Title: Elephant megacarcasses increase local nutrient pools in African savanna soils and plants

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Abstract

African elephants (*Loxodonta africana*) are the largest extant terrestrial mammals, with bodies containing enormous quantities of nutrients. Yet we know little about how these nutrients move through the ecosystem after an elephant dies. Here, we investigated the initial effects (1-26 months post-death) of elephant megacarcasses on savanna soil and plant nutrient pools in Kruger National Park, South Africa. We hypothesized that: (H1) elephant megacarcass decomposition would release nutrients into soil, resulting in higher concentrations of soil nitrogen (N), phosphorus (P), and cations near the center of carcass sites; (H2) carbon (C) inputs to the soil would stimulate microbial activity, resulting in increased soil respiration potential near the center of carcass sites; and (H3) carcass-derived nutrients would be absorbed by plants, resulting in higher foliar nutrient concentrations near the center of carcass sites. To test our hypotheses, we identified 10 elephant carcass sites split evenly between nutrient-poor granitic and nutrient-rich basaltic soils. At each site, we ran transects in the four cardinal directions from the center of the carcass site, collecting soil and grass (*Urochloa trichopus,* formerly *U. mosambicensis*) samples at 0, 2.5, 5, 10, and 15 m. We then analyzed samples for CNP and cation concentrations and quantified soil microbial respiration potential. We found that concentrations of soil nitrate, ammonium, $\delta^{15}N$, phosphate, and sodium were elevated closer to the center of carcass sites (H1). Microbial respiration potentials were positively correlated with soil organic C, and both respiration and organic C decreased with distance from the carcass (H2). Finally, we found evidence that plants were readily absorbing carcass-derived nutrients from the soil, with foliar %N, $\delta^{15}N$, iron, potassium, magnesium, and sodium significantly elevated closer to the center of carcass sites (H3). Together, these results indicate that elephant megacarcasses release ecologically consequential pulses of nutrients into the soil that influence soil microbial activity

and are absorbed by plants into the above-ground nutrient pools. These localized nutrient pulses may drive spatiotemporal heterogeneity in plant diversity, herbivore behavior, and ecosystem processes.

Sect. 1 Introduction

Living animals affect nutrient flows through ecosystems (Schmitz et al. 2018), but we have only recently acknowledged that the nutrients from animal carcasses could also influence ecosystem processes (Barton et al. 2013; Monk et al. 2024). In marine ecosystems, whale carcasses function as unique hotspots of nutrient cycling, biodiversity, and ecosystem processes (Roman et al. 2014). In terrestrial systems, mass mortality events (e.g., wildebeest, cicadas) create nutrient hotspots (Yang, 2004; Subalusky et al. 2020), while individual small and medium-sized carcasses release pulses of nutrients into the soil (Town, 2000; Barton et al. 2016; Olea et al. 2019). Yet, terrestrial ecosystem ecology lacks knowledge about the role of megacarcasses (carcasses of animals such as elephants and rhinoceros that are >1000 kg at death) as potential drivers of spatiotemporal heterogeneity in nutrient cycling and ecosystem processes. Importantly, these megacarcasses may be functionally different than smaller carcasses due to the extraordinarily high concentration of nutrients and residence time of the decomposing animal (see reviews by Barton et al. 2013; Barton, 2016; Barton & Bump 2019). This question around the role of megacarcasses is particularly relevant given the megaherbivore losses that occurred during the Pleistocene extinctions and that are still occurring today (Ripple et al. 2015). We are only beginning to understand how the 'extinction aftershock' of losing the largest species impacts ecosystems (Owen-Smith, 1989; Flannery, 1990), and no study has yet investigated how the loss of megacarcasses might influence the dynamics of terrestrial ecosystems (Doughty et al. 2013; Doughty et al. 2016).

We can only evaluate the importance of terrestrial megacarcasses for nutrient cycling in ecosystems where megaherbivores still exist, such as African savannas. The African savanna elephant (*Loxodonta africana*) is the largest extant land animal and is known for its key ecological effects in savannas while alive (e.g., dispersing seeds, creating plant refuges, preventing woody encroachment) (Skarpe et al. 2004; Asner et al. 2009; Campos-Arceiz & Blake, 2011; Coverdale et al. 2016; Guy et al. 2021). Yet, the elephant's large body mass may mean that it also has an outsized impact in these ecosystems even after death. A 4000-kg elephant megacarcass likely represents ~2000 kg carbon (C), ~300 kg nitrogen (N), and ~125 kg phosphorus (P) deposited in the savanna landscape (estimated from stoichiometry of elephants and other mammals in Sterner & Elser, 2002). The N deposition from one elephant megacarcass (in a 700 m^2 impact zone assuming a 15 m disturbance radius) is roughly equivalent to the N delivered to 10,000 m^2 of savanna from ~100 years from atmospheric deposition (Mphepya et al. 2006).

If megacarcasses provide large nutrient pulses, then they likely create hotspots of important below- and aboveground processes. Belowground, soil respiration and organic matter decomposition might increase with nutrient inputs from carcasses (Risch et al. 2020). Concentrations of C, N, P, and potassium (K) are often elevated near carcasses of medium-sized animals (e.g., bison, moose, kangaroo, vicuña) (Towne, 2000; Bump et al. 2009a; Macdonald et al. 2014; Risch et al. 2020; Monk et al. 2024), and nutrients such as P and calcium (Ca) continue leaching from bones even after soft tissues have been consumed or degraded (Coe, 1978; Keenan & Beeler, 2023). Aboveground, plant growth in African savannas is strongly limited by nutrient availability, most commonly N and P, but also by cations such as Ca, K, and magnesium (Mg) (Jobbágy & Jackson, 2004; Ries & Shugart, 2008; Pellegrini, 2016), and there is evidence of cation limitation of plants (particularly K^+ and Ca^{2+}) on African savannas (Lathwell & Grove, 1996; Agbenin & Yakubu, 2006). Thus, the large influx of nutrients released from megacarcasses might increase the mobilization of nutrients by plants, potentially increasing nutrient accessibility for vertebrate and invertebrate herbivores (Yang, 2008; Grant & Scholes, 2006; Anderson et al. 2010; Joern et al. 2012). Indeed, carcasses of smaller vertebrates (e.g., salmon, deer) can increase the proportions of nitrogen and $\delta^{15}N$ (an indicator of animal-driven N) in plants within just a few months post-death (Hocking & Reynolds, 2012; van Klink et al. 2020).

