

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

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25 **Abstract**

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

48 that influence soil microbial activity and are absorbed by plants into the above-ground nutrient  
49 pools. These localized nutrient pulses may drive spatiotemporal heterogeneity in plant diversity,  
50 herbivore behavior, and ecosystem processes.

51 **Sect. 1 Introduction**

52 Living animals affect nutrient flows through ecosystems (Schmitz et al. 2018), but we have only  
53 recently acknowledged that the nutrients from animal carcasses could also influence ecosystem  
54 processes (Barton et al. 2013; Monk et al. 2024). In marine ecosystems, whale carcasses function  
55 as unique hotspots of nutrient cycling, biodiversity, and ecosystem processes (Roman et al.  
56 2014). In terrestrial systems, mass mortality events (e.g., wildebeest, cicadas) create nutrient  
57 hotspots (Yang, 2004; Subalusky et al. 2020), while individual small and medium-sized  
58 carcasses release pulses of nutrients into the soil (Town, 2000; Barton et al. 2016; Olea et al.  
59 2019). Yet, terrestrial ecosystem ecology lacks knowledge about the role of megacarcasses  
60 (carcasses of animals such as elephants and rhinoceros that are >1000 kg at death) as potential  
61 drivers of spatiotemporal heterogeneity in nutrient cycling and ecosystem processes. Importantly,  
62 these megacarcasses may be functionally different than smaller carcasses due to the  
63 extraordinarily high concentration of nutrients and residence time of the decomposing animal  
64 (see reviews by Barton et al. 2013; Barton, 2016; Barton & Bump 2019). This question around  
65 the role of megacarcasses is particularly relevant given the megaherbivore losses that occurred  
66 during the Pleistocene extinctions and that are still occurring today (Ripple et al. 2015). We are  
67 only beginning to understand how the ‘extinction aftershock’ of losing the largest species  
68 impacts ecosystems (Owen-Smith, 1989; Flannery, 1990), and no study has yet investigated how  
69 the loss of megacarcasses might influence the dynamics of terrestrial ecosystems (Doughty et al.  
70 2013; Doughty et al. 2016).

71 We can only evaluate the importance of terrestrial megacarcasses for nutrient cycling in  
72 ecosystems where megaherbivores still exist, such as African savannas. The African savanna  
73 elephant (*Loxodonta africana*) is the largest extant land animal and is known for its key

74 ecological effects in savannas while alive (e.g., dispersing seeds, creating plant refuges,  
75 preventing woody encroachment) (Skarpe et al. 2004; Asner et al. 2009; Campos-Arceiz &  
76 Blake, 2011; Coverdale et al. 2016; Guy et al. 2021). Yet, the elephant's large body mass may  
77 mean that it also has an outsized impact in these ecosystems even after death. A 4000-kg  
78 elephant megacarcass likely represents ~2000 kg carbon (C), ~300 kg nitrogen (N), and ~125 kg  
79 phosphorus (P) deposited in the savanna landscape (estimated from stoichiometry of elephants  
80 and other mammals in Sterner & Elser, 2002). The N deposition from one elephant megacarcass  
81 (in a 700 m<sup>2</sup> impact zone assuming a 15 m disturbance radius) is roughly equivalent to the N  
82 delivered to 10,000 m<sup>2</sup> of savanna from ~100 years from atmospheric deposition (Mphepya et al.  
83 2006).

84         If megacarcasses provide large nutrient pulses, then they likely create hotspots of  
85 important below- and aboveground processes. Belowground, soil respiration and organic matter  
86 decomposition might increase with nutrient inputs from carcasses (Risch et al. 2020).  
87 Concentrations of C, N, P, and potassium (K) are often elevated near carcasses of medium-sized  
88 animals (e.g., bison, moose, kangaroo, vicuña) (Towne, 2000; Bump et al. 2009a; Macdonald et  
89 al. 2014; Risch et al. 2020; Monk et al. 2024), and nutrients such as P and calcium (Ca) continue  
90 leaching from bones even after soft tissues have been consumed or degraded (Coe, 1978; Keenan  
91 & Beeler, 2023). Aboveground, plant growth in African savannas is limited by nutrient  
92 availability, most commonly N and P (Ries & Shugart, 2008; Pellegrini, 2016), and  
93 micronutrients such as sodium (Na) and potassium (K) may co-limit plant productivity as well  
94 (Epron et al. 2012; Chen et al. 2024). Thus, the large influx of nutrients released from  
95 megacarcasses might increase the mobilization of nutrients by plants, potentially increasing  
96 nutrient accessibility for vertebrate and invertebrate herbivores (Yang, 2008; Grant & Scholes,

97 2006; Anderson et al. 2010; Joern et al. 2012). Indeed, carcasses of smaller vertebrates (e.g.,  
98 salmon, deer) can increase the proportions of nitrogen and  $\delta^{15}\text{N}$  (an indicator of animal-driven N)  
99 in plants within just a few months [postmortem](#) (Hocking & Reynolds, 2012; van Klink et al.  
100 2020).

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

118

119 **Sect. 2 Methods**

## 120 2.1 Study system and sample collection

121 We performed this research in the southern part of the Kruger National Park (KNP), South  
122 Africa (24.996 S, 31.592 E, ~275m elevation). The two dominant soil types in KNP are granitic  
123 soils ([Inceptisols](#)) and basaltic soils ([Versitols or Andisols](#)) (Khomo et al. 2017). The clay-rich  
124 basaltic soils have relatively large surface area, enabling them to retain larger quantities of water  
125 than granitic soils, which drain water more quickly and therefore are lower in water-soluble  
126 nutrients (Buitenwerf, Kulmatiski, & Higgins, 2014; Rughöft et al. 2016). The landscape of  
127 KNP is a mix of savanna grasslands and broadleaf woodlands, with an overstory dominated by  
128 trees from the genus *Combretum* (red bushwillow, *C. apiculatum*; russet bushwillow, *C.*  
129 *hereroense*; leadwood, *C. imberbe*) and trees formerly known as acacias (knobthorn,  
130 *Senegalensis nigrescens*; umbrella thorn, *Vachellia tortillis*). The park hosts a full suite of  
131 African savanna animals, including ~30,000 elephants (*Loxodonta africana*) (Coetsee &  
132 Ferreira, 2023), with a mortality rate of ~2% (~600 elephants per year). The targeted region of  
133 KNP has a high density of scavengers and predators, including white-backed vultures (*Gyps*  
134 *africanus*), spotted hyenas (*Crocuta crocuta*), and lions (*Panthera leo*) (Owen-Smith & Mills,  
135 2007).

136         During the wet season in March 2023, we identified ten elephant carcass sites (1-26  
137 months [postmortem](#)), five on relatively nutrient-rich basaltic soil and five on nutrient-poor  
138 granitic soil. KNP section rangers provided precise GPS locations of where elephant carcasses  
139 had been found. Most elephants died of old age, illness, injury, or, in the case of one young bull,  
140 fighting over territory. Carcass sites were recognizable *in situ* by a persistent bonefield,  
141 undigested gut contents, and an absence of herbaceous vegetation. At each site, we hammered a  
142 rebar post into the center of the megacarcass disturbance and ran 15 m transects out from the



