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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 micronutrients 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 move from soil into 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 gravesite, collecting soil and grass (*Urochloa mosambicensis*) samples at 0, 2.5, 5, 10, and 15 m. We then analyzed samples for CNP and micronutrient concentrations and quantified soil microbial respiration potential. We found that concentrations of soil nitrate, ammonium, ^{15}N, P, sodium, and potassium 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, ^{15}N, iron, potassium, 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, which then move into above-ground nutrient pools

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in plants. These localized nutrient pulses may drive spatiotemporal heterogeneity in plant diversity, herbivore behavior, and ecosystem processes.

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Sect. 1 Introduction

Living animals affect nutrient flows and ecosystem processes (Schmitz et al. 2018), but we have only recently acknowledged that animal carcasses could also influence nutrient availability (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 another potential driver of spatiotemporal heterogeneity in nutrient cycling and ecosystem processes – megacarcasses (animals such as elephants and rhinoceros that are >1000 kg at death) – which 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 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 terrestrial ecosystem dynamics (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,

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preventing woody encroachment) (Skarpe et al. 2004; Asner et al. 2009; Campos-Arceiz & Blake, 2011; Coverdale et al. 2016; Guy et al. 2021). The elephant's large body mass may mean that it also has an outsized impact 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 (Rische et al. 2020). Concentrations of C, N, P, and potassium (K) are 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 micronutrients such as Ca, K, and magnesium (Mg) (Jobbágy & Jackson, 2004; Ries & Shugart, 2008; Pellegrini, 2016). Thus, the large influx of nutrients released from megacarcasses might increase the mobilization of nutrients by plants, potentially increasing nutrient accessibility for above-ground 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 ^{15}N in plants within just a few months post-death (Hocking & Reynolds, 2012; van Klink et al. 2020).

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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, 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 mosambicensis*) at 0, 2.5, 5, 10, and 15 m. We then analyzed soil samples for CNP content, quantified soil microbial respiration potential, and measured %N and ^{15}N in grass tissue. We hypothesized that: (H1) elephant megacarcass decomposition would release nutrients into soil, resulting in higher concentrations of soil N, P, and micronutrients 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 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 landscape 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

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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. These 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 *Urochloa mosambicensis,* 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). 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. On the day of collection, we used 5 g of each soil sample for soil respiration measurements (described below). The rest of each sample was stored plastic bags in a -20°C freezer until nutrient analyses. Leaf samples were stored in paper bags at room temperature until dried for analyses (see below).

2.3 Hypothesis testing

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We tested our first hypothesis that elephant megacarcass decomposition would release nutrients into the soil by performing soil nutrient analyses. First, 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 ion concentrations of ammonium $[NH_4]^+$, nitrate $[NO_3]^-$, phosphate $[PO_4]^{3-}$, and plant-available P using a 1:2 water extract analysis. To determine whether soil micronutrients were distinct and elevated at the center of carcass sites relative soil further from the center, Eco-Analytica used mass spectrometry to measure concentrations of sodium (Na), magnesium (Mg), iron (Fe), calcium (Ca), and potassium (K), which are micronutrients important to both plant reproduction and herbivore nutrition (Pandey, 2010; Chen et al. 2015; Hu et al. 2021; Kaspari, 2021; Sardans & Peñuelas, 2021). 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 ^{15}N, obtained using a Vario Isotope Select Elemental Analyzer connected to a thermal conductivity detector and an Isoprime precision isotope ratio mass spectrometer (IRMS).

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, Langensebold, Germany). To quantify soil respiration and water content, we used an incubation method (Lemoine et al. 2024) 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

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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 µg h^{-1}g dry $soil^{-1}$.