To assess the effects of megacarcasses on local nutrient pools (Figure 1), we measured the initial contributions of elephant carcasses (1-26 months post-death) to soil and plant nutrients in the Kruger National Park (KNP), South Africa. Further, we examined the effects of elephant carcasses on the two main soil types in KNP: sandy, relatively nutrient-poor granitic soils and clayey, relatively nutrient-rich basaltic soils (Venter et al. 2003). At each site, we ran transects in each cardinal direction from the center of the site where an elephant died, collecting samples of soil and a palatable grass species (*Urochloa trichopus*) at 0, 2.5, 5, 10, and 15 m. We then analyzed soil samples for CNP and cation content, quantified soil microbial respiration potential, and measured %N, $\delta^{15}N$, and macro- and micronutrient content in grass tissue. We hypothesized that: (H1) elephant megacarcass decomposition would release nutrients into soil, resulting in higher concentrations of soil N, P, and cations near the center of carcass sites; (H2) C inputs to the soil would stimulate microbial activity, resulting in increased soil respiration potential near the center of carcass sites; and (H3) carcass-derived nutrients would move from soil into plants, resulting in higher foliar nutrient concentrations near the center of carcass sites. We predicted that enrichment effects from megacarcasses would be greater on sites with fresher carcasses relative to older carcasses and on nutrient-poor granitic sites compared to nutrient-rich basaltic sites.

Sect. 2 Methods

2.1 Study system and sample collection

We performed this research in the southern part of the Kruger National Park (KNP), South Africa (24.996 S, 31.592 E, ~275m elevation). The two dominant soil types in KNP are granitic soils (inceptisols) and basaltic soils (versitols or andisols) (Khomo et al. 2017). The clay-rich basaltic soils have relatively large surface area, enabling them to retain larger quantities of water than granitic soils, which drain water more quickly and therefore are lower in water-soluble nutrients (Buitenweref, Kulmatiski, & Higgins, 2014; Rughöft et al. 2016). The landscape of KNP is a mix of savanna grasslands and broadleaf woodlands, with an overstory dominated by trees from the genus *Combretum* (red bushwillow, *C. apiculatum*; russet bushwillow, *C. hereroense*; leadwood, *C. imberbe*) and trees formerly known as acacias (knobthorn, *Senegalensis nigrescens*; umbrella thorn, *Vachellia tortillis*). The park hosts a full suite of African savanna animals, including ~30,000 elephants (*Loxodonta africana*) (Coetsee & Ferreira, 2023), with a mortality rate of ~2% (~600 elephants per year). The targeted region of KNP has a high density of scavengers and predators, including white-backed vultures (*Gyps africanus*), spotted hyenas (*Crocuta crocuta*), and lions (*Panthera leo*) (Owen-Smith & Mills, 2007).

During the wet season in March 2023, we identified ten elephant carcass sites (1-26 months post-death), five on relatively nutrient-rich basaltic soil and five on nutrient-poor granitic soil. KNP section rangers provided precise GPS locations of where elephant carcasses had been found. Most elephants died of old age, illness, injury, or, in the case of one young bull, fighting over territory. Carcass sites were recognizable *in situ* by a persistent bonefield, undigested gut contents, and an absence of herbaceous vegetation. At each site, we hammered a rebar post into the center of the megacarcass disturbance and ran 15 m transects out from the post in each of the four cardinal directions. We collected green leaf material from *U. trichopus,* a common and abundant palatable grass species, and used an auger to collect soil samples to a depth of 10 cm at five points along each transect (0.5, 2.5, 5, 10, and 15 m) (Bump, Peterson, & Vucetich, 2009; Holdo & Mack, 2014; Gray & Bond, 2015; Monk et al. 2024). We treated the 10-15m distances as representative of background concentrations of nutrients based on pilot data showing that the effect of elephant carcasses on soil nutrient concentrations was undetectable at this distance away from the carcass site, similar to studies on the carcasses of other large vertebrates (e.g., Towne, 2000; Bump et al. 2009). We pooled and homogenized the samples to yield one composite leaf and one composite soil sample per sampling distance from each carcass site. Soil samples were sieved in a 5-mm metal sieve which was cleaned in between samples with 70% ethanol. Soil samples were stored in a cooler during fieldwork. On the day they were collected, we used 5 g of each soil sample for soil respiration measurements (described below). The rest of each sample was stored in plastic bags in a -20°C freezer until nutrient analyses; they were stored in coolers with ice blocks during the transition from the freezer at the field site to the freezers at the labs. We chose to freeze samples rather than storing at room temperature based on literature demonstrating that the impacts of freezing on soil nitrate and ammonium concentrations are fairly minimal, except in specific cases of high soil acidity or peaty soils that were not present at our field site (Esala, 1995; Turner & Romero, 2009; Sollen-Norrlin & Rintoul-Hynes, 2024). Leaf samples were stored in paper bags at room temperature until dried for analyses (see below).

2.3 Hypothesis testing

We tested our first hypothesis that elephant carcass decomposition would release nutrients into the soil by performing soil nutrient analyses. We sent 250 g of each soil sample to Eco-Analytica laboratory at the North-West University in Potchefstroom, South Africa for measurements of soil concentrations of ammonium $[NH_4]^+$, nitrate $[NO_3]^-$, phosphate $[PO_4]^{3-}$, and plant-available P. Samples were air-dried and sieved through < 2mm mesh prior to chemical analysis. Plant-available P was extracted from 4 g of soil and 30 ml extraction fluid (1:7.5 ratio) using an acid–fluoride solution (P Bray-1), measured colorimetrically using a Systea EasyChem200 analyser, and expressed as mg/kg. The detection limit was 0.5 mg/kg, and plant available P measurements <0.5 mg/kg were replaced with half the detection limit (0.25 mg/kg) (Croghan & Egeghy, 2003; Keenan & Beeler, 2023). Water-soluble nitrate and phosphate anions were extracted from volume on volume 100 ml soil and 200 ml deionized water, analyzed by ion chromatography on a Metrohm 930 Compact Flex System, and measured as mg/L. Ammonium (also 1:2 water extract) was analyzed colorimetrically using a Systea EasyChem200 analyzer and measured as mg/L. Detection limits for soil ions were 0.01 mg/L, and soil ion concentrations measured as <0.01 mg/L were replaced with half the detection limit (0.005 mg/L). To convert the nitrate, ammonium, and phosphate units from mg/L to mg/kg, we multiplied by 2, based on the 1:2 soil to water extraction ratio.