143 post in each of the four cardinal directions. We collected green leaf material from *U. trichopus*, a  
144 common and abundant palatable grass species, and used an auger to collect soil samples to a  
145 depth of 10 cm at five points along each transect (0.5, 2.5, 5, 10, and 15 m) (Bump, Peterson, &  
146 Vucetich, 2009; Holdo & Mack, 2014; Gray & Bond, 2015; Monk et al. 2024). We treated the  
147 10-15m distances as representative of background concentrations of nutrients based on pilot data  
148 showing that the effect of elephant carcasses on soil nutrient concentrations was undetectable at  
149 this distance away from the carcass site, similar to studies on the carcasses of other large  
150 vertebrates (e.g., Towne, 2000; Bump et al. 2009). We pooled and homogenized the samples to  
151 yield one composite leaf and one composite soil sample per sampling distance from each carcass  
152 site. Soil samples were sieved in a 5-mm metal sieve which was cleaned in between samples  
153 with 70% ethanol. Soil samples were stored in a cooler during fieldwork. On the day they were  
154 collected, we used 5 g of each soil sample for soil respiration measurements (described below).  
155 The rest of each sample was placed in a plastic bag on the day of collection and stored in a -20°C  
156 freezer for up to 1 month; samples were stored in coolers with ice blocks during the transition  
157 from the freezer at the field site to the lab for analysis. We chose to freeze samples rather than  
158 storing at room temperature based on literature demonstrating that the impacts of freezing on soil  
159 nitrate and ammonium concentrations are fairly minimal, except in specific cases of high soil  
160 acidity or peaty soils that were not present at our field site (Esala, 1995; Turner & Romero, 2009;  
161 Sollen-Norrin & Rintoul-Hynes, 2024). Leaf samples were stored in paper bags at room  
162 temperature until dried for analyses (see below).

163

### 164 **2.3 Hypothesis testing**

165 We tested our first hypothesis that elephant carcass decomposition would release nutrients into  
166 the soil by performing soil nutrient analyses. We sent 250 g of each soil sample to Eco-Analytica  
167 laboratory at the North-West University in Potchefstroom, South Africa for measurements of soil  
168 concentrations of ammonium  $[\text{NH}_4]^+$ , nitrate  $[\text{NO}_3]^-$ , phosphate  $[\text{PO}_4]^{3-}$ , and plant-available P.  
169 Samples were air-dried and sieved through  $< 2\text{mm}$  mesh prior to chemical analysis. Plant-  
170 available P was extracted from 4 g of soil and 30 ml extraction fluid (1:7.5 ratio) using an acid-  
171 fluoride solution (P Bray-1) (FAO, 2021), measured colorimetrically using a Syssta  
172 EasyChem200 analyser, and expressed as mg/kg. The detection limit was 0.5 mg/kg, and plant  
173 available P measurements  $< 0.5$  mg/kg were replaced with half the detection limit (0.25 mg/kg)  
174 (Croghan & Egeghy, 2003). Water-soluble nitrate and phosphate anions were extracted from  
175 volume on volume 100 mg soil and 200 ml deionized water (Sonneveld & van den Ende, 1981),  
176 analyzed by ion chromatography on a Metrohm 930 Compact Flex System, and measured as  
177 mg/L. Ammonium (also 1:2 water extract) was analyzed colorimetrically using a Syssta  
178 EasyChem200 analyzer and measured as mg/L. Detection limits for soil ions were 0.01 mg/L,  
179 and soil ion concentrations measured as  $< 0.01$  mg/L were replaced with half the detection limit  
180 (0.005 mg/L). To convert the nitrate, ammonium, and phosphate units from mg/L to mg/kg, we  
181 multiplied by 2, based on the 1:2 soil to water extraction ratio.

182 To determine whether soil micronutrients were distinct and elevated at the center of  
183 carcass sites relative to soil further from the center, we measured concentrations of sodium (Na),  
184 magnesium (Mg), iron (Fe), calcium (Ca), potassium (K), and phosphorus (P). Air-dried and  
185 sieved ( $> 2$  mm) soil samples, weighed to 0.2 g, were microwaved in 9 ml 65% nitric acid  
186 ( $\text{HNO}_3$ ) and 3 ml 32% hydrochloric acid (HCl) according to EPA 3051b in a Milestone, Ethos  
187 microwave digester with UP, Maxi 44 rotor. A period of 20 minutes allowed the system to reach

188 1800 MW at a temperature of 200 °C which was maintained for 15 minutes. After cooling, the  
189 samples were brought up to a final volume of 50 ml and analyzed on an Agilent 7500 CE ICP-  
190 MS fitted with CRC (Collision Reaction Cell) technology for interference removal. The  
191 instrument is optimized using a solution containing Li, Y, Ce, and Tl (1 ppb) for standard low-  
192 oxide/low interference levels ( $\leq 1.5\%$ ) while maintaining high sensitivity across the mass range.  
193 The instrument was calibrated using ULTRASPEC® certified custom mixed multi-element stock  
194 standard solutions containing all the elements of interest (De Bruyn Spectroscopic Solutions,  
195 South Africa). Calibrations spanned the range of 0 – 30 ppm for the mineral elements Ca, Mg,  
196 Na, and K and 0 – 0.3 ppm for the rest of the trace elements. Elemental concentrations were  
197 expressed as mg/kg.

198         Finally, to determine whether elevated N levels in soils were derived from the carcass, we  
199 sent 10 g of each sample to the BIOGRIP laboratory within the Central Analytical Facility at  
200 Stellenbosch University for measurements of soil %N and  $\delta^{15}\text{N}$ , obtained using a Vario Isotope  
201 Select Elemental Analyzer connected to a thermal conductivity detector and an Isoprime  
202 precisions isotope ratio mass spectrometer (IRMS). Samples were oven-dried at 60°C for 48  
203 hours and milled to a fine powder using a Retsch MM400 mill (Germany). The powdered  
204 samples were weighed (2 – 60 mg) prior to combustion at 950°C. The gasses were reduced to  $\text{N}_2$   
205 (undiluted) in the reduction column, which was held at 600°C. A high organic carbon (HOC) soil  
206 standard ( $0.52 \pm 0.02\%$  N), along with two international reference standards (USGS40 ( $\delta^{15}\text{N} -$   
207  $4.52\%$  AIR) and USGS41 ( $\delta^{15}\text{N} + 47.57\%$  AIR)) were used for calibration. The N elemental  
208 content was expressed relative to atmospheric N as  $\text{N}_2$   $\delta^{15}\text{NAIR}$  (‰). The quantification limit for  
209  $\delta^{15}\text{N}$  on the IRMS is 1 nA (nanoAmp), and the quantification limit for %N is 0.06%. The

210 precision for %N was 0.02% and for  $\delta^{15}\text{N}$  is  $\pm 0.11\%$ , determined using the HOC standard, which  
211 was run multiple times throughout the analysis.

212 To test our second hypothesis that nutrient inputs to the soil would stimulate microbial  
213 activity, we measured soil organic C, water content, and microbial respiration potential. We sent  
214 10 g of each sample to the BIOGRIP laboratory for measurements of soil organic C using a  
215 Vario TOC Cube (Elementar, Germany). Samples (dried and milled as above) were weighed (10  
216 – 60 mg), acidified using 10% HCl to remove the total inorganic C (carbonates), and dried  
217 overnight at 60°C. All samples were analyzed through combustion at 950°C. The released CO<sub>2</sub>  
218 was measured by a non-dispersive infrared (NDIR) sensor. A high organic C ( $7.45 \pm 0.14\%$  C)  
219 soil standard from Elemental Microanalysis Ltd (UK) was included during the analysis. The  
220 quantification limit for %C is 0.14%. The precision for the %C was 0.09% and was determined  
221 using the low organic C (LOC) standard ( $1.86 \pm 0.14\%$  C), which was run multiple times  
222 throughout the analysis.

223 To quantify soil respiration and water content, we used an incubation method (Lemoine  
224 et al. 2023) in which 5 g ( $\pm 0.2$  g) of each sample was placed into a 100 ml clear glass bottle,  
225 sealed, and flushed with CO<sub>2</sub>-free air. Following flushing, we incubated the bottles for one hour  
226 at 25°C. We then recorded CO<sub>2</sub> concentrations using an LI-850 CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer.  
227 After soil respiration measurements, we determined sample dry weight by drying each sample at  
228 60°C for 24-48 hours until stable mass was achieved. We subtracted dry weight from starting  
229 weight to obtain soil water content. Finally, we used the dry weights and the Ideal Gas Law to  
230 standardize all respiration measurements to CO<sub>2</sub>  $\mu\text{g h}^{-1}\text{g dry soil}^{-1}$ .

