th percentile foliar Na concentrations for C_3 and C_4 plants across sub-Saharan Africa (<15°N)[74].

Foliar sodium concentration and herbivore sodium intake

To evaluate the extent to which foliar Na concentration influences Na intake by large herbivores across sub-Saharan Africa, we assessed Na concentration in the faeces of wild mammal herbivores (>2 kg). Ideally, obtaining information from both urinary and faecal excretion pathways is preferred. However, collecting uncontaminated urine from wild large mammals is extremely difficult[23], so we focus our assessment on faeces only. Several studies have shown that faecal Na concentration correlates with Na intake[36–40]. There is a paucity of large-herbivore faecal samples analysed for Na in published literature sources covering sub-Saharan Africa. Consequently, we combined the scant data (n = 319; 6 species) found using the search terms ['sodium', 'Africa', 'faeces', 'feces'] in Google Scholar and Web of Science (June 2022) with unpublished data from previous field studies (146 samples from Laikipia, 1998–2000; 75 samples from Hluhluwe–Imfolozi Game Reserve, 2018; and 86 samples from Gorangosa National Park, 2021–2022) and our own specific field campaign (n = 730; Supplementary Table 3). All unpublished data represented samples of fresh dung from one individual animal and were analysed using either an inductively coupled plasma optical emission spectrometer or an inductively coupled plasma mass spectrometer (see Supplementary Text 1 for details). In total, we collated 1,356 geolocated faecal Na concentration values from 28 herbivore species across 20 wildlife reserves spanning ~4,000 km from equatorial Kenya to the Eastern Cape of South Africa.

To assess the relationship between predicted dietary Na intake and field-measured faecal Na concentration, we first determined the percentage of C_3 and C_4 plants in the diets of large-herbivore species (Artiodactyla, Perissodactyla, Proboscidea) in sub-Saharan Africa for which we had observations using data from the literature (Supplementary Table 4). We then extracted the corresponding geographical median and 95th percentile foliar Na concentration estimates for both C_3 and C_4 functional groups at the location of each individual faecal sample. From this, we estimated the unselective and selective dietary Na concentrations for each species i at each site s as:

$$\text{Forage_Na}_{i,s} = (D_{C3_i} \times C_{C3_s}) + (D_{C4_i} \times C_{C4_s}) \quad (1)$$

where D_{C3_i} and D_{C4_i} are, respectively, the measured mean percentages of C_3 and C_4 plants in the diet of species i and C_{C3_s} and C_{C4_s} are, respectively, the modelled Na concentrations of C_3 and C_4 plants at site s (using the median Na concentration for the unselective scenario and the 95th percentile for the selective scenario). Mean faecal Na was calculated per species and protected area to avoid pseudo-replication. We then fitted a GAMM using the 'mgcv' package[75], including diet Na as a fixed effect for the unselective and selective scenarios separately, with genus included as a random effect. A strong positive relationship between diet Na and faecal Na would indicate that forage Na availability is the primary determinant of herbivore Na intake, and is not masked by alternative sources of Na (for example, geophagy).

Modelling sodium availability and herbivore density

To assess the potential effect of Na constraints on natural large-herbivore density, we obtained large-herbivore density data from ref. 27, which collated census records for protected areas across sub-Saharan Africa, and filtered these to retain those records that appear to best reflect intact herbivore populations in these reserves (for example, by omitting periods known to have been affected by poaching- or drought-induced population crashes[27]). Repeat censuses within a reserve were averaged, yielding 1,119 records from 64 wild mammalian herbivore species across 123 protected areas (Supplementary Fig. 8); *Hippopotamus amphibius* was removed from the database as this species is semiaquatic. These data provide an approximation of variation in natural species-level densities across sub-Saharan Africa, but unavoidably include prevailing anthropogenic (for example, management strategies and poaching) and natural (for example, predation, disease, interspecific competition and climatic cycles) influences that we could not directly control for. As herbivore density data were right skewed (a universal pattern in species abundance distributions), we $\log_{10}$ transformed values to satisfy assumptions of data normality[76].

Few species had sufficient data to develop species-specific statistical models. Accordingly, we followed methods of Santini et al.[24]—with modifications outlined below—to develop a cross-species model based on species traits and environmental conditions. Specifically, we used GAMMs with spatially explicit environmental covariates as proxies for resource quantity, quality and variability (see Supplementary Table 5 for covariate details and sources). To account for prevailing anthropic factors, we considered eight potential proxies related to human accessibility, hunting motivation, protection of large-herbivore species and broader anthropogenic ecosystem modifications (Supplementary Text 1). There was, however, substantial correlation between some factors; we therefore focused on three covariates which maximized the various axes of potential human impact on large-herbivore density: distance to nearest city, human development index and hunting pressure. To account for differences in historical and socio-economic factors not captured by these anthropogenic fixed effects, we also included region (west, central, east and southern Africa) as a random effect. All environmental and anthropic data were extracted using QGIS 3.20.3. In addition, we included three species traits that are known correlates of local herbivore density[24,27,31]: body mass, omnivory percentage, habitat preference (a categorical variable with three levels from ref. 27 and applied to the vegetation map of ref. 77). To control for potential phylogenetic non-independence of our estimates, we followed Santini et al.[24] by conducting a principal component analysis on the phylogenetic distance