To determine whether soil anions were distinct and elevated at the center of carcass sites relative to soil further from the center, concentrations of sodium (Na), magnesium (Mg), iron (Fe), calcium (Ca), potassium (K), and phosphorus (P) cations were measured using microwave-assisted digestion. Air-dried and sieved (>2 mm) soil samples, weighed to 0.2 g, were microwaved in 9 ml 65% nitric acid (HNO_3) and 3 ml 32% hydrochloric acid (HCl) according to EPA 3051b in a Milestone, Ethos microwave digester with UP, Maxi 44 rotor. A period of 20 minutes allowed the system to reach 1800 MW at a temperature of 200 °C which was maintained for 15 minutes. After cooling, the samples were brought up to a final volume of 50 ml and analyzed on an Agilent 7500 CE ICP-MS fitted with CRC (Collision Reaction Cell) technology for interference removal. The instrument is optimized using a solution containing Li, Y, Ce, and Tl (1 ppb) for standard low-oxide/low interference levels (≤ 1.5%) while maintaining high sensitivity across the mass range. The instrument was calibrated using ULTRASPEC® certified custom mixed multi-element stock standard solutions containing all the elements of interest (De Bruyn Spectroscopic Solutions, South Africa). Calibrations spanned the range of 0 – 30 ppm for the mineral elements Ca, Mg, Na, and K and 0 – 0.3 ppm for the rest of the trace elements. Elemental concentrations were expressed as mg/kg.

Finally, to determine whether elevated N levels in soils were derived from the carcass, we sent 10 g of each sample to the BIOGRIP laboratory within the Central Analytical Facility at Stellenbosch University for measurements of soil %N and δ^{15}N, obtained using a Vario Isotope Select Elemental Analyzer connected to a thermal conductivity detector and an Isoprime precisions isotope ratio mass spectrometer (IRMS). Samples were oven-dried at 60°C for 48 hours and milled to a fine powder using a Retsch MM400 mill (Germany). The powdered samples were weighed (2 – 60 mg) prior to combustion at 950°C. The gasses were reduced to N_2 (undiluted) in the reduction column, which was held at 600°C. A high organic carbon (HOC) soil standard (0.52 ± 0.02 %N), along with two international reference standards (USGS40 (δ^{15}N -4.52% AIR) and USGS41 (δ^{15}N +47.57% AIR)) were used for calibration. The N elemental content was expressed relative to atmospheric N as N_2 δ^{15}NAIR (‰). The quantification limit for δ^{15}N on the IRMS is 1 nA (nanoAmp), and the quantification limit for %N is 0.06%. The precision for %N was 0.02% and for $\delta^{15}N$ is ±0.11%, determined using the HOC standard, which was run multiple times throughout the analysis.

To test our second hypothesis that nutrient inputs to the soil would stimulate microbial activity, we measured soil organic C, water content, and microbial respiration potential. We sent 10 g of each sample to the BIOGRIP laboratory for measurements of soil organic C using a Vario TOC Cube (Elementar, Germany). Samples (dried and milled as above) were weighed (10 – 60 mg), acidified using 10% HCl to remove the total inorganic C (carbonates), and dried overnight at 60°C. All samples were analyzed through combustion at 950°C. The released CO_2 was measured by a non-dispersive infrared (NDIR) sensor. A high organic C (7.45 ± 0.14 %C) soil standard from Elemental Microanalysis Ltd (UK) was included during the analysis. The quantification limit for %C is 0.14%. The precision for the %C was 0.09% and was determined using the low organic C (LOC) standard (1.86 ± 0.14 %C), which was run multiple times throughout the analysis.

To quantify soil respiration and water content, we used an incubation method (Lemoine et al. 2023) in which 5 g (± 0.2 g) of each sample was placed into a 100 ml clear glass bottle, sealed, and flushed with CO_2-free air. Following flushing, we incubated the bottles for one hour at 25°C. We then recorded CO_2 concentrations using an LI-850 CO_2/H_2O infrared gas analyzer. After soil respiration measurements, we determined sample dry weight by drying each sample at 60°C for 24-48 hours until stable mass was achieved. We subtracted dry weight from starting weight to obtain soil water content. Finally, we used the dry weights and the Ideal Gas Law to standardize all respiration measurements to CO_2 $\mu g\ h^{-1} g$ dry soil^{-1}.

To test our third hypothesis that carcass-derived nutrients would be incorporated by plants, we measured foliar nutrient concentrations in *U. trichopus*. Two grams of each dried leaf sample was sent to the BIOGRIP laboratory for preparation and measurements of %N and $\delta^{15}N$ via stable isotope analysis as described above. A Sorghum flour standard (1.47 ± 0.25 %N) from Elemental Microanalysis Ltd (UK) was used for calibration, along with two international reference standards (USGS40 and USGS41). The quantification limit for $\delta^{15}N$ on the IRMS is 1 nA, and the quantification limit for %N is 1.3%. The precision for the %N was 0.02% and for $\delta^{15}N$ is ±0.08‰. Limits were determined using the sorghum flour standard, which was run multiple times throughout the analysis. Additionally, we sent 5 g per sample to Cedara Analytical Services Laboratory to quantify micronutrients in grass tissue (P, Na, Mg, K, Ca, and Fe) using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES 5800, Agilent, USA). Samples were dried (110°C overnight) and milled to a fine powder. Subsamples (0.5 g) were ashed at 450°C for 4 hours, and the ash was re-wet using 2 mL conc. HCl (32%). Samples were evaporated to dryness then re-suspended in 25 mL 1M HCl before filtering. Lastly, the filtrate was diluted with de-ionized water in a ratio of 5:20 filtrate to water. To calibrate the ICP-OES, solutions containing known amounts of each element were measured (10-20 ppm for Na and C, 200-1500 ppm for Fe, 0.5-3.75% for K, and 0.125-0.5% for P), prepared from 1000 ppm primary single standards. At three of the ten sites, we did not find sufficient plant material at the central point for analysis, resulting in a sample size of N = 7 for the center (distance = 0.5m) measurement for leaf nutrient analyses.