231 To test our third hypothesis that carcass-derived nutrients would be incorporated by  
232 plants, we measured foliar nutrient concentrations in *U. trichopus*. Two grams of each dried leaf

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

251       To test whether each response variable for the three hypotheses was significantly  
252 associated with soil type and/or distance from the carcass center, we performed a model selection  
253 procedure. For each response variable, we ran five generalized linear mixed models using the  
254 gamma family (link = log) in the package *lme4* (Bates et al. 2015): (i) soil type + distance + soil  
255 type  $\times$  distance interaction, (ii) soil type + distance, (iii) soil type, (iv) distance, and (v) a null

256 model indicating no significant difference in slope or intercept after accounting for carcass site.  
257 All models included carcass site as a random effect to account for individual variation. Each  
258 model included 50 observations (10 sites x 5 distances per site). For samples in which the  
259 nutrient level was listed as 0 or undetectable, we accounted for the uncertainty by using half the  
260 detection level as described above. The narrow distribution of ages (1-26 months since death)  
261 with the sample size of  $N = 10$  sites made testing for the effect of age challenging, so we did not  
262 include carcass age in the models. We compared the models for each response variable using  
263 Akaike Information Criterion (AICc). Models with a  $\Delta AICc \leq 2$  were considered roughly  
264 equivalent in fit (Burnham and Anderson, 2002).

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

271         To determine whether leaf and soil micronutrient composition differed with distance and  
272 soil type, we ran permutational analysis of variance (perMANOVA) in *vegan* (Oksanen et al.  
273 2022). We ran the same model separately for soil and leaf micronutrient composition (soil type +  
274 distance). To determine which micronutrients contributed most to compositional differences  
275 across distances and soil types, we calculated samplewise Bray-Curtis dissimilarity and  
276 performed principal component analysis. We also tested for differences in variance in  
277 micronutrient composition across distances and soil types using “betadisper” in *vegan* (Oksanen

278 et al. 2022). We ran linear models to test for correlations between leaf and soil concentrations of  
279 each micronutrient. Each model included distance as a covariate and site as a random effect.

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

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

285

## 286 **Sect. 3 Results**

### 287 **3.1 Hypothesis 1: Effects of megacarcasses on soil nutrient pools**

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

301 Contrary to our first hypothesis, soil **micronutrient** composition did not differ  
302 significantly with distance from the carcass center; nor did most individual **micronutrients** (Table  
303 S1). The perMANOVA results showed that soil **micronutrient** composition did not differ  
304 significantly with distance ( $R^2 = 0.00$ ,  $F_{4,44} = 0.0$ ,  $P = 1.000$ ) (Figure S2A), but it did differ  
305 significantly with soil type ( $R^2 = 0.71$ ,  $F_{1,44} = 108.8$ ,  $P = 0.001$ ) (Figure S2B). There was no  
306 significant difference in variance with distance ( $F_{4,45} = 0.0$ ,  $P = 0.996$ ) or soil type ( $F_{1,48} = 2.6$ ,  $P$   
307  $= 0.115$ ). Principal components analysis showed that dimension 1 explained 53.6% of the  
308 variation between soil types and was driven primarily by differences in Mg, Ca, and Fe.  
309 Dimension 2 explained 25.9% of variation and was driven primarily by differences in K. Soil Na  
310 (Figure S3A) was marginally greater in granitic soils and decreased with distance from the  
311 carcass, with the effect greater in granitic soils. Soil K (Figure S3B) was greater in basaltic soils  
312 and decreased marginally with distance. Soil Fe, Mg, and Ca (Figure S3C-E) were greater in  
313 basaltic soils, with minimal effects of distance.

314

### 315 **3.2 Hypothesis 2: Effects of megacarcasses on soil carbon and respiration**

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

321

### 322 **3.3 Hypothesis 3: Effects of megacarcasses on plant nutrient pools**



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

330 Leaf micronutrient composition did not differ significantly with distance ( $R^2 = 0.13$ ,  $F_{4,40}$   
331  $= 1.9$ ,  $P = 0.062$ ; Figure S5A) but did differ with soil type ( $R^2 = 0.17$ ,  $F_{1,40} = 9.7$ ,  $P = 0.001$ ;  
332 Figure S5B). There was no significant difference in variance with distance ( $F_{4,41} = 0.5$ ,  $P =$   
333  $0.713$ ) or soil type ( $F_{1,44} = 1.9$ ,  $P = 0.173$ ). Dimension 1 explained 42.8% of the variance across  
334 soil types and was primarily driven by Mg, Na, and P. Dimension 2 explained 26.6% of the  
335 variance and was driven mainly by K, Ca, and Fe. Foliar Na (Figure S6A) and Mg (Figure S6B)  
336 were both greater in basaltic soils and decreased with distance from the carcass center. Foliar K  
337 (Figure S6C) and Fe (Figure S6D) both decreased with distance as well but did not differ with  
338 soil type. The null model was in the top set for foliar Ca, indicating no significant relationship  
339 between foliar Ca concentrations and soil type or distance from the carcass center. Individual  
340 micronutrients (K, Ca, Mg, Fe) were not correlated between leaf and soil samples, with the  
341 exception of Na (Table S3).

342

### 343 **3.4 Effects of carcass age on soil ions and respiration potential**

344 Soil ammonium ( $\alpha = 0.018$ ,  $P < 0.001$ ), phosphate ( $\alpha = 0.023$ ,  $P < 0.001$ ), and respiration  
345 potential ( $\alpha = 0.058$ ,  $P < 0.001$ ) all decreased significantly with carcass age (Figure 5A-C). The

346 exponential decay model for nitrate failed to converge due to an outlier with extremely high soil  
347 nitrate (1454 mg/kg) at 258 days [postmortem](#) (Figure 5D). We ran a t-test to test for a difference  
348 in mean carcass age between soil types and found no significant difference between the two  
349 groups ( $P = 0.294$ ).

350

#### 351 **Sect. 4 Discussion**

352 Here, we show that elephant megacarcasses influence soil and foliar nutrients during at least the  
353 first two years following mortality. Consistent with our hypotheses, soil nitrate (Figure 2B),  
354 ammonium (Figure 2C),  $\delta^{15}\text{N}$  (Figure 2D), and P (Figure 2E-F) concentrations were all elevated  
355 at the center of carcass sites and decreased with distance from the center. Soil %N, nitrate,  
356 ammonium, and plant-available P concentrations at the 15m point were consistent with those  
357 found in other studies of soil nutrient content in Kruger (Aranibar et al. 2003; Rughöft et al.  
358 2016), confirming that the 15m point serves as an effective baseline control in this experiment.  
359 Microbial respiration potential was also elevated towards the center of carcass sites and was  
360 correlated with the abundance of organic C (Figure 3). Finally, %N (Figure 4A) and  $\delta^{15}\text{N}$  in a  
361 common grass (Figure 4B) were both elevated closer to the centers of carcass sites compared to  
362 grass farther from carcasses. Together, these results indicate that carcass-derived nutrients move  
363 into soil and subsequently get absorbed by plants over relatively short time scales, cycling  
364 essential nutrients such as N from carrion into the soil and then back into aboveground nutrient  
365 pools.