To test our third hypothesis that carcass-derived nutrients would move from soil into plants, we measured foliar nutrient concentrations in *U. mosambicensis*. We dried each leaf sample in a drying oven at 60°C for 48 hours, ground dried samples with a Retsch MM400 mill (Germany), and sent 2 g of each dry sample to the BIOGRIP laboratory for measurements of %N and ^{15}N via stable isotope analysis as described above. 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 a microwave-assisted digestion procedure (Ethos UP, Magna Analytical) and an Agilent ICP-MS mass spectrometer. 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 = 0-0.5m) 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 first ran a Shapiro-Wilk normality test to determine whether the variable was normally distributed. If not, we normalized the data via log-transformation, adding 0.001 to each variable before transformation to address zeros in the dataset. Soil %N, nitrate, ammonium, ^{15}N, phosphate, plant-available P, organic C, respiration, water, and micronutrients were non-normally distributed and required log transformations (Figure S1). Leaf micronutrients were normally distributed except for Fe and Ca (Figure S2), which we log-transformed for individual analysis. Next, we ran five generalized linear mixed models in the package *lme4* (Bates et al. 2015) for each response variable: (*i*) soil type + distance

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+ 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. 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 $\Delta AICc \leq 2$ 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. Finally, 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.

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

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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). Our results were inconclusive for soil %N (Figure 2A) and nitrate concentration (Figure 2B); there was substantial support for the null model and an alternative model in both instances. For %N, soil type was the top model, with %N higher in basaltic soils, but there was also some support for the null model (ΔAICc = 1.80). The top model for soil nitrate was distance and showed nitrate decreasing with distance from the center of the carcass site, but the null model also had some support in this case as well (ΔAICc = 1.68). The top model for ammonium concentration (Figure 2C) was soil type + distance, indicating that ammonium concentrations were greatest in granitic soils and decreased with distance from the carcass regardless of soil type. The top models for ^{15}N (Figure 2D) were (i) distance and (ii) soil + distance. ^{15}N was greatest in granitic soils and decreased with distance regardless of soil type, indicating that the proportion of animal-sourced N was greater near the center of the carcass site. The top model for phosphate (Figure 2E) was soil type + distance + soil type × distance interaction. Phosphate concentrations were greater in granitic soils, but only towards the center of carcass sites. Phosphate concentrations dropped precipitously from 0-2.5 m distance and then were similar in both soil types. For plant-available P (Figure 2F), all four biological models (excluding the null) fell within the set of top models. Plant-available P was greater in basaltic soils and decreased with distance from the center in both soil types, but the effect of distance was stronger in granitic soils.

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Contrary to our first hypothesis, soil micronutrient composition did not differ significantly with distance from the carcass center; nor did most individual micronutrients (Table S1). The perMANOVA results showed that soil micronutrient composition did not differ significantly with distance ($R^2 = 0.00$, $F_{4,44} = 0.1$, $P = 1.000$) (Figure S3A), but it did differ significantly with soil type ($R^2 = 0.71$, $F_{1,44} = 108.8$, $P = 0.001$) (Figure S3B). 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. The top model for Na (Figure S4A) was distance, indicating a significant decrease in soil Na with distance from the carcass. The top model for K (Figure S4B) was soil type + distance + soil type × distance interaction. Soil K was greater in basaltic soils and decreased with distance only in granitic soils. The remaining three micronutrients (Ca, Fe, and Mg) all had soil type as the top model, appearing in higher concentrations in basaltic soils (Figure S4C-E).

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

Consistent with our second hypothesis, soil respiration potential was positively correlated with soil organic carbon concentration ($P = 0.039$) and decreased significantly with distance ($P = 0.020$) but did not differ with soil type ($P = 0.408$) (Figure 3). Results for soil water content (Figure S5) were inconclusive. The top model for water was soil, showing higher water content in granitic soils, but there was also strong support for the null model (ΔAICc = 0.42).

3.3 Hypothesis 3: Effects of megacarcasses on plant nutrient pools

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Consistent with our third hypothesis, we found evidence that N from carcasses had moved from soils into plants. Leaf %N (Figure 4A) and ^{15}N (Figure 4B) both decreased significantly with distance from the carcass site, indicating that the high N content in leaves closer to the center of a megacarcass site likely had an animal origin. These trends did not hold true for P (Figure 4C), another major limiting nutrient for savanna plants; the top model for leaf P was the null, indicating no difference in leaf P content with soil type or distance from the carcass (Figure 4C).