To test whether each response variable for the three hypotheses was significantly associated with soil type and/or distance from the carcass center, we performed a model selection procedure. For each response variable, we ran five generalized linear mixed models using the gamma family (link = log) in the package *lme4* (Bates et al. 2015): (*i*) soil type + distance + soil type × distance interaction, (*ii*) soil type + distance, (*iii*) soil type, (*iv*) distance, and (v) a null model indicating no significant difference in slope or intercept after accounting for carcass site. All models included carcass site as a random effect to account for individual variation. Each model included 50 observations (10 sites x 5 distances per site). For samples in which the nutrient level was listed as 0 or undetectable, we accounted for the uncertainty by using half the detection level as described above. The narrow distribution of ages (1-26 months since death) with the sample size of N = 10 sites made testing for the effect of age challenging, so we did not include carcass age in the models. We compared the models for each response variable using Akaike Information Criterion (AICc). Models with a ΔAICc ≤ 2 were considered roughly equivalent in fit (Burnham and Anderson, 2002).

In addition to these models, for our second hypothesis we regressed soil respiration potential against soil organic C, expecting that the two would be positively correlated. We ran a generalized linear mixed model with soil respiration potential as the response variable. The model included soil organic C + distance + soil type, with carcass site as a random effect. We did not include an interaction with soil type in this model due to sample size restrictions. Respiration potential and organic C were both log-transformed to achieve normality.

To determine whether leaf and soil micronutrient composition differed with distance and soil type, we ran permutational analysis of variance (perMANOVA) in *vegan* (Oksanen et al. 2022). We ran the same model separately for soil and leaf micronutrient composition (soil type + distance). To determine which micronutrients contributed most to compositional differences across distances and soil types, we calculated samplewise Bray-Curtis dissimilarity and performed principal component analysis. We also tested for differences in variance in micronutrient composition across distances and soil types using “betadisper” in *vegan* (Oksanen et al. 2022). We ran linear models to test for correlations between leaf and soil concentrations of each micronutrient. Each model included distance as a covariate and site as a random effect.

Finally, to test the impact of carcass age on key soil metrics, we ran exponential decay functions for soil ammonium, nitrate, phosphate, and respiration verses carcass age for samples from the center of the carcass site (0.5m sampling location). We also performed a t-test to verify that there was no difference in mean carcass age across soil types.

All statistical analyses were performed in R version 4.2.1 (R Core Team, 2022).

Sect. 3 Results

3.1 Hypothesis 1: Effects of megacarcasses on soil nutrient pools

We found partial support for our first hypothesis that soil N and P concentrations would be higher closer to the center of carcass sites (Table S1). Soil %N (Figure 2A) was overall greater in basaltic soils, and it decreased with distance from the carcass site on granitic soils. Soil nitrate (Figure 2B) decreased with distance from the carcass site but did not differ between soil types. Ammonium (Figure 2C) also decreased with distance, but only in granitic soils. $\delta^{15}N$ (Figure 2D) was greater in granitic soils and decreased with distance in both soil types, indicating that the proportion of animal-sourced N in the soil was greater near the center of the carcass site. Soil phosphate, plant available P, and mineral P (Figure 2E-G) all exhibited significant soil × distance interactions. Phosphate (Figure 2E) was highly elevated at the center of carcass sites and decreased steeply with distance, but only in granitic soils. Plant-available P (Figure 2F) decreased with distance in both soil types, but the effect was strongest in granitic soils. Finally, mineral P (Figure 2G) was greater in basaltic soils, and there was a small decrease with distance in granitic soils but not in basaltic soils.

Contrary to our first hypothesis, soil cation composition did not differ significantly with distance from the carcass center; nor did most individual cations (Table S1). The perMANOVA results showed that soil cation composition did not differ significantly with distance ($R^2 = 0.00$, $F_{4,44} = 0.0$, $P = 1.000$) (Figure S2A), but it did differ significantly with soil type ($R^2 = 0.71$, $F_{1,44} = 108.8$, $P = 0.001$) (Figure S2B). There was no significant difference in variance with distance ($F_{4,45} = 0.0$, $P = 0.996$) or soil type ($F_{1,48} = 2.6$, $P = 0.115$). Principal components analysis showed that dimension 1 explained 53.6% of the variation between soil types and was driven primarily by differences in Mg, Ca, and Fe. Dimension 2 explained 25.9% of variation and was driven primarily by differences in K. Soil Na (Figure S3A) was marginally greater in granitic soils and decreased with distance from the carcass, with the effect greater in granitic soils. Soil K (Figure S3B) was greater in basaltic soils and decreased marginally with distance. Soil Fe, Mg, and Ca (Figure S3C-E) were greater in basaltic soils, with minimal effects of distance.

3.2 Hypothesis 2: Effects of megacarcasses on soil carbon and respiration

Consistent with our second hypothesis, soil respiration potential was marginally positively correlated with soil organic carbon concentration and decreased significantly with distance but did not differ with soil type (Figure 3). We found no evidence for differences in soil water content (Figure S4A) or soil pH (Figure S4B) with distance or soil type. In both cases, the null ranked among the set of top models (Table S1).

3.3 Hypothesis 3: Effects of megacarcasses on plant nutrient pools

Consistent with our third hypothesis, we found elevated foliar nutrient concentrations in *U. trichopus* at elephant carcass sites. Leaf %N (Figure 4A) and $\delta^{15}N$ (Figure 4B) both decreased with distance from the carcass center. $\delta^{15}N$ exhibited a significant soil × distance interaction in which it was overall greater in basaltic soils, but the difference between the two soil types was greater closer to the carcass site. Foliar P was greater in basaltic soils and decreased only marginally with distance in the granite soils. Finally, the foliar N:P ratio was greater in granitic soils and decreased with distance in the basaltic soils.