366 [The initial influx of ammonium from elephant carcasses may have time-dependent](#)  
367 [impacts on plant abundance at elephant carcass sites. The mean ammonium level at the center of](#)  
368 [carcass sites \(34.8 mg/kg\) was higher than the level generally considered toxic to plants \(Britto](#)

369 & Kronzucker, 2002). Yet, we found living grass—typically *U. trichopus*—in the center of the  
370 carcass site at seven out of ten of our sites (ammonium range 10-172 mg/kg) and at the 2.5m  
371 distance for all sites (ammonium range 0-72 mg/kg). The three sites without vegetation in the  
372 center had the highest ammonium levels (70-144 mg/kg), suggesting that *U. trichopus* has a  
373 higher degree of ammonium tolerance than some sympatric grass species but may still be limited  
374 by the high ammonium levels at the centers of these three relatively fresh carcass sites. However,  
375 the recentness of the disturbance from the carcass likely also plays a role in determining plant  
376 abundance near the center of the carcass. Because of the elephant carcass site age distribution,  
377 (mean 350 days postmortem; range 24-811 days), this study may not have captured the full  
378 impact of ammonium release from carcasses during the early stages of decomposition. Soil  
379 ammonium spiked early and decreased rapidly (Figure 5A), and future research on carcasses  
380 within the first few weeks postmortem would enhance our understanding of these early nutrient  
381 dynamics.

382 Soil nitrate (Figure 2B) and soil respiration potential (Figure 3) were also elevated near  
383 the center of carcass sites, indicating higher activity rates for nitrifying bacteria and heterotrophic  
384 microbes (Prosser, 2011). These results are consistent with other work on carrion, where  
385 microbial activity tends to be greater in soils near carcasses as compared to surrounding soil  
386 (Bump et al. 2009b). However, carcass effects on soil microbial respiration exhibit a high degree  
387 of intra-system variation (Risch et al. 2020), and the potentially short window during which  
388 increased respiration occurs may make capturing these variations challenging. For example, soil  
389 respiration potential at the center of the three youngest carcass sites was on average 2x higher  
390 than the seven older sites (18.43 and 9.62  $\mu\text{g CO}_2$  per hour per gram of dry soil, respectively;  
391 Figure 5D). Thus, the impact of increased organic C on soil microbial processes may be

392 relatively short lived and only last a matter of months (Keenan et al. 2018; Keenan, Schaeffer, &  
393 DeBruyn, 2019). These trends are consistent with soil ammonium and phosphate, both of which  
394 are highest at the youngest carcass sites (<200 days [postmortem](#); Figure 5A-B). Soil microbial  
395 respiration rate is also highly elevated early on, but it decreases at a faster rate over time than soil  
396 ions (Figure 5C). Thus, soil dynamics during the first several months after death may play a  
397 crucial role in determining the long-term impacts of megacarcasses on savannas and therefore  
398 provides a promising avenue for future research.

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

415           The elevated plant-available P at the center of carcass sites likely came primarily from  
416 phosphate released from decomposing tissue (Yong et al. 2019). Bone decomposition, which is  
417 also likely a major source of P from animal carcasses (Subalusky et al. 2020), occurs over long  
418 time scales (Coe, 1978; Subalusky et al. 2020) and therefore should result in the slow release of  
419 P and a gradual decrease in the N:P ratio (Parmenter & MacMahon, 2009; Quaggiotto et al.  
420 2019). Indeed, initial inorganic N influxes to the Mara River in Kenya from mass wildebeest die-  
421 offs are 10-fold greater than concurrent increases in P, which instead releases slowly over about  
422 seven years of bone decomposition (Subalusky et al. 2017). Research following megacarcasses  
423 over longer timeframes [postmortem](#) is needed to clarify when P from enriched soil is absorbed  
424 by plants and at what stage megacarcass bones begin contributing to soil P dynamics. It is also  
425 possible that bone dispersal by scavengers may result in less P leaching from bones close to  
426 where the elephant died and more P being distributed across the landscape at distances far from  
427 the carcass site.

428           The contributions of megacarcasses to soil [nutrient](#) pools were strongly associated with  
429 soil type. Our results confirmed the previously-established trend that basaltic soils are overall  
430 more cation rich than granitic soils, with greater concentrations of P, K, Fe, Mg, and Ca (Figure  
431 2G; Figure S3B-E; Gertenbach, 1983; Craine, Morrow, & Stock, 2008; Wigley et al. 2014).  
432 However, soil ammonium,  $\delta^{15}\text{N}$ , and phosphate were all higher in the granitic soils towards the  
433 center of carcass sites, decreasing steeply to be similar to basaltic soils about 10 m from the  
434 carcass center (Figure 2C-E). These results indicate that the impact of organic matter from  
435 megacarcasses may be stronger in relatively nutrient-poor and sandy granitic soil compared with  
436 nutrient-rich and clayey basaltic soil. We were surprised that grass on basaltic soil did not  
437 consistently exhibit greater [nutrient concentrations](#). One potential explanation is that grass may

438 primarily be limited by macronutrients like N and P on both soil types (Craine et al. 2008;  
439 Holdo, 2013) rather than by [micronutrients](#). Thus, even with increased [micronutrient](#) availability  
440 their actual uptake may not differ substantially. Studies on ungulate carcasses (e.g., muskoxen,  
441 moose, zebra) have shown increased foliar N at carcass sites (Danell et al. 2002; Bump et al.  
442 2009b; Turner et al. 2014), but to date there is little research on the flow of [micronutrients](#) from  
443 carrion to plants and none on the pipeline from megacarcasses to plants. Moreover, it remains to  
444 be seen whether increases in foliar N and other nutrients affect herbivory rates at carcass sites  
445 and how long such effects may last.

446         The magnitude of [nitrogen](#) inputs from megacarcasses, as well as the substantial size and  
447 duration of their impact zones, means their impacts on ecosystem processes may be functionally  
448 distinct from smaller carrion. [Soil nitrate concentrations at elephant carcass sites are orders of](#)  
449 [magnitude higher than at carcass sites of smaller carrion \(e.g., rabbits, white-tailed deer,](#)  
450 [kangaroo\) \(Quaggiato et al. 2019; Bump et al. 2009; Barton et al. 2016\). Even for large ungulates](#)  
451 [such as moose, total soil inorganic nitrogen \(ammonium + nitrate\) at carcass sites is a mean 300](#)  
452 [mg/kg \(Bump, Peterson, & Vucetich, 2009\), substantially lower than the mean total soil](#)  
453 [inorganic nitrogen at elephant carcass sites \(2.5m distance; 473 mg/kg\). Termite mounds,](#)  
454 [another long-lasting source of savanna nutrient heterogeneity, have mean soil nitrate](#)  
455 [concentrations \(197 mg/kg\) lower than elephant carcass sites, but maximum nitrate](#)  
456 [concentrations that are on par with them \(974 mg/kg\) \(Seymour et al. 2014\), again indicating that](#)  
457 [elephant carcasses are one of the strongest known individual contributors of soil nitrogen in](#)  
458 [African savanna ecosystems, which may have important implications for savanna ecology.](#)  
459 Indeed, there is evidence that carcass size strongly impacts scavenger food web structure  
460 (Moleón et al. 2015; Morris et al. 2023). Moreover, the attraction of animals to carcasses via

461 scavenging, predation, or mourning (Goldenberg & Wittemyer, 2020) could have positive  
462 feedbacks on nutrient cycling (Bump, Peterson, & Vucetich, 2009; Monk et al. 2024), which  
463 may be magnified by carcass size. Thus, the impacts of megacarcasses on savanna ecosystem  
464 processes may be dissimilar to the effects of small carrion and more similar to other more  
465 persistent contributors to savanna ecosystem processes, such as termite mounds (Davies et al.  
466 2016), cattle bomas (Augustine, 2003), and even mass animal mortality events (Subalusky et al.  
467 2017, 2020).