matrix of Abraham et al.[57] and extracting the first two eigenvectors (PC1 and PC2), which accounted for >92% of total variance. To control for potential spatial autocorrelation in model residuals, we updated methods used by Santini et al.[24] and used a soap-film smoother[78] to include bounded latitude and longitude variables as latent geographical factors not already being taken into consideration. Finally, to control for potential bias arising from uneven numbers of records among species, we included species identity as a random intercept[24]. Details of all environmental, anthropic and species-trait covariates used are provided in Supplementary Text 1 and Supplementary Tables 4 and 5.

We then compared GAMMs with and without the inclusion of Na availability. We used the 'bam' function from the 'mgcv' package[75] and fit smoothing splines, or nonlinear functions, to all continuous variables. On the basis of identified relationships in the literature, we also included interactive effects between body mass and resource seasonality[41] and hunting pressure[42] using a tensor product (Supplementary Table 5). We used three knots (k) to prevent model overfitting, except for body mass and forage availability ($k = 4$), which are known to have more complex relationships[24,26]. We set λ to a high value equal to 1 to further reduce the complexity of smoothing splines[79]. Redundant terms were removed using the 'select = TRUE' automated doubled penalty procedure[80]. To evaluate whether the inclusion of Na availability improves model performance, we separately included dietary Na availability under the unselective and selective scenarios as an additional fixed effect. We calculated dietary Na availability for each species in each grid cell using equation (1) and associated foliar Na concentration maps. As larger animals may be more vulnerable to sodium deficiencies[5], we also considered model variants with the inclusion of diet Na as a tensor product with body mass. We assessed model performance using marginal R^2 and AICc, considering an improvement if δ AICc was >2 (ref. 81; Table 2).

Our analysis revealed that including dietary Na as an interative effect with body mass produced the best model, with species >1,000 kg being most constrained in low-Na environments. Consequently, we repeated the above analysis for a model specifically trained on observations from megaherbivore species only (*Loxodonta* spp., *G. camelopardalis*, *D. bicornis* and *C. simum*). As we focused on large species only, we simplified the model by removing variables and interactions related to body mass, and also omnivory as there was no variation in this predictor. Comparable effects of dietary Na between models would provide further confidence in our result that Na potentially constrains megaherbivore density. To ensure that our best all-herbivore and megaherbivore models were robust, we checked model residuals[82], assessed pairwise concurvity (a measure of co-linearity in GAMMs, where values > 0.8 should be treated with caution owing to reduced interpretability[79]) and spatial autocorrelation by fitting a variogram and calculating Moran's I statistic. To ensure that our models were not overfit, we also undertook spatial-block, taxonomic-block and random-block cross-validation using the 'spatialsample' package[83]. In all cases, our best models were sufficiently robust in our examination and did not have spatial autocorrelation (see Supplementary Text 3 for discussion of model robustness).

For the best all-herbivore and megaherbivore-only models, we assessed the relative importance of each predictor by partitioning the variance explained across predictors. Following Santini et al.[24], we estimated the square correlation coefficient between the prediction of a model with one variable randomized and the actual observed data. Each of these estimates was subtracted from the full variance explained, to estimate the relative importance of each variable. We repeated this process ten times and calculated a final mean relative importance, expressed as a percentage. We examined how different covariates impacted the final GAMMs by generating partial dependence plots[82]. Finally, to assess the extent to which dietary Na availability constrains megaherbivore density across their pre-colonial era range[45], we spatially mapped areas where dietary Na concentrations fall below 100 mg kg^{-1}, a threshold value predicted by our megaherbivore-only GAMM below which density decreases. As dietary Na concentration values decrease below this threshold, the potential for Na acting as a constraint on megaherbivore density increases.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data reported in this study are available via figshare at https://doi.org/10.6084/m9.figshare.25639080 (ref. 84). Source data are provided with this paper.

Code availability

All associated code generated in this study is available via figshare at https://doi.org/10.6084/m9.figshare.25639080 (ref. 84).

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Author contributions

A.J.A., C.E.D., T.P.-J., E.R.T. and M.B.J.H. developed and framed the research question. A.J.A., J.C., T.P.-J., A.B.W. and C.D. conducted fieldwork specifically for this project. A.B.W. and P.D.J. conducted laboratory analysis. A.J.A., G.P.H. and L.L.T. collated datasets required for this study. E.L.R., D.A., C.A.C., P.J.F., R.M.H., G.P.H., C.J., F.V.L., Y.M., A.M., N.N., N.O.-S., A.B.P., R.M.P., H.H.T.P., J.M.R., L.S., F.V.D.P., M.P.V. and J.-C.S. contributed data. A.J.A., C.M., M.C., E.S.D., T.P.-J. and C.R. performed statistical analysis. A.J.A. wrote the first draft of the paper, and all authors contributed substantially to revisions.