Leaf micronutrient composition did not differ significantly with distance ($R^2 = 0.13$, $F_{4,40} = 1.9$, $P = 0.062$; Figure S5A) but did differ with soil type ($R^2 = 0.17$, $F_{1,40} = 9.7$, $P = 0.001$; Figure S5B). There was no significant difference in variance with distance ($F_{4,41} = 0.5$, $P = 0.713$) or soil type ($F_{1,44} = 1.9$, $P = 0.173$). Dimension 1 explained 42.8% of the variance across soil types and was primarily driven by Mg, Na, and P. Dimension 2 explained 26.6% of the variance and was driven mainly by K, Ca, and Fe. Foliar Na (Figure S6A) and Mg (Figure S6B) were both greater in basaltic soils and decreased with distance from the carcass center. Foliar K (Figure S6C) and Fe (Figure S6D) both decreased with distance as well but did not differ with soil type. The null model was in the top set for foliar Ca, indicating no significant relationship between foliar Ca concentrations and soil type or distance from the carcass center. Individual micronutrients (K, Ca, Mg, Fe) were not correlated between leaf and soil samples, with the exception of Na (Table S3).

3.4 Effects of carcass age on soil ions and respiration potential

Soil ammonium ($\alpha = 0.018$, $P < 0.001$), phosphate ($\alpha = 0.023$, $P < 0.001$), and respiration potential ($\alpha = 0.058$, $P < 0.001$) all decreased significantly with carcass age (Figure 5A-C). The exponential decay model for nitrate failed to converge due to an outlier with extremely high soil nitrate (1454 mg/kg) at 258 days post-death (Figure 5D). We ran a t-test to test for a difference in mean carcass age between soil types and found no significant difference between the two groups ($P = 0.294$).

Sect. 4 Discussion

Here, we show that elephant megacarcasses influence soil and foliar nutrients during at least the first two years following mortality. Consistent with our hypotheses, soil nitrate (Figure 2B), ammonium (Figure 2C), $\delta^{15}N$ (Figure 2D), and P (Figure 2E-F) concentrations were all elevated at the center of carcass sites and decreased with distance from the center. Soil %N, nitrate, ammonium, and plant-available P concentrations at the 15m point were consistent with those found in other studies of soil nutrient content in Kruger (Aranibar et al. 2003; Rughöft et al. 2016), confirming that the 15m point serves as an effective baseline control in this experiment. Microbial respiration potential was also elevated towards the center of carcass sites and was correlated with the abundance of organic C (Figure 3). Finally, %N (Figure 4A) and $\delta^{15}N$ in a common grass (Figure 4B) were both elevated closer to the centers of carcass sites compared to grass farther from carcasses. Together, these results indicate that carcass-derived nutrients move into soil and subsequently get absorbed by plants over relatively short time scales, cycling essential nutrients such as N from carrion into the soil and then back into aboveground nutrient pools.

The initial influx of ammonium from elephant carcasses is consistent with literature on smaller carrion but much greater in magnitude in these much larger carcasses (Parmenter & McMachon, 2009; Quaggiotto et al. 2019; Yong et al. 2019). The mean ammonium level at the center of carcass sites (17.4 mg/L) was 5x the level generally considered toxic to plants (3.5 mg/L; Britto & Kronzucker, 2002). Yet, we found living grass—typically *U. trichopus*—in the center of the carcass site at seven out of ten of our sites (ammonium range 5-86 mg/L) and at the 2.5m distance for all sites (ammonium range 0-36 mg/L). The three sites without vegetation in the center had the highest ammonium levels (35-72 mg/L), suggesting that *U. trichopus* has a higher degree of ammonium tolerance than some sympatric grass species but may still be limited by the extreme ammonium levels at the centers of these three relatively fresh carcass sites. However, the recentness of the disturbance from the carcass likely also plays a role in determining plant abundance near the center of the carcass. These results indicate that ammonium remains elevated at elephant carcass sites for at least the first two years post-death and may reduce, but not eliminate, plant growth over this time period.

Soil nitrate (Figure 2B) and soil respiration potential (Figure 3) were also elevated near the center of carcass sites, indicating higher rates of activity of heterotrophic microbes (Prosser, 2011). These results are consistent with other work on carrion, where microbial activity tends to be greater in soils near carcasses as compared to surrounding soil (Bump et al. 2009b). However, carcass effects on soil microbial respiration exhibit a high degree of intra-system variation (Risch et al. 2020), and the potentially short window during which increased respiration occurs may make capturing these variations challenging. For example, soil respiration potential at the center of the three youngest carcass sites was on average 2x higher than the seven older sites (18.43 and 9.62 µg CO_2/hr, respectively; Figure 5D). Thus, the impact of increased organic C on soil microbial processes may be relatively short lived and only last a matter of months (Keenan et al. 2018; Keenan, Schaeffer, & DeBruyn, 2019). These trends are consistent with soil ammonium and phosphate, both of which are highest at the youngest carcass sites (<200 days post death; Figure 5A-B). Soil microbial respiration rate is also highly elevated early on, but it decreases at a faster rate over time than soil ions (Figure 5C). Thus, soil dynamics during the first several months after death may play a crucial role in determining the long-term impacts of megacarcasses on savannas and therefore provides a promising avenue for future research.

Elevated soil phosphate (Figure 2E) and plant-available P (Figure 2F) at the center of carcass sites were also consistent with expectations from the literature (Bump et al. 2009a; Parmenter & MacMahon, 2009). However, elevated P levels in soil did not translate to elevated P in grass leaves (Figure 4C), which could suggest a lag between trends in soil and plants that is longer for P than for N. This lag could occur because phosphate easily forms chemical bonds with other soil ions (e.g., iron and aluminum in acidic soils and calcium in basic soils). Nitrate does not form these bonds and therefore has greater water solubility and mobility in soils and may be more readily taken up by plants (Wiersum, 1962; Arai & Sparks, 2007). However, it is also possible that P limitation in Kruger is not as strong as it is in some other African savanna systems (Pellegrini, 2016). The foliar N:P ratios measured in this experiment were higher closer to the center of the carcass site (median 9.38 at 0 m and 4.83 at 15 m), indicating that N limitation may be relatively stronger further from the carcass site, and P limitation may be relatively stronger closer to the center (Figure 4D, Table S2). These relatively high foliar N:P ratios at the center of carcass sites are similar to those found in N fertilization studies in Kruger (Craine et al. 2008), further supporting the idea that the influx of N from megacarcasses may shift the soil from relatively more N limited to more P limited.