Leaf micronutrient composition did not differ significantly with distance ($R^2 = 0.08$, $F_{4,40} = 1.7$, $P = 0.115$; Figure S6A) but did differ with soil type ($R^2 = 0.43$, $F_{1,40} = 34.7$, $P = 0.001$; Figure S6B). Dimension 1 explained 44.4% of the variance across soil types and was primarily driven by Mg and Na. Dimension 2 explained 30.0% of the variance and was driven mainly by Ca. The top model for Na (Figure 5A) was soil type by distance, showing that leaf Na decreased with distance and was greater in basaltic soils. Leaf K (Figure 5B) and Fe (Figure 5C) both had distance as the top model and decreased significantly with distance from the carcass. The top models for Ca (Figure 5D) and Mg (Figure 5E) were the nulls, indicating no significant difference in these nutrients with distance or soil type. However, none of the individual micronutrients were correlated between soil and leaf samples (Table S3).

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), ^{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. Microbial respiration potential was also elevated towards the center of carcass sites and was strongly correlated with

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the influx of organic C (Figure 3A). Finally, %N (Figure 4A) and ^{15}N in grass (Figure 4B) were both elevated closer to the centers of carcass sites compared to grass farther from carcasses. Similarly, micronutrients Na and K in both soils and grasses were elevated closer to the center of carcass sites. Together, these results indicate that carcass-derived nutrients move into soil and subsequently into plants over relatively short time scales, cycling essential nutrients such as N from carrion into the soil and back into aboveground nutrient pools.

The initial influx of ammonium from elephant carcasses is consistent with literature on smaller carrion (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 *Urochloa mosambicensis*—in the center of the carcass site at seven out of ten of our sites and at the 2.5m distance for all sites. The three sites without vegetation in the center had the highest ammonium levels (35-72 mg/L), suggesting that *U. mosambicensis* 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. 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 3A) were also elevated near the center of carcass sites, implying that the higher rates of soil microbial biomass and activity are resulting in the oxidation of ammonium to nitrate (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 (elk, bison; Risch et al.

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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 ugCO_2/hr, respectively). Thus, the impact of increased organic C on soil microbial processes may be relatively short lived and last a matter of months.

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 P has low water solubility relative to N and therefore is less mobile in soils (Wiersum, 1962).

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 occurs over years (Coe, 1978) 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 moves into 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 the P leaching from bones at distances far from the carcass site, reducing their local effects at sites of elephant mortality.

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The contributions of megacarcasses to soil nutrient pools were strongly associated with soil type. Results confirmed that basaltic soils are overall more nutrient rich, with greater concentrations of micronutrients (P, Ca, Fe, and Mg; Figure S4B-E). However, soil ammonium (Figure 2C) and phosphate (Figure 2E) concentrations were both greater in granitic soils, indicating that organic matter from megacarcasses may persist longer in nutrient-poor and sandy granitic soil compared with nutrient-rich and clayey basaltic soil. With the exception of Na (Figure 5A), soil type had no significant effect on leaf micronutrient concentrations (Figure 5B-E). We were surprised that grass on more nutrient-rich soil did not exhibit greater nutrient concentrations. 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 micronutrients. Thus, even with increased micronutrient 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 micronutrients 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.

Sect. 5 Conclusions

This research is an initial step in understanding the ecological legacies of megacarcasses on savanna nutrient pools. During the first two years post-death, megacarcasses released pulses of N, P, and key micronutrients, which all influence primary production when limited. These nutrients stimulated soil microbial activity and enriched foliar N, and the effects were strongest

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in nutrient-poor soil. These carcass-derived nutrient hotspots represent a previously unstudied function of megaherbivores on savannas – one that we need to better understand as megaherbivore populations continue to decline across their native ranges.

Code Availability: Computer code will be posted on Dryad Digital Repository.

Data Availability: Data will be archived on Dryad Digital Repository.

Author Contributions: Deron E. Burkepile, Nathan P. Lemoine, Izak P. J. Smit, Tercia Strydom, Aimee Tallian, Johan T. du Toit, Dave I. Thompson, and Joshua P. Schimel conceived the study. Michelle L. Budny, Johan T. du Toit, Nathan P. Lemoine, Joshua P. Schimel, Izak P. J. Smit, Tercia Strydom, Aimee Tallian, Dave I. Thompson, Helga van Coller, and Deron E. Burkepile collected samples. Courtney G. Reed, Nathan P. Lemoine, Dave I. Thompson, and Deron E. Burkepile analyzed the data. Courtney G. Reed drafted the manuscript, and all authors contributed to editing.