468

## 469 **Sect. 5 Conclusions**

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

478

479 **Data and Code Availability:** Data and computer code are archived on Dryad Digital Repository  
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481

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487 Deron E. Burkepile analyzed the data. Courtney G. Reed drafted the manuscript, and all authors  
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489

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501

## 502 **References**

- 503 1. Agbenin, J. O. & Yakubu, S. Potassium-calcium and potassium-magnesium exchange  
504 equilibria in an acid savanna soil from northern Nigeria. *Geoderma*, 136, 542-554,  
505 <https://doi.org/10.1016/j.geoderma.2006.04.008>, 2006.



- 506 2. Anderson, T. M., Hopcraft, J. G. C., Eby, S., Ritchie, M., Grace, J. B., & Olf, H. Landscape-  
507 scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore  
508 hotspots. *Ecol.*, 91, 1519–1529, <https://doi.org/10.1890/09-0739.1>, 2010.
- 509 3. Aranibar, J. N., Macko, S. A., Anderson, I. C., Potgieter, A. L. F., Sowry, R. & Shugart, H.  
510 H. Nutrient cycling responses to fire frequency in the Kruger National Park (South Africa) as  
511 indicated by stable isotope analysis. *Isotopes Environ. Health Stud.*, 39, 141-158,  
512 <https://doi.org/10.1080/1025601031000096736>, 2003.
- 513 4. Aria, Y. & Sparks, D. L. Phosphate reaction dynamics in soils and soil components: a  
514 multiscale approach. *Adv. Agron.*, 94, 135-179, [https://doi.org/10.1016/S0065-](https://doi.org/10.1016/S0065-2113(06)94003-6)  
515 [2113\(06\)94003-6](https://doi.org/10.1016/S0065-2113(06)94003-6), 2007.
- 516 5. Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., Jacobson, J.,  
517 Colgan, M. S., & Martin, R. E. Large-scale impacts of herbivores on the structural diversity  
518 of African savannas. *PNAS*, 106, 4947–4952, <https://doi.org/10.1073/pnas.0810637106>,  
519 2009.
- 520 6. Augustine, D. J. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in  
521 an East African savanna. *J. Appl. Ecol.*, 40, 137-149, [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2664.2003.00778.x)  
522 [2664.2003.00778.x](https://doi.org/10.1046/j.1365-2664.2003.00778.x), 2003.
- 523 7. Barton, P. S., Cunningham, S. A., Lindenmayer, D. B., & Manning, A. D. The role of carrion  
524 in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*,  
525 171, 761–772, <https://doi.org/10.1007/s00442-012-2460-3>, 2013.
- 526 8. Barton, P.S. Carrion Ecology, Evolution, and Their Applications. Edited by: M.E. Benbow,  
527 J.K. Tomberlin, A.M. Tarone. CRC Press, Boca Raton, FL, USA. 2016.

- 528 9. Barton, P. S., McIntyre, S., Evans, M. J., Bump, J. K., Cunningham, S. A., & Manning, A. D.  
529 Substantial long-term effects of carcass addition on soil and plants in a grassy eucalypt  
530 woodland. *Ecosphere*, 7, e01537, <https://doi.org/10.1002/ecs2.1537>, 2016.
- 531 10. Barton, P.S., Bump, J.K. Carrion decomposition. In: Carrion Ecology and Management.  
532 Edited by: P.P. Olea, P. Mateo-Tomas, J.A. Sanchez-Zapata. Springer, NY, USA, 101-124,  
533 2019.
- 534 11. Bates, D., Mächler, M., Bolker, B., & Walker, S. Fitting linear mixed-effects models using  
535 lme4. *J. Stat. Softw.*, 67, 1–48, <https://doi.org/10.18637/jss.v067.i01>, 2015.
- 536 12. Britto, D. T., & Kronzucker, H. J. NH<sub>4</sub><sup>+</sup> toxicity in higher plants: a critical review. *J. Plant*  
537 *Physiol.*, 159, 567–584, <https://doi.org/10.1078/0176-1617-0774>, 2002.
- 538 13. Buitenwerf, R., Kulmatiski, A. & Higgins, S. I. Soil water retention curves for the major soil  
539 types of the Kruger National Park. *Koedoe*, 56, a1228,  
540 <http://dx.doi.org/10.4102/koedoe.v56i1.1228>, 2014.
- 541 14. Bump, J. K., Peterson, R. O., & Vucetich, J. A. Wolves modulate soil nutrient heterogeneity  
542 and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecol.*, 90, 3159–  
543 3167, <https://doi.org/10.1890/09-0292.1>, 2009.
- 544 15. Bump, J. K., Webster, C. R., Vucetich, J. A., Peterson, R. O., Shields, J. M., & Powers, M.  
545 D. (2009). Ungulate carcasses perforate ecological filters and create biogeochemical hotspots  
546 in forest herbaceous layers allowing trees a competitive advantage. *Ecosyst.*, 12, 996–1007,  
547 <https://doi.org/10.1007/s10021-009-9274-0>, 2009.
- 548 16. Burnham, K. P. & Anderson, D. R. Model Selection and Multimodel Inference. Springer  
549 New York, NY. <http://doi.org/10.1007/b97636>, 2002.

- 550 17. Campos-Arceiz, A., & Blake, S. Megagardeners of the forest – the role of elephants in seed  
551 dispersal. *Acta Oecol.*, 37, 542–553, <https://doi.org/10.1016/j.actao.2011.01.014>, 2011.
- 552 18. Chen, J., Gutjahr, C., Bleckmann, A., & Dresselhaus, T. Calcium signaling during  
553 reproduction and biotrophic fungal interactions in plants. *Mol. Plant*, 8, 595–611,  
554 <https://doi.org/10.1016/j.molp.2015.01.023>, 2015.
- 555 19. Chen, B., Fang, J., Piao, S., Ciais, P., Black, T. A., Wang, F., Niu, S., Zeng, Z. & Luo, Y. A  
556 meta-analysis highlights globally widespread potassium limitation in terrestrial ecosystems.  
557 *New Phytologist*, 241, 154-165, <https://doi.org/10.1111/nph.19294>, 2024.
- 558 20. Coe, M. The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya.  
559 *J. Arid Environ.*, 1, 71–86, [https://doi.org/10.1016/S0140-1963\(18\)31756-7](https://doi.org/10.1016/S0140-1963(18)31756-7), 1978.
- 560 21. Coetsee, M. & Ferreira, S. Bridging science, management, and opinion: GLTFCA elephant  
561 management [Conference presentation]. Savanna Science Network Meeting, Skukuza,  
562 Kruger National Park, South Africa, 2023 March 5-9.
- 563 22. Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A., Goheen,  
564 J. R., Palmer, T. M., & Pringle, R. M. Elephants in the understory: opposing direct and  
565 indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecol.*, 97,  
566 3219–3230, <https://doi.org/10.1002/ecy.1557>, 2016.
- 567 23. Craine, J. M., Morrow, C., & Stock, W. D. Nutrient concentration ratios and co-limitation in  
568 South African grasslands. *New Phytol.*, 179, 829–836, <https://doi.org/10.1111/j.1469-8137.2008.02513.x>, 2008.
- 570 24. Croghan C. & Egeghy P. P., Methods of dealing with values below the limit of detection  
571 using SAS. *Southern SAS User Group*, 22, 2003.