The elevated plant-available P at the center of carcass sites likely came primarily from phosphate released from decomposing tissue (Yong et al. 2019). Bone decomposition, which is also likely a major source of P from animal carcasses (Subalusky et al. 2020), occurs over long time scales (Coe, 1978; Subalusky et al. 2020) and therefore should result in the slow release of P and a gradual decrease in the N:P ratio (Parmenter & MacMahon, 2009; Quaggiotto et al.

2019). Indeed, initial inorganic N influxes to the Mara River in Kenya from mass wildebeest die-offs are 10-fold greater than concurrent increases in P, which instead releases slowly over about seven years of bone decomposition (Subalusky et al. 2017). Research following megacarcasses over longer timeframes post-death is needed to clarify when P from enriched soil is absorbed by plants and at what stage megacarcass bones begin contributing to soil P dynamics. It is also possible that bone dispersal by scavengers may result in less P leaching from bones close to where the elephant died and more P being distributed across the landscape at distances far from the carcass site.

The contributions of megacarcasses to soil macronutrient and cation pools were strongly associated with soil type. Our results confirmed the previously-established trend that basaltic soils are overall more cation rich than granitic soils, with greater concentrations of P, K, Fe, Mg, and Ca (Figure 2G; Figure S3B-E; Gertenbach, 1983; Craine, Morrow, & Stock, 2008; Wigley et al. 2014). However, soil ammonium, δ^{15}N, and phosphate were all higher in the granitic soils towards the center of carcass sites, decreasing steeply to be similar to basaltic soils about 10 m from the carcass center (Figure 2C-E). These results indicate that the impact of organic matter from megacarcasses may be stronger in relatively nutrient-poor and sandy granitic soil compared with nutrient-rich and clayey basaltic soil. We were surprised that grass on basaltic soil did not consistently exhibit greater concentrations of cations and macronutrients. One potential explanation is that grass may primarily be limited by macronutrients like N and P on both soil types (Craine et al. 2008; Holdo, 2013) rather than by cations. Thus, even with increased cation availability their actual uptake may not differ substantially. Studies on ungulate carcasses (e.g., muskoxen, moose, zebra) have shown increased foliar N at carcass sites (Danell et al. 2002; Bump et al. 2009b; Turner et al. 2014), but to date there is little research on the flow of cations from carrion to plants and none on the pipeline from megacarcasses to plants. Moreover, it remains to be seen whether increases in foliar N and other nutrients affect herbivory rates at carcass sites and how long such effects may last.

The magnitude of nutrient inputs from megacarcasses, as well as the substantial size and duration of their impact zones, means their impacts on ecosystem processes may be functionally distinct from smaller carrion. Indeed, there is evidence that carcass size strongly impacts scavenger food web structure (Moleón et al. 2015; Morris et al. 2023). Moreover, the attraction of animals to carcasses via scavenging, predation, or mourning (Goldenberg & Wittemyer, 2020) could have positive feedbacks on nutrient cycling (Bump, Peterson, & Vucetich, 2009; Monk et al. 2024), which may be magnified by carcass size. Thus, the impacts of megacarcasses on savanna ecosystem processes may be dissimilar to the effects of small carrion and more similar to other more persistent contributors to savanna ecosystem processes, such as termite mounds (Davies et al. 2016), cattle bomas (Augustine, 2003), and even mass animal mortality events (Subalusky et al. 2017, 2020).

Sect. 5 Conclusions

This study is an important first step in understanding the ecological legacies of megacarcasses on savanna ecosystem processes. During the first two years post-death, elephant carcasses released pulses of ammonium, nitrate, and phosphate, all of which influence savanna primary productivity. These nutrients stimulated soil microbial activity and enriched foliar N, and the effects were strongest in nutrient-poor soil, with potential long-term impacts on savanna nutrient heterogeneity. These carcass-derived nutrient hotspots represent a previously unstudied function of megaherbivores on savannas—one that we need to better understand in order to comprehend the full impacts of megaherbivore population declines in the Anthropocene.

Data and Code Availability: Data and computer code are archived on Dryad Digital Repository (https://doi.org/10.5061/dryad.wpzgmsbwm).

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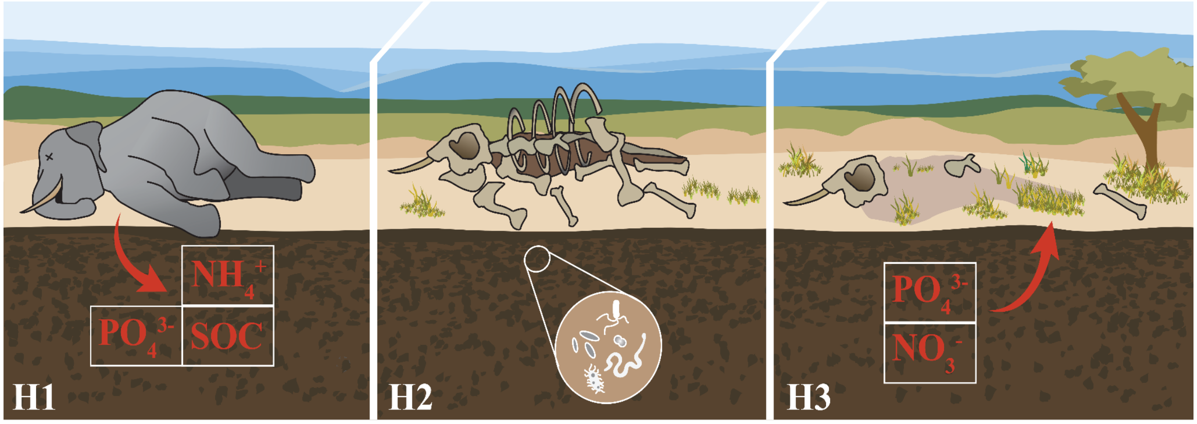

Figure 1. Hypothesized impacts of elephant megacarcasses on soil and plant nutrients. First (H1), we hypothesized that elephant carcasses would release pulses of nutrients into the soil, resulting in higher concentrations of soil ions such as nitrogen (ammonium, $[NH_4]^+$), phosphorus (phosphate, $[PO_4]^{3-}$), and soil organic C. Second (H2), we hypothesized that C inputs from the carcass would result in increased soil microbial respiration potential. Third (H3), we hypothesized that plants would take up nutrients from the carcass soil, resulting in plants with distinct nutrient profiles and increased concentrations of key limiting nutrients such as N and P. Image credit: Kirsten Boeh.