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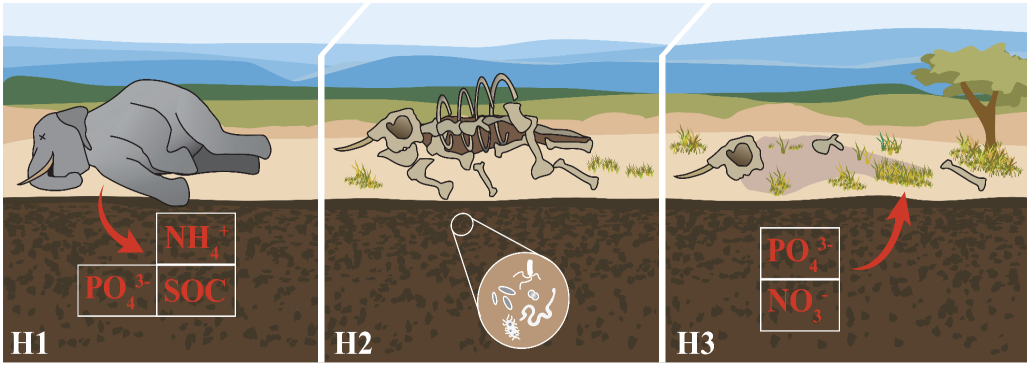

552

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

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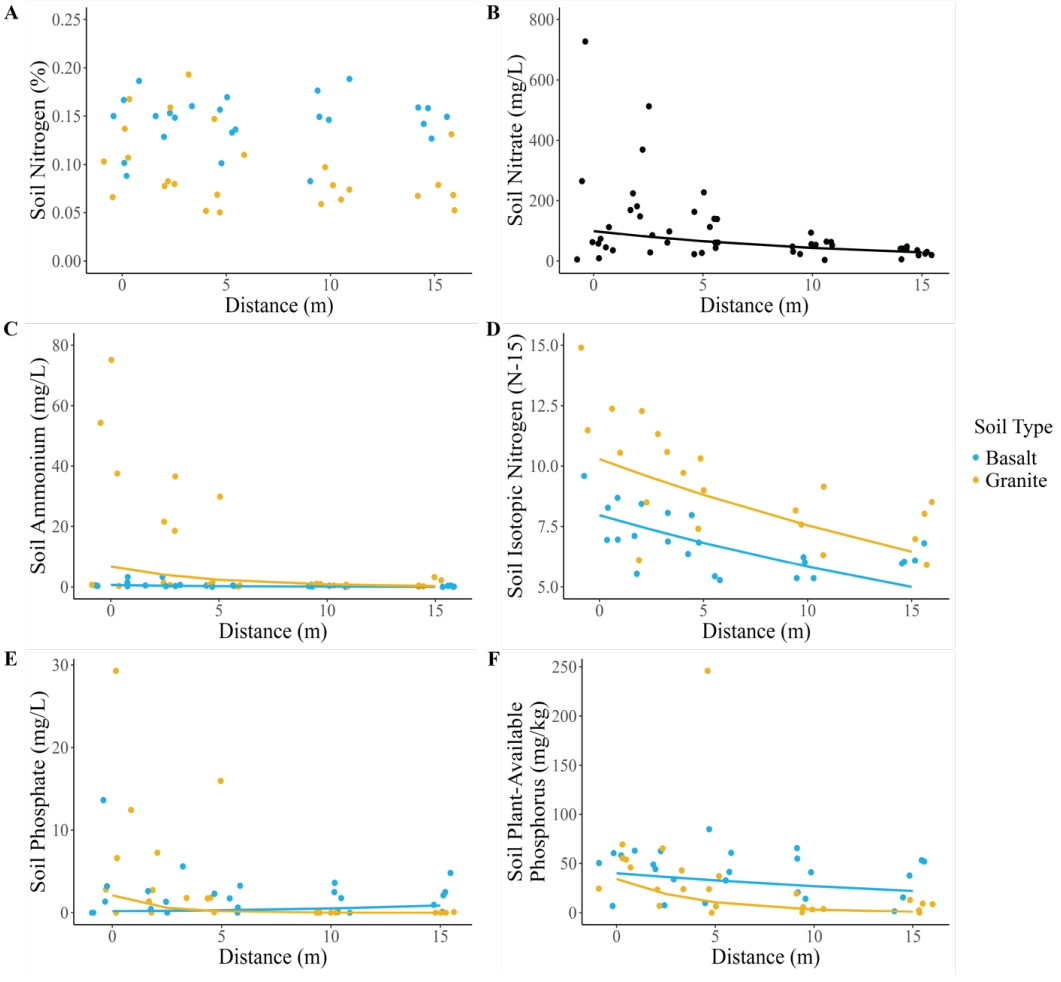