- 572 25. Danell, K., Berteaux, D., & Bråthen, K. A. Effect of muskox carcasses on nitrogen  
573 concentration in tundra vegetation. *Arctic*, 55, 389–392, <http://www.jstor.org/stable/40512497>,  
574 2002.
- 575 26. Davies, A. B., Levick, S. R., Robertson, M. P., van Rensburg, B. J., Asner, G. P. & Parr, C.  
576 L. Termite mounds differ in their importance for herbivores across savanna types, seasons  
577 and spatial scales. *Oikos*, 125, 726-734, <https://doi.org/10.1111/oik.02742>, 2016.
- 578 27. Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E. S., Malhi, Y.,  
579 Dunning, J. B., Jr, & Svenning, J.-C. Global nutrient transport in a world of giants. *PNAS*,  
580 113, 868–873, <https://doi.org/10.1073/pnas.1502549112>, 2016.
- 581 28. Doughty, C. E., Wolf, A., & Malhi, Y. The legacy of the Pleistocene megafauna extinctions  
582 on nutrient availability in Amazonia. *Nat. Geosci.*, 6, 761–764,  
583 <https://doi.org/10.1038/ngeo1895>, 2013.
- 584 29. Epron, D., Laclau, J-P., Almeida, J. C. R., Gonçalves, J. L. M., Ponton, S., Sette, Jr., C. R.,  
585 Delgado-Rojas, J. S., Bouillet, J-P. & Nouvellon, Y. Do changes in carbon allocation account  
586 for the growth response to potassium and sodium applications in tropical Eucalyptus  
587 plantations? *Tree Physiology*, 32, 667-679, <https://doi.org/10.1093/treephys/tpr107>, 2012.
- 588 30. Esala, M. J. Changes in the extractable ammonium- and nitrate-nitrogen contents of soil  
589 samples during freezing and thawing. *Commun. Soil Sci. Plant Anal.*, 26, 61-68,  
590 <https://doi.org/10.1080/00103629509369280>, 1995.
- 591 31. FAO. Standard operating procedure for soil available phosphorus - Bray I and Bray II  
592 method. <http://www.fao.org/3/cb3460en/cb3460en.pdf>, 2021.

- 593 32. Flannery, T. F. Pleistocene faunal loss: implications of the aftershock for Australia's past and  
594 future. *Archaeol. Ocean.*, 25, 45–55, <https://doi.org/10.1002/j.1834-4453.1990.tb00232.x>,  
595 1990.
- 596 33. Gertenbach, W. Landscapes of the Kruger National Park. *Koedoe*, 26, 9-121,  
597 <https://doi.org/10.4102/koedoe.v26i1.591>, 1983.
- 598 34. Goldenberg, S. Z. & Wittemyer, G. Elephant behavior toward the dead: A review and  
599 insights from field observations. *Primates*, 61, 119-128, [https://doi.org/10.1007/s10329-019-](https://doi.org/10.1007/s10329-019-00766-5)  
600 [00766-5](https://doi.org/10.1007/s10329-019-00766-5), 2020.
- 601 35. Grant, C. C., & Scholes, M. C. The importance of nutrient hot-spots in the conservation and  
602 management of large wild mammalian herbivores in semi-arid savannas. *Biol. Conserv.*, 130,  
603 426–437, <https://doi.org/10.1016/j.biocon.2006.01.004>, 2006.
- 604 36. Gray, E. F. & Bond, W. Soil nutrients in an African forest/savanna mosaic: Drivers or  
605 driven? *S. Afr. J. Bot.*, 101, 66-72, <https://doi.org/10.1016/j.sajb.2015.06.003>, 2015.
- 606 37. Guy, T. J., Hutchinson, M. C., Baldock, K. C. R., Kayser, E., Baiser, B., Staniczenko, P. P.  
607 A., Goheen, J. R., Pringle, R. M., & Palmer, T. M. Large herbivores transform plant-  
608 pollinator networks in an African savanna. *Curr. Biol.*, 2964–2971,  
609 <https://doi.org/10.1016/j.cub.2021.04.051>, 2021.
- 610 38. Hocking, M. D. & Reynolds, J. D. Nitrogen uptake by plants subsidized by Pacific salmon  
611 carcasses: a hierarchical experiment. *Can. J. For. Res.*, 42, 908-917,  
612 <https://doi.org/10.1139/x2012-045>, 2012.
- 613 39. Holdo, R. M. Effects of fire history and N and P fertilization on seedling biomass, specific  
614 leaf area, and root:shoot ratios in a South African savannah. *S. Afr. J. Bot.*, 86, 5–8,  
615 <https://doi.org/10.1016/j.sajb.2013.01.005>, 2013.

- 616 40. Holdo, R. M. & Mack, M. C. Functional attributes of savanna soils: contrasting effects of  
617 tree canopies and herbivores on bulk density, nutrients and moisture dynamics. *J. Ecol.*, 102,  
618 1171-1182, <https://doi.org/10.1111/1365-2745.12290>, 2014.
- 619 41. Hu, L., Wu, Z., Robert, C. A. M., Ouyang, X., Züst, T., Mestrot, A., Xu, J., & Erb, M. Soil  
620 chemistry determines whether defensive plant secondary metabolites promote or suppress  
621 herbivore growth. *PNAS*, 118, e2109602118, <https://doi.org/10.1073/pnas.2109602118>,  
622 2021.
- 623 42. Joern, A., Provin, T., & Behmer, S. T. Not just the usual suspects: insect herbivore  
624 populations and communities are associated with multiple plant nutrients. *Ecol.*, 93, 1002–  
625 1015, <https://doi.org/10.1890/11-1142.1>, 2012.
- 626 43. Kaspari, M. The invisible hand of the periodic table: how micronutrients shape ecology.  
627 *Annu. Rev. Ecol. Evol. Syst.*, 52, 199–219, [https://doi.org/10.1146/annurev-ecolsys-012021-](https://doi.org/10.1146/annurev-ecolsys-012021-090118)  
628 [090118](https://doi.org/10.1146/annurev-ecolsys-012021-090118), 2021.
- 629 44. Keenan, S. W., Schaeffer, S. M., Jin, V. L. & DeBruyn, J. M. Mortality hotspots: nitrogen  
630 cycling in forest soils during vertebrate decomposition. *Soil Biol. Biochem.*, 121, 165-176,  
631 <https://doi.org/10.1016/j.soilbio.2018.03.005>, 2018.
- 632 45. Keenan, S. W., Schaeffer, S. M., and DeBruyn, J. M. Spatial changes in soil stable isotopic  
633 composition in response to carrion decomposition. *Biogeosciences*, 16, 3929–3939,  
634 <https://doi.org/10.5194/bg-16-3929-2019>, 2019.
- 635 46. Keenan, S. W., & Beeler, S. R. Long-term effects of buried vertebrate carcasses on soil  
636 biogeochemistry in the Northern Great Plains. *PloS One*, 18, e0292994,  
637 <https://doi.org/10.1371/journal.pone.0292994>, 2023.

- 638 47. Khomo, L., Trumbore, S., Bern, C. R. & Chadwick, O. A. Timescales of carbon turnover in  
639 soils with mixed crystalline mineralogies. *SOIL*, 3, 17-30, [https://doi.org/10.5194/soil-3-17-](https://doi.org/10.5194/soil-3-17-2017)  
640 [2017](https://doi.org/10.5194/soil-3-17-2017), 2017.
- 641 48. Lathwell, D. J. & Grove, T. L. Soil-plant relationships in the tropics. *Annu. Rev. Ecol. Syst.*,  
642 17, 1-16, <https://www.jstor.org/stable/2096986>, 1986.
- 643 49. Lemoine, N. P., Budny, M. L., Rose, E., Lucas, J., & Marshall, C. W. Seasonal soil moisture  
644 thresholds inhibit bacterial activity and decomposition during drought in a tallgrass prairie.  
645 *Oikos*, 2024, e10210, <https://doi.org/10.1111/oik.10201>, 2023.
- 646 50. Macdonald, B. C. T., Farrell, M., Tuomi, S., Barton, P. S., Cunningham, S. A., & Manning,  
647 A. D. Carrion decomposition causes large and lasting effects on soil amino acid and peptide  
648 flux. *Soil Biol. Biochem.*, 69, 132–140, <https://doi.org/10.1016/j.soilbio.2013.10.042>, 2014.
- 649 51. Moleón, M., Sánchez-Sapata, J. A., Sebastián-González, E. & Owen-Smith, N. Carcass size  
650 shapes the structure and functioning of an African scavenging assemblage. *Oikos*, 124, 1391-  
651 1403, <https://doi.org/10.1111/oik.02222>, 2015.
- 652 52. Monk, J. D., Donadio, E., Smith, J. A., Perrig, P. L., Middleton, A. D., & Schmitz, O. J.  
653 Predation and biophysical context control long-term carcass nutrient inputs in an Andean  
654 ecosystem. *Ecosyst.*, 27, 346–359, <https://doi.org/10.1007/s10021-023-00893-7>, 2024.
- 655 53. Morris, A. W., Smith, I., Chakrabarti, S., Lala, F., Nyaga, S. & Bump, J. K. Eating an  
656 elephant, one bite at a time: predator interactions at carrion bonanzas. *Food Webs*, 37,  
657 e00304, <https://doi.org/10.1016/j.fooweb.2023.e00304>, 2023.
- 658 54. Mphepya, J. N., Galy-Lacaux, C., Lacaux, J. P., Held, G., & Pienaar, J. J. Precipitation  
659 chemistry and wet deposition in Kruger National Park, South Africa. *J. Atmos. Chem.*, 53,  
660 169–183, <https://doi.org/10.1007/s10874-005-9005-7>, 2006.