Competing interests

The authors declare no competing interests.

Additional information

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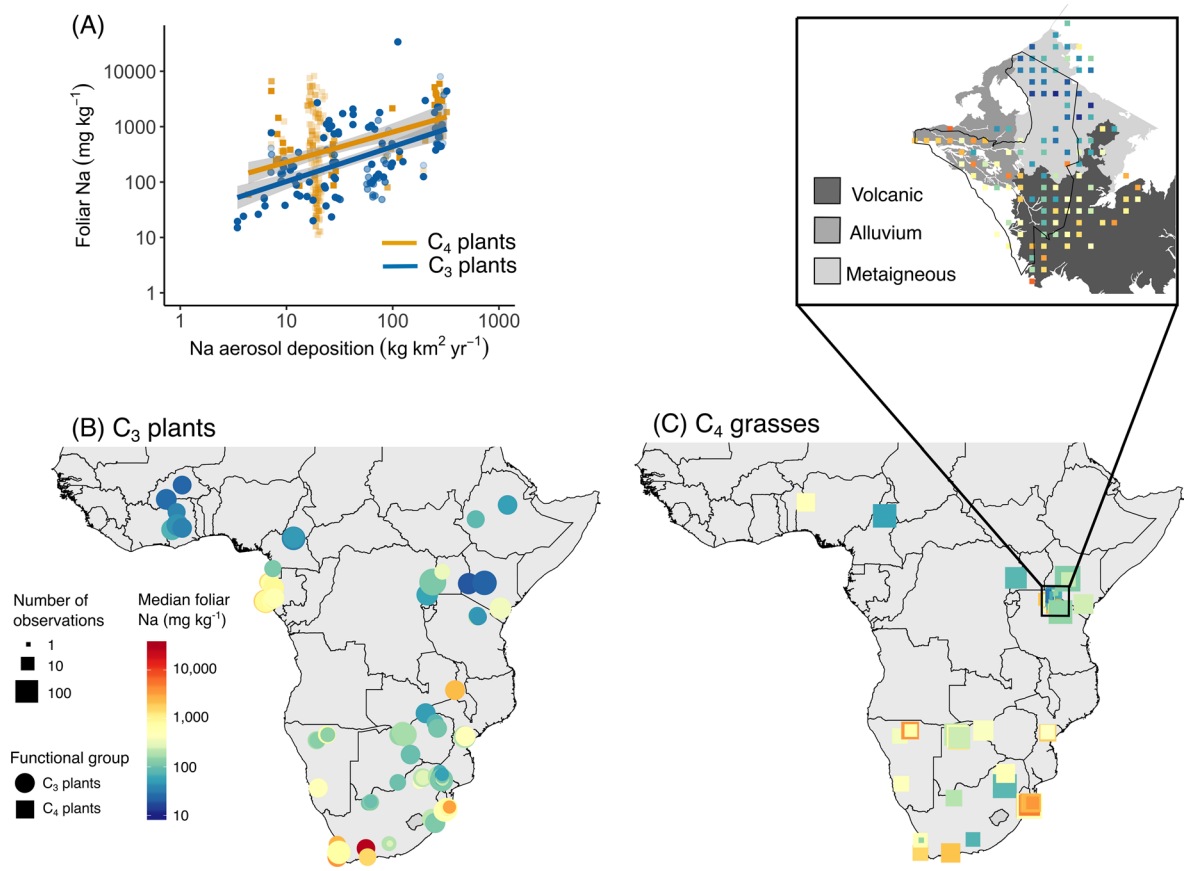
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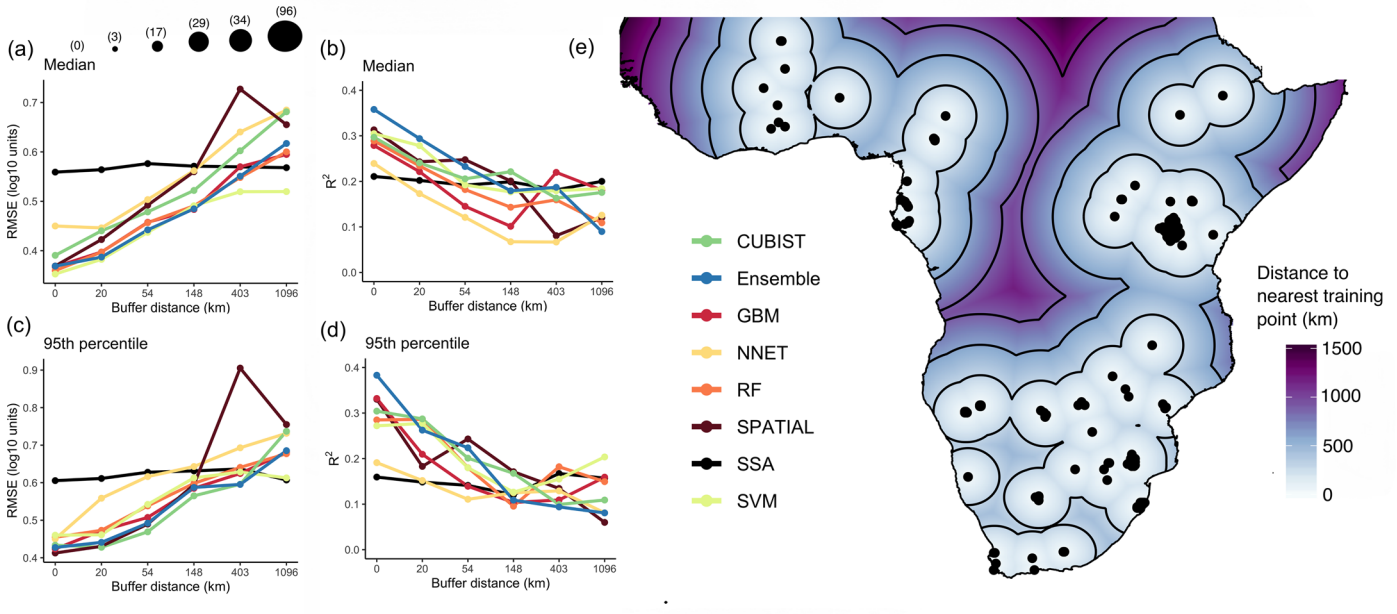
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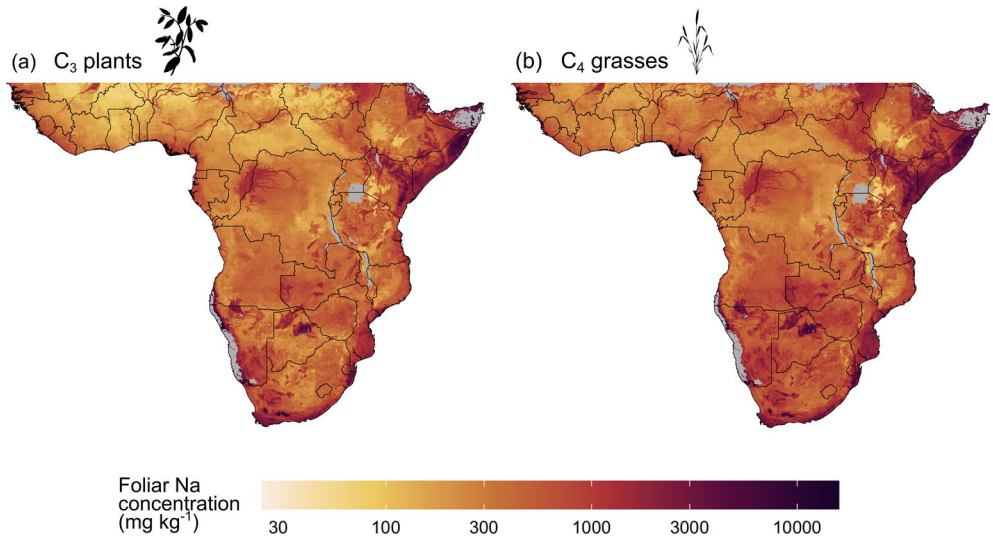
Extended Data Fig. 1 | Plant sodium (Na) concentrations across sub-Saharan Africa. (**A**) Relationship between median community foliar Na concentration and aerosol deposition (see Fig. S3b). Increased opacity of points represents an increased number of measurements recorded within the foliar community. Trend lines for C_3 and C_4 plant functional groups represent ordinary least squares fits weighted by the $\log_{10}+1$ number of measurements recorded within each community (cf. Figure 1). Error bars represent Standard Error. Median measured community foliar Na concentration for C_3 plants (**B**) and C_4 grasses (**C**) located across sub-Saharan Africa. The cluster of grass points in the Serengeti-Mara ecosystem is illustrated at higher spatial resolution for clarity. Map elements created with Natural Earth (https://www.naturalearthdata.com).