Figure 2. Soil N and P responses to elephant carcasses. (A) Soil N (%) was greater in basaltic soils but did not differ with distance from the center of the carcass site. (B) Soil nitrate decreased with distance but did not differ with soil type. (C) Ammonium and (D) ^{15}N were both greater in granitic soils and decreased with distance from the carcass. (E) Soil phosphate and (F) plant-available P both decreased with distance, and the effects were stronger in granitic soils. Log-transformed data have been back-transformed for visualization. Points represent individual measurements and are offset to be visible when they would otherwise overlap. Each plot includes only visualization (i.e., lines/colors) for parameters that were included in the set of top models.

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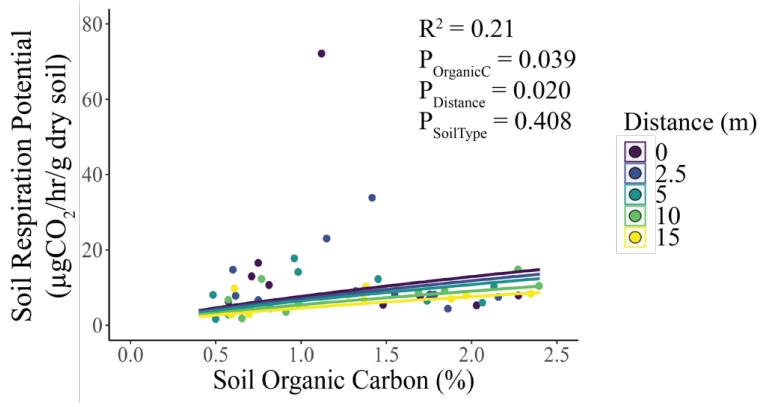

570

571 **Figure 3.** Soil respiration potential was positively correlated with soil organic C (%) and
572 decreased significantly with distance from the carcass. Log-transformed data have been back-
573 transformed for visualization. Points represent individual measurements and are offset to be
574 visible when they would otherwise overlap.

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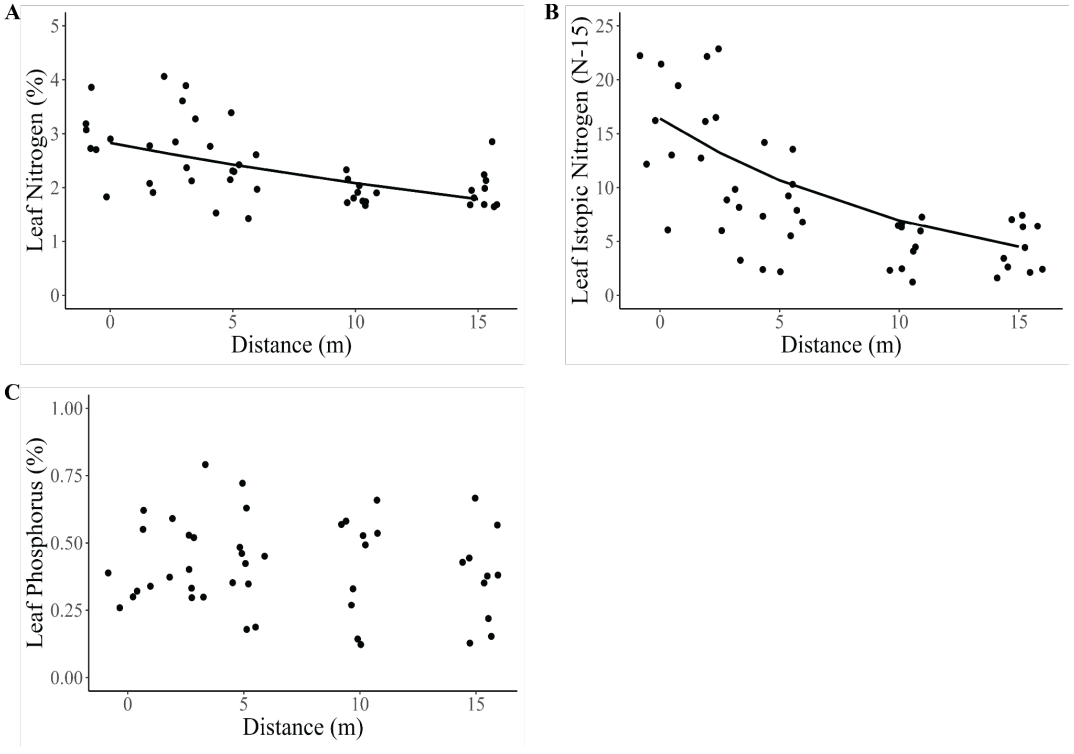