- 661 55. Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P,  
662 Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G,  
663 Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B,  
664 Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A,  
665 Ter Braak C, Weedon J. Community Ecology Package. R package version 2.6-4,  
666 <https://CRAN.R-project.org/package=vegan>, 2022.
- 667 56. Olea, P.P, Mateo-Tomas, P., Sanchez-Zapata, J.A. (eds.) Carrion Ecology and Management.  
668 Springer, NY, USA, 2019.
- 669 57. Owen-Smith, N. Megafaunal extinctions: the conservation message from 11,000 years B.P.  
670 *Conserv. Biol.*, 3, 405–412, <https://www.jstor.org/stable/2386221>, 1989.
- 671 58. Owen-Smith, N., & Mills, M. G. L. Predator-prey size relationships in an African large-  
672 mammal food web. *J. Anim. Ecol.*, 77, 173–183, <https://doi.org/10.1111/j.1365->  
673 [2656.2007.01314.x](https://doi.org/10.1111/j.1365-2656.2007.01314.x), 2008.
- 674 59. Pandey, N. Role of micronutrients in reproductive physiology of plants. *Plant Stress*, 4, 1-13.  
675 <https://www.semanticscholar.org/paper/af9a8662b83613f6e0d5e538ed33f3add4a1d5a1>,  
676 2010.
- 677 60. Parmenter, R. R., & MacMahon, J. A. Carrion decomposition and nutrient cycling in a  
678 semiarid shrub–steppe ecosystem. *Ecol. Monogr.*, 79, 637–661, <https://doi.org/10.1890/08->  
679 [0972.1](https://doi.org/10.1890/08-0972.1), 2009.
- 680 61. Pellegrini, A. F. A. Nutrient limitation in tropical savannas across multiple scales and  
681 mechanisms. *Ecol.*, 97, 313–324, <https://doi.org/10.1890/15-0869.1>, 2016.
- 682 62. Prosser, J. I. Soil Nitrifiers and Nitrification. In Nitrification. ASM Press, pp. 347-383, 2014.

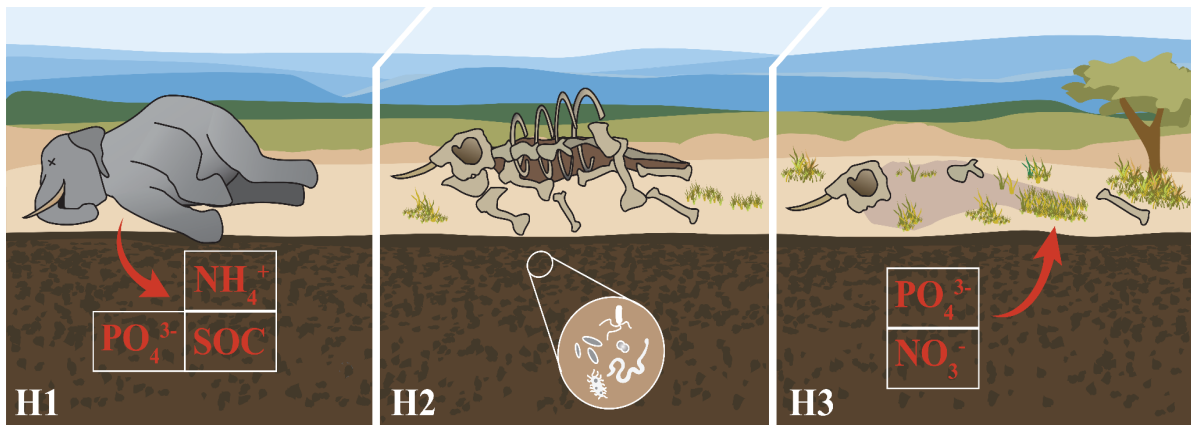


- 683 63. Quaggiotto, M.-M., Evans, M. J., Higgins, A., Strong, C., & Barton, P. S. Dynamic soil  
684 nutrient and moisture changes under decomposing vertebrate carcasses. *Biogeochemistry*,  
685 146, 71–82, <https://doi.org/10.1007/s10533-019-00611-3>, 2019.
- 686 64. R Core Team. R: A language and environment for statistical computing. R Foundation for  
687 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>, 2022.
- 688 65. Ries, L. P., & Shugart, H. H. Nutrient limitations on understory grass productivity and  
689 carbon assimilation in an African woodland savanna. *J. Arid Environ.*, 72, 1423–1430,  
690 <https://doi.org/10.1016/j.jaridenv.2008.02.013>, 2008.
- 691 66. Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M.  
692 W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E.,  
693 Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. Collapse of the world’s largest  
694 herbivores. *Sci. Adv.*, 1, e1400103, <https://doi.org/10.1126/sciadv.1400103>, 2015.
- 695 67. Risch, A. C., Frossard, A., Schütz, M., Frey, B., Morris, A. W., & Bump, J. K. Effects of elk  
696 and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone,  
697 USA. *Funct. Ecol.*, 34, 1933–1944, <https://doi.org/10.1111/1365-2435.13611>, 2020.
- 698 68. Roman, J., Estes, J. A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J. B.,  
699 Nicol, S., Pershing, A., & Smetacek, V. *Whales as marine ecosystem engineers. Front. Ecol.*  
700 *Environ.*, 12, 377–385, <https://doi.org/10.1890/130220>, 2014.
- 701 69. Rughöft, S., Hermann, M., Lazar, C. S., Cesarz, S., Levick, S. R., Trumbore, S. E. & Küsel,  
702 K. Community composition and abundance of bacterial, archaeal and nitrifying populations  
703 in savanna soils on contrasting bedrock material in Kruger National Park, South Africa.  
704 *Front. Microbiol.*, 7, <https://doi.org/10.3389/fmicb.2016.01638>, 2016.