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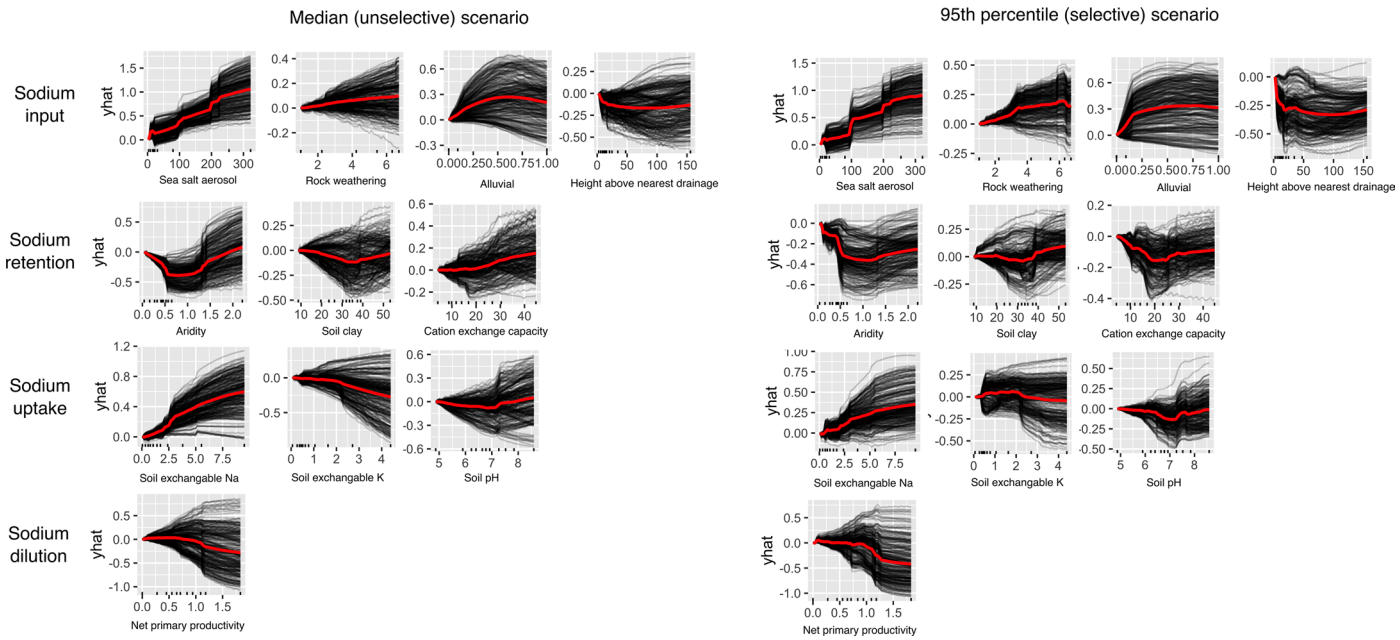
Extended Data Fig. 2 | Performance of machine learning models used to predict plant sodium (Na) concentrations across sub-Saharan Africa. Root mean squared error (RMSE) and R^2 model performance metrics of the buffered leave-one-out cross validation (BLOOCV) for (**a**, **b**) median and (**c**, **d**) 95th percentile foliar Na concentration prediction models. The black circles above the first graph represents the average number of training points removed from within each buffer distance. CUBIST = cubist model; GBM = Gradient boosted model; NNET = neural network model; RF = random forest model; SPATIAL = kernel smoothing model; SSA = sea salt aerosol model; SVM = support vector machine model. **e**) Spatial mapping of distance to the nearest training point across sub-Saharan Africa. Contour lines represent 300 km intervals. Map elements created with Natural Earth (https://www.naturalearthdata.com).

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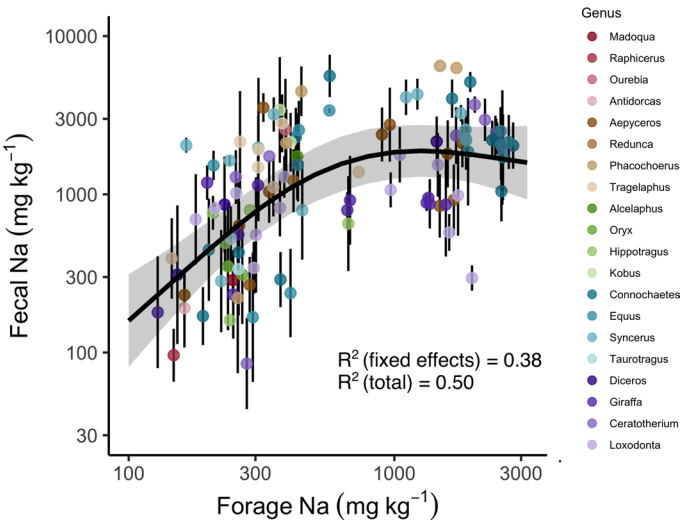
Extended Data Fig. 3 | Spatial mapping of 95th percentile plant foliar sodium (Na) concentration for (a) C_3 and (b) C_4 plant functional groups at a 0.1° resolution across sub-Saharan Africa. This is representative of plant Na availability to herbivores under a selective foraging scenario. To better visualise geographic patterns, concentrations have been plotted on a $\log_{10}$ scale. Silhouettes from PhyloPic under a Creative Commons license CC0 1.0: plant, T. Michael Keesey; grass, Mason McNair; map elements created with Natural Earth (https://www.naturalearthdata.com).