Figure 4. Leaf N and P responses to elephant carcasses. (A) Leaf %N and (B) ^{15}N both decreased with distance from the carcass site, while (C) leaf P did not differ significantly with distance or soil type. Log-transformed data have been back-transformed for visualization. Points represent individual measurements and are offset to be visible when they would otherwise overlap. 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.

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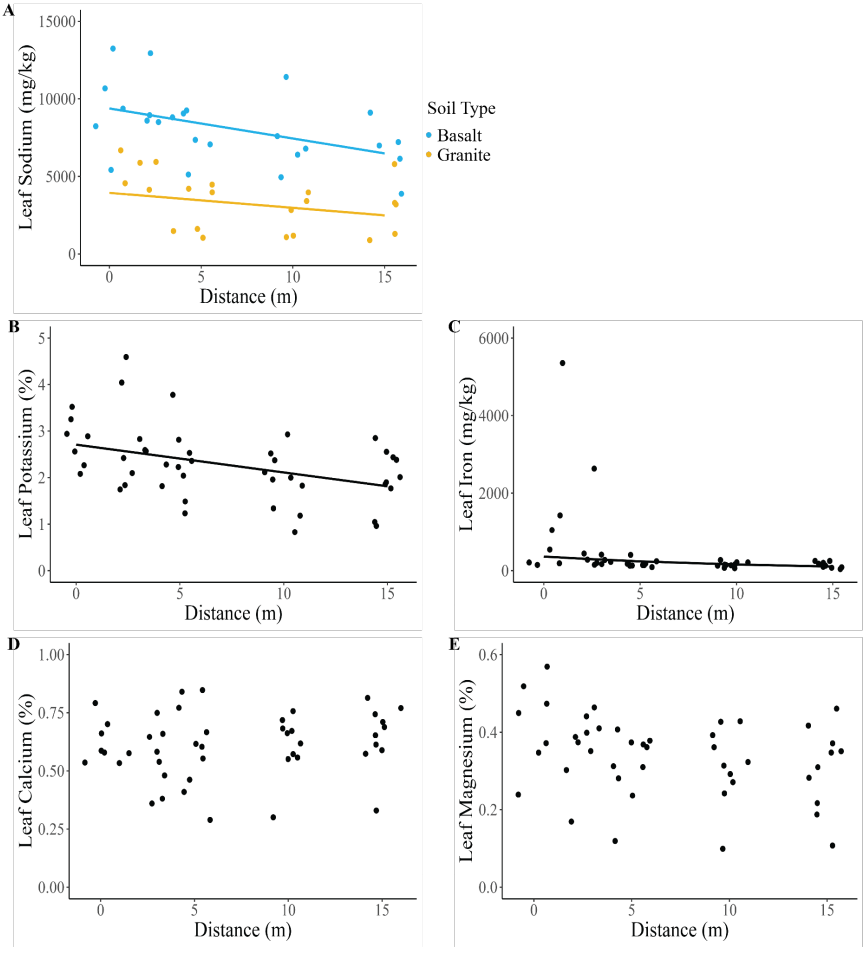

582

583 **Figure 5.** Generalized linear mixed model results for leaf micronutrients. (A) Leaf Na was
584 greatest in basaltic soil and decreased significantly with distance. (B) Leaf K and (C) Fe both
585 decreased significantly with distance. (D) Ca and (E) Mg did not differ significantly with
586 distance or soil type. Log-transformed data have been back-transformed for visualization. Points
587 represent individual measurements and are offset to be visible when they would otherwise
588 overlap.