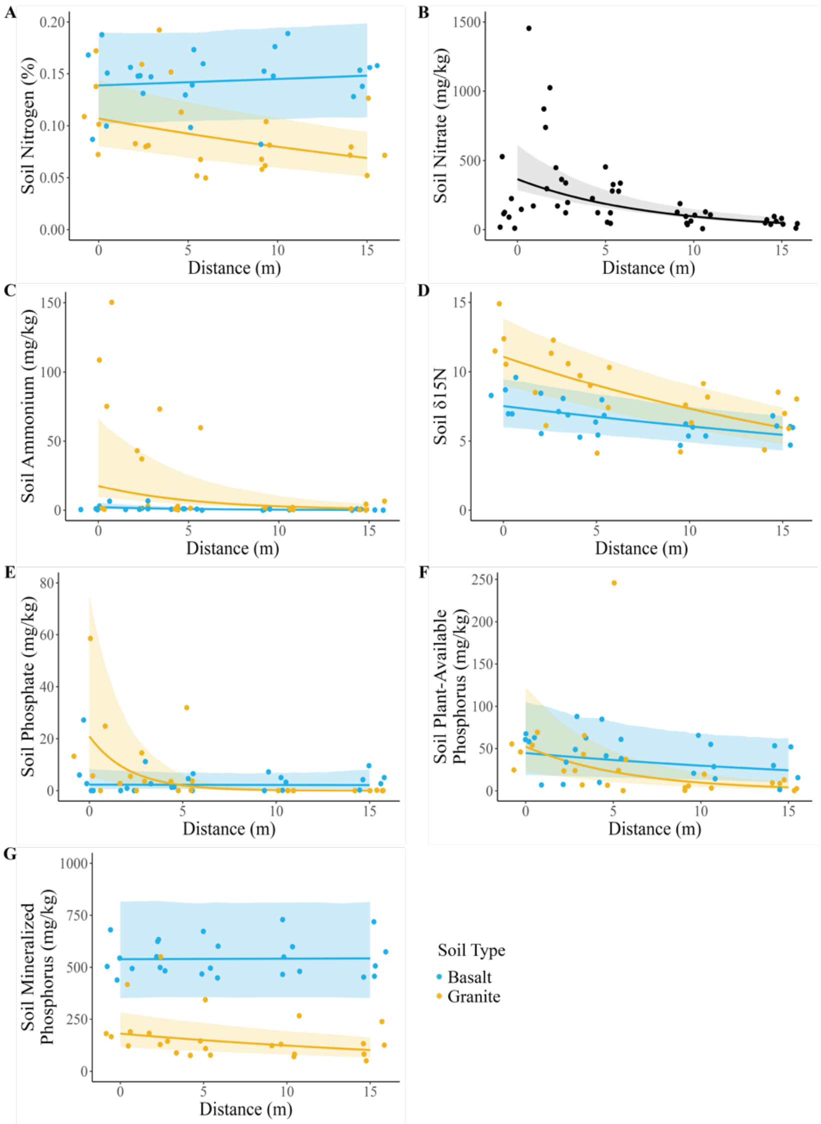

Figure 2. Soil N and P responses to elephant carcasses. (A) Soil N (%) was greater in basaltic soils, and in granitic soils it decreased with distance from the carcass site. (B) Soil nitrate nitrogen decreased with distance but did not differ with soil type. (C) Soil ammonium nitrogen and (D) $\delta^{15}N$ were both greater in granitic soils and decreased with distance from the carcass. (E) Soil phosphate, (F) plant-available P, and (G) mineralized P decreased with distance in granitic soils but not basaltic soils. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap. Lines show predictions calculated from the top model (see Table S1). Shading indicates the 95% confidence interval.

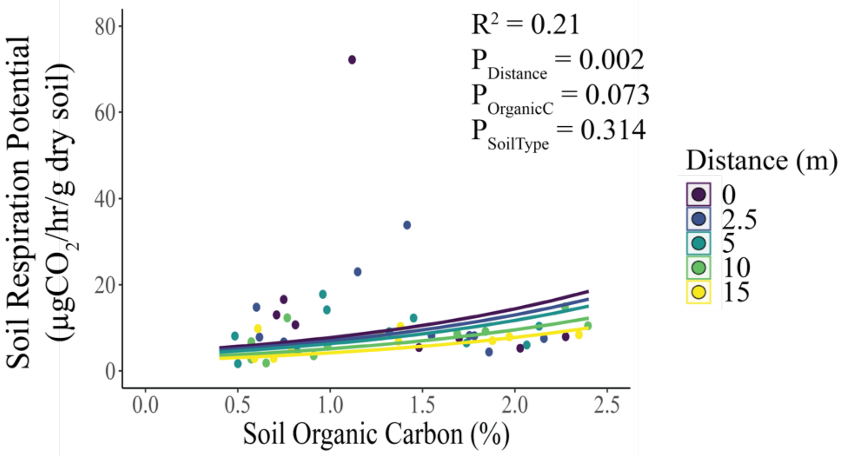

Figure 3. Soil respiration potential was marginally positively correlated with soil organic C (%) and decreased significantly with distance from the carcass. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap. Lines represent model predictions.