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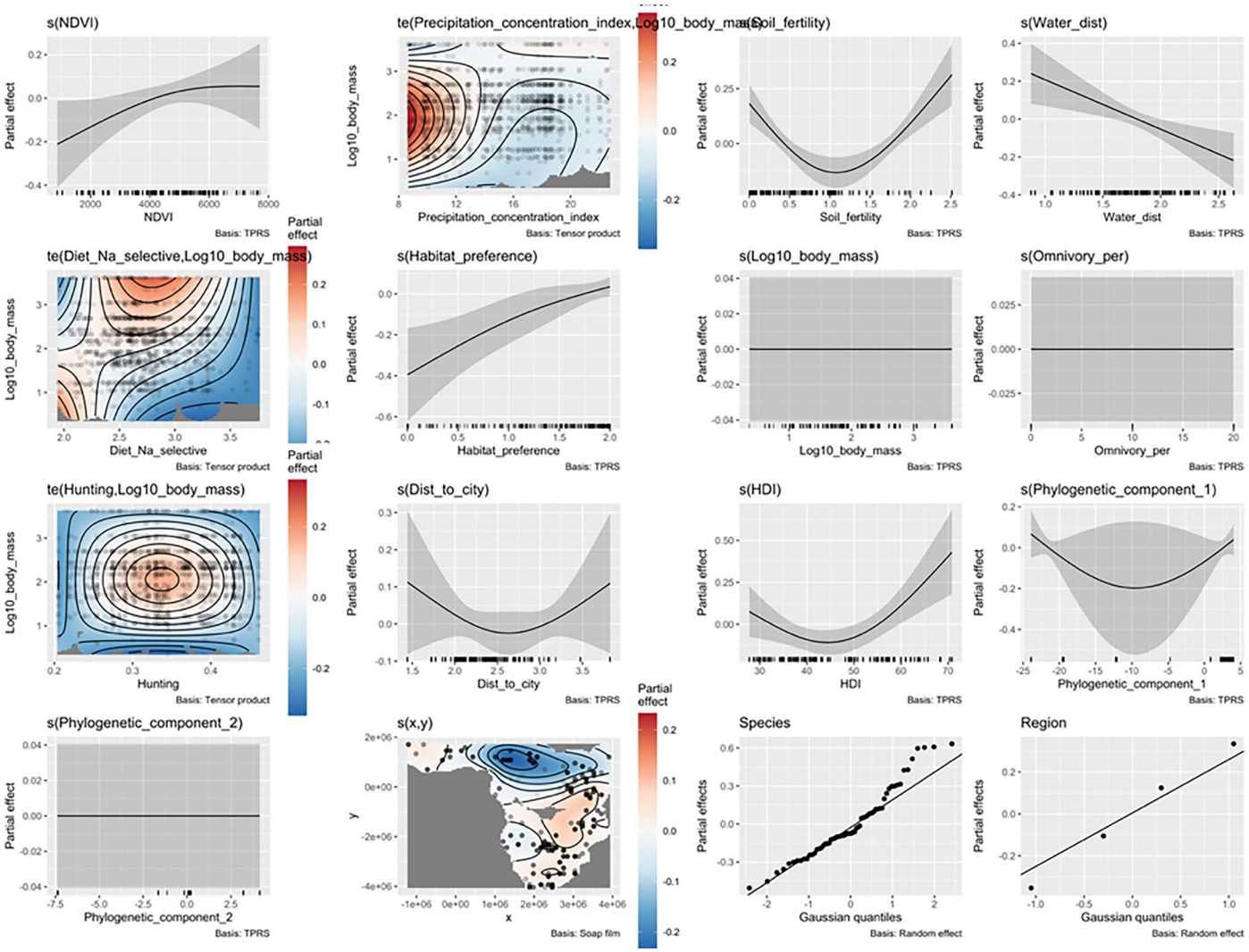
Extended Data Fig. 4 | Drivers of foliar sodium (Na) concentration across sub-Saharan Africa. Partial dependence plots for predicting foliar median (unselective foraging scenario) and 95th percentile (selective foraging scenario) sodium (Na) concentration using the ensemble model. The relationship between foliar Na concentration (yhat) and each variable is highlighted by the red line. Note: the scale for aridity is non-intuitive, with lower scores reflecting more arid environments.

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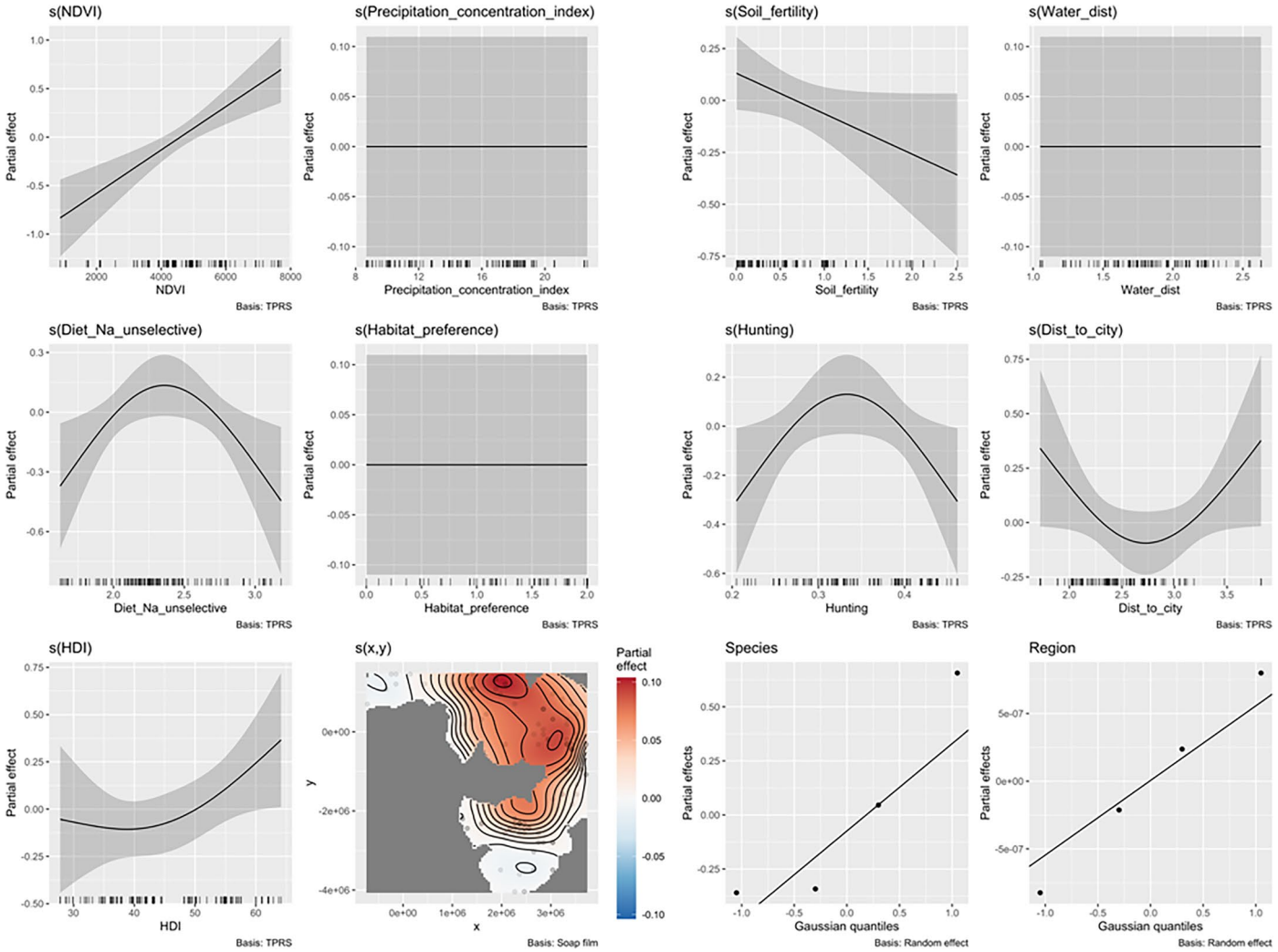
Extended Data Fig. 5 | Herbivore sodium (Na) intake as a function of plant Na gradients. Relationship between modelled dietary forage Na concentration and field-measured herbivore faecal Na concentration using the unselective foraging scenario. Points and vertical error bars represent the mean ± 1 SD faecal Na concentration per genus per protected area. The total number of independent points is n = 111 from 20 genera across 20 protected areas. Note that axes are on $\log_{10}$ scales to emphasise attention on low-values that may be indicative of Na limitation. The black line represents the fit of a linear mixed effects model with species included as a random effect. The marginal R^2 (fixed effects) denotes the proportion of variance explained by dietary Na availability. Analogous results for the 95th percentile (selective) scenario are in Fig. 2a.

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Extended Data Fig. 6 | Drivers of large-herbivore density across sub-Saharan Africa. Partial dependence plots for covariates in the best generalised additive mixed model (GAMM) for estimating large-herbivore density using all available observations. Plots indicate how large-herbivore density is predicted to change across the range of each covariate. Error bars represent 95% confidence intervals. For interaction plots, blue colours indicate density decrease, and red colours density increase. Map elements created with Natural Earth (https://www.naturalearthdata.com).