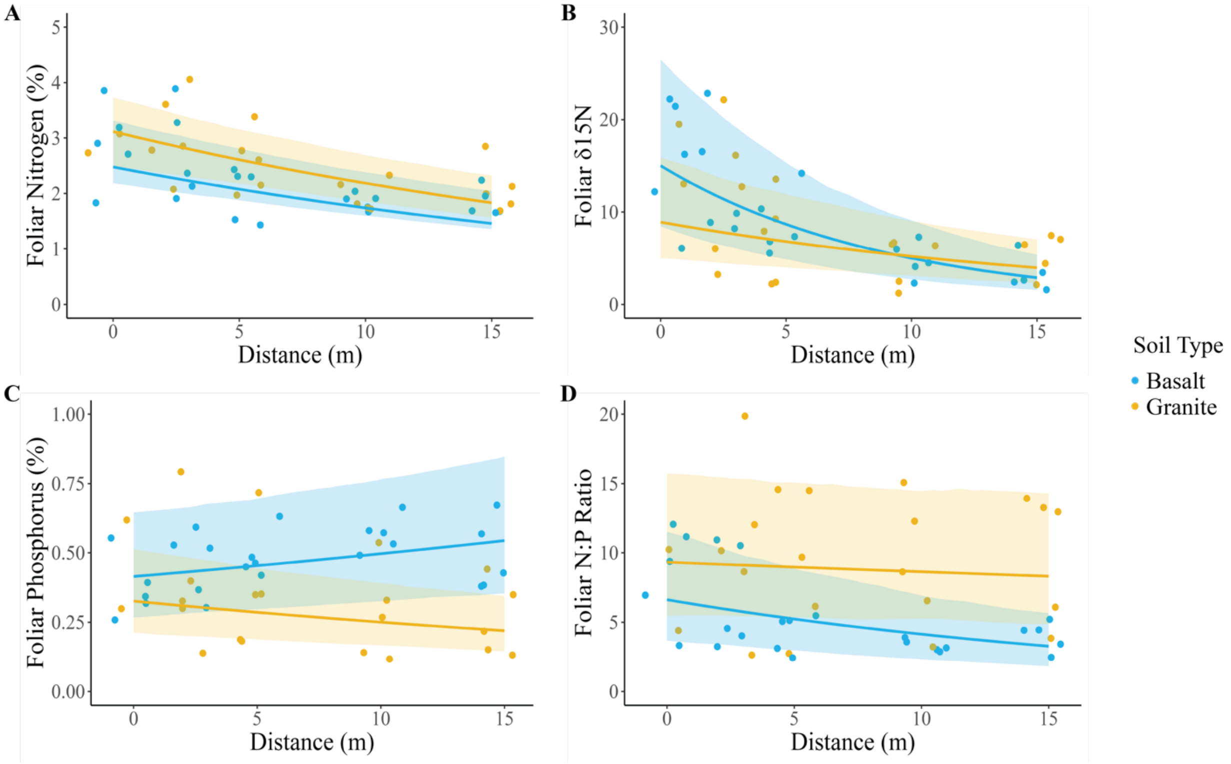

Figure 4. Foliar N and P responses to elephant carcasses. (A) Foliar %N and (B) δ^{15}N both decreased with distance from the carcass center. (C) Foliar P was greater in basaltic soils and decreased with distance in granitic soils. (D) Foliar N:P ratio was greater in granitic soils and decreased with distance from the carcass center. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap. Lines show predictions calculated from the top model (see Table S2). Shading indicates the 95% confidence interval. Three of the ten sites had bare ground at the 0 m distance, resulting in a sample size of 7 sites for that distance and 10 for the other distances.

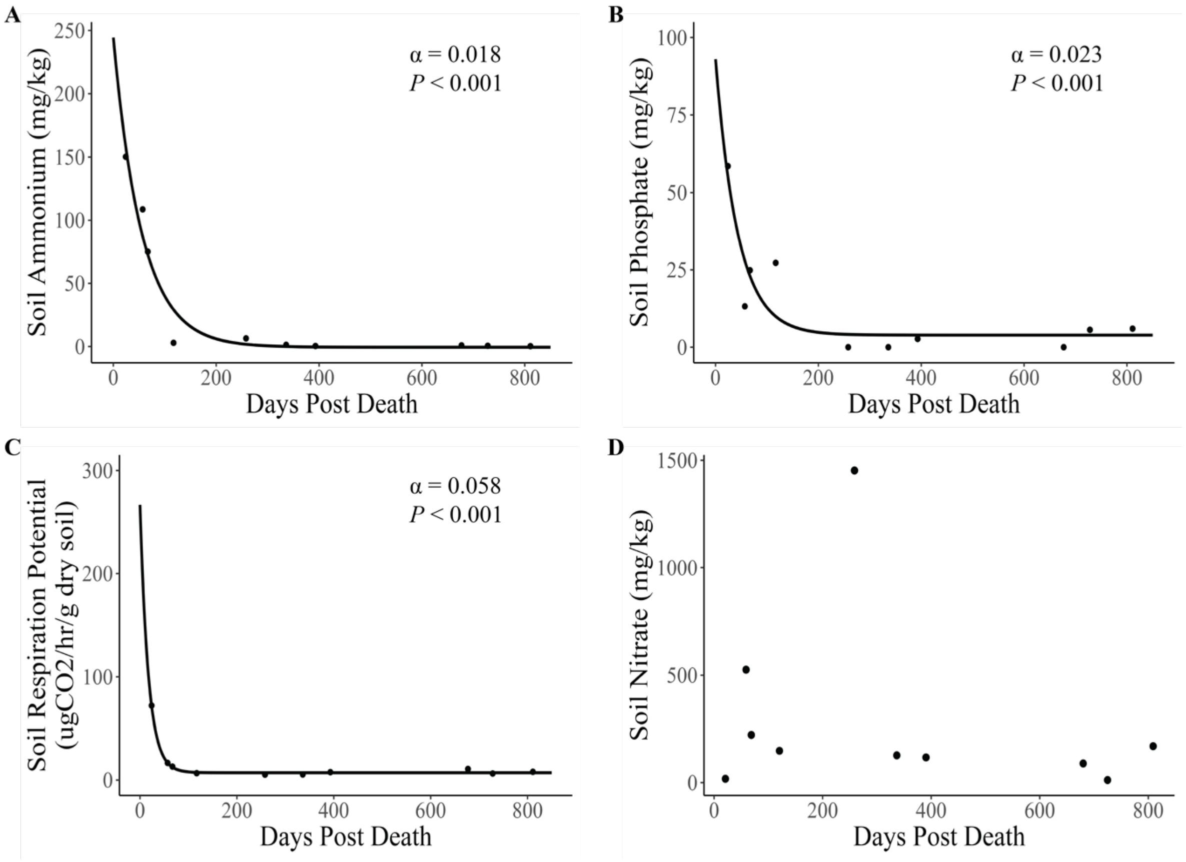

Figure 5. Relationship between carcass age and key soil metrics (soil ion concentrations and respiration potential). Lines represent predictions from exponential decay models, with α equal to the rate of decay. (A) Soil ammonium, (B) phosphate, and (C) respiration potential all decreased significantly with carcass age. The model for (D) soil nitrate failed to converge. Points represent individual measurements taken at the center of the carcass site (distance = 0.5m).