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Extended Data Fig. 7 | Drivers of megaherbivore density across sub-Saharan Africa. Partial dependence plots for covariates in the best generalised additive mixed model (GAMM) for estimating large-herbivore density using megaherbivore observations only. Plots indicate how megaherbivore density is predicted to change across the range of each covariate. Error bars represent 95% confidence intervals. For interaction plots, blue colours indicate density decrease, and red colours density increase. Map elements created with Natural Earth (https://www.naturalearthdata.com).

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☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used.
Data analysis	R Statistical Software 4.3.1 R packages: readr 2.1.4 dplyr 1.1.2 sf 1.0-13 RColorBrewer 1.1-3 ggplot2 3.5.1 gbm 2.2.2 caret 6.0-94 caretEnsemble 2.0.2 vip 0.3.2 pdp 0.8.1 raster 3.6-20 lme4 1.1-33 fitdistrplus 1.2-2 performance 0.13.0 DHARMa 0.4.7

car 3.1-2
jtools 2.3.0
pals 1.7
mgcv 1.8-42
flextable 0.9.4
viridis 0.6.3
gratia 0.8.1
gstat 2.1-1
flexOR 1.0.0
corrplot 0.95
spdep 1.3-8
spatialsample 0.6.0
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Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	N/A
Reporting on race, ethnicity, or other socially relevant groupings	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We assessed the role of sodium as a constraint for large herbivore populations in Africa. First, we developed high-resolution maps of plant sodium concentration across sub-Saharan Africa using a large database of plant sodium concentrations and an ensemble of machine learning tools. Using these maps, we modeled dietary sodium availability for large herbivore populations spatially. Linking this with a large dataset of sodium concentration in herbivore faeces, we validated the assumption that herbivore sodium intake is regulated by plant sodium concentrations. Finally, we assessed if/where plant sodium concentrations constrain large herbivore abundance using a large dataset of herbivore population density across the region.

Research sample	Vascular plants, split into two groups: C3- and C4-photosynthesising plants. Large mammalian herbivores (>3kg)
Sampling strategy	Data was first mined from literature sources. However, in cases where data were scant, additional observations were collected from unpublished field studied and a specific field survey specifically for this paper. All available data known to the authors were collated
Data collection	All available data was collated.
Timing and spatial scale	Data was collected during the period 1982-present day.
Data exclusions	Data associated with plants using the CAM photosynthesis pathway was excluded, as this data group was very small (n<10).
Reproducibility	Plant and faecal data were collected from across many field sites, which were mostly assessed once. However, for field sites where multiple field campaigns were deployed, we compared results for reproducibility. For herbivore density measurements, densities were calculated over multiple years.
Randomization	Samples were grouped by functional traits (e.g., photosynthetic pathway, diet) or by species.
Blinding	We did not use blinding during our analysis.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Samples were collected by foot, vehicle or horseback. Conditions varied by wildlife reserve and season. Temperature varied from cool to very hot, precipitation varied from minimal to moderate.
Location	Southern Africa
Access & import/export	All samples were collected in wildlife reserves with permission from governing bodies.
Disturbance	Samples (plant and faeces) were collected non-invasively, aiming to disturb the soil, plant and wildlife communities as little as possible.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	N/A
Wild animals	N/A
Reporting on sex	It was not possible to collect information on the sex of individuals in this study. Sex may be important for analysis as nutritional requirements could vary between sex. However, in this paper we were most interested in overall population effects, which were captured within our sampling protocol. Effects of sex were mentioned in the Discussion.

Field-collected samples	Fresh faecal samples were collected in the field from large herbivore mammal species and stored in labeled plastic bags. All samples were immediately frozen at -20C. Samples were transported as frozen to various laboratories for analysis. All faecal samples were disposed of using university disposal services.
Ethics oversight	Data used in this study was reviewed and approved by the University of Pretoria Research and Animal Use and Care Committees (Reference EC043-18, EC043-18-A1 and NAS115/2021).Provincial permits for transport of faecal samples between provinces of South Africa were obtained from Province of the Eastern Cape Rural Development and Agrarian Reform Veterinary Services, Province of the Eastern Cape Department of Agriculture, Limpopo Provincial Government Department of Agriculture and the South African Department of Agriculture, Forestry and Fisheries (DAFF-18/02/2019 and DAFF-12/11/1/1/8(1933NC).

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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☒	☐	Ecosystems
☒	☐	Any other significant area

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Does the work involve any of these experiments of concern:

No	Yes	
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☒	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
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☒	☐	Increase transmissibility of a pathogen
☒	☐	Alter the host range of a pathogen
☒	☐	Enable evasion of diagnostic/detection modalities
☒	☐	Enable the weaponization of a biological agent or toxin
☒	☐	Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	No seed stocks were collected as we assessed leaf samples only.
Novel plant genotypes	Leaf samples from common plants were collected only; specific genotypes were not assessed.
Authentication	Experienced field botanists were used to collect all plant samples and ensure that plant samples were correctly identified.