- 705 70. Sardans, J., & Peñuelas, J. Potassium control of plant functions: ecological and agricultural  
706 implications. *Plants*, 10, <https://doi.org/10.3390/plants10020419>, 2021.
- 707 71. Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M.,  
708 Davies, A. B., & Goetz, S. J. Animals and the zoogeochemistry of the carbon cycle. *Science*,  
709 362, <https://doi.org/10.1126/science.aar3213>, 2018.
- 710 72. Seymour, C. L., Milewski, A. V., Mills, A. J., Joseph, G. S., Cumming, G. S., Cumming, D.  
711 H. M. & Mahlangu, Z. Do the large termite mounds of *Macrotermes* concentrate  
712 micronutrients in addition to macronutrients in nutrient-poor African savannas? *Soil Biology*  
713 *and Biogeochemistry*, 68, 95-105, <https://doi.org/10.1016/j.soilbio.2013.09.022>, 2014.
- 714 73. Skarpe, C., Aarrestad, P. A., Andreassen, H. P., Dhillion, S. S., Dimakatso, T., du Toit, J. T.,  
715 Duncan, Halley, J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G.,  
716 Ditshoswane, M., Moe, S. R., Mojaphoko, R., Mosugelo, D., Motsumi, S., Neo-Mahupeleng,  
717 G., ... Wegge, P. The return of the giants: ecological effects of an increasing elephant  
718 population. *Ambio*, 33, 276–282, <http://www.jstor.org/stable/4315497>, 2004.
- 719 74. Sollen-Norrin, M. & Rintoul-Hynes, N. L. J. Soil sample storage conditions affect  
720 measurements of pH, potassium, and nitrogen. *SSSAJ*, 88, 930-941,  
721 <https://doi.org/10.1002/saj2.20653>, 2024.
- 722 75. Sonneveld, C. & van den Ende, J. Soil analysis by means of a 1:2 volume extract. *Plant and*  
723 *Soil*, 63, 523-526, <https://www.jstor.org/stable/42933277>, 1971.
- 724 76. Sterner, R. W., & Elser, J. J. Ecological Stoichiometry: The Biology of Elements from  
725 Molecules to the Biosphere. Princeton University Press.  
726 <http://www.jstor.org/stable/j.ctt1jktrp3>, 2002.

- 727 77. Subalusky, A. L., Dutton, C. L., Rosi, E. J., & Post, D. M. Annual mass drownings of the  
728 Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River.  
729 *PNAS*, 114, 7647–7652, <https://doi.org/10.1073/pnas.1614778114>, 2017.
- 730 78. Subalusky, A.L., Dutton, C.L., Rosi, E.J, Puth, L.M., Post, D.M. River of bones: wildebeest  
731 skeletons leave a legacy of mass mortality in Mara River, Kenya. *Front. Ecol. Evol.*, 8,  
732 <https://doi.org/10.3389/fevo.2020.00031>, 2020.
- 733 79. Towne, E. G. Prairie vegetation and soil nutrient responses to ungulate carcasses. *Oecologia*,  
734 122, 232–239, <https://www.jstor.org/stable/4222536>, 2000.
- 735 80. Turner, B. L. & Romero, T. E. Short-term changes in extractable inorganic nutrients during  
736 storage of tropical rainforest soils. *SSSAJ*, 73, 1972-1979,  
737 <https://doi.org/10.2136/sssaj2008.0407>, 2009.
- 738 81. Turner, W. C., Kausrud, K. L., Krishnappa, Y. S., Cromsigt, J. P. G. M., Ganz, H. H.,  
739 Mapaure, I., Cloete, C. C., Havarua, Z., Küsters, M., Getz, W. M., & Stenseth, N. C. Fatal  
740 attraction: vegetation responses to nutrient inputs attract herbivores to infectious anthrax  
741 carcass sites. *Proc. R. Soc. B*, 281, <https://doi.org/10.1098/rspb.2014.1785>, 2014.
- 742 82. van Klink, R., van Laar-Wiersma, J., Vorst, O., & Smit, C. Rewilding with large herbivores:  
743 Positive direct and delayed effects of carrion on plant and arthropod communities. *PloS One*,  
744 15, e0226946, <https://doi.org/10.1371/journal.pone.0226946>, 2020.
- 745 83. Venter, F. J., Scholes, R. J. & Eckhardt, H. C. Abiotic template and its associated vegetation  
746 pattern. In: J. T. Du Toit, K. H. Rogers, H. C. Biggs, eds. *The Kruger experience: ecology*  
747 *and management of savanna heterogeneity*. Washington, DC, USA: Island Press, 83–129,  
748 2003.

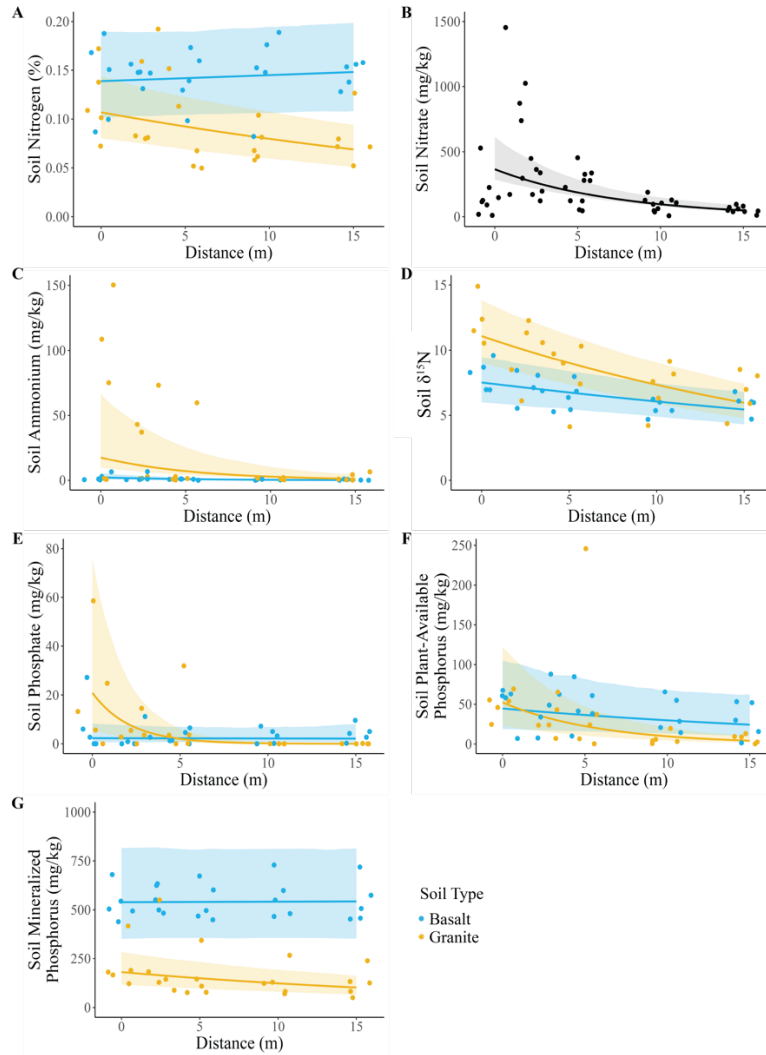
- 749 84. Wiersum, L. K. Uptake of nitrogen and phosphorus in relation to soil structure and nutrient  
750 mobility. *Plant Soil*, 16, 62–70, <https://doi.org/10.1007/BF01378158>, 1962.
- 751 85. Wigley, B. J., Coetsee, C., Fritz, C. & Bond, W. J. Herbivores shape woody plant  
752 communities in the Kruger National Park: lessons from three long-term exclosures: original  
753 research. *Koedoe*, 56, <http://dx.doi.org/10.4102/koedoe.v56i1.1165>, 2014.
- 754 86. Yang, L. H. Periodical cicadas as resource pulses in North American forests. *Science*, 306,  
755 1565–1567, <https://doi.org/10.1126/science.1103114>, 2004.
- 756 87. Yang, L. H. Pulses of dead periodical cicadas increase herbivory of American bellflowers.  
757 *Ecol.*, 89, 1497–1502, <https://doi.org/10.1890/07-1853.1>, 2008.
- 758 88. Yong, S. K., Jalaludin, N. H., Brau, E., Shamsudin, N. N., & Heo, C. C. Changes in soil  
759 nutrients (ammonia, phosphate and nitrate) associated with rat carcass decomposition under  
760 tropical climatic conditions. *Soil Res.*, 57, 482–488, <https://doi.org/10.1071/SR18279>, 2019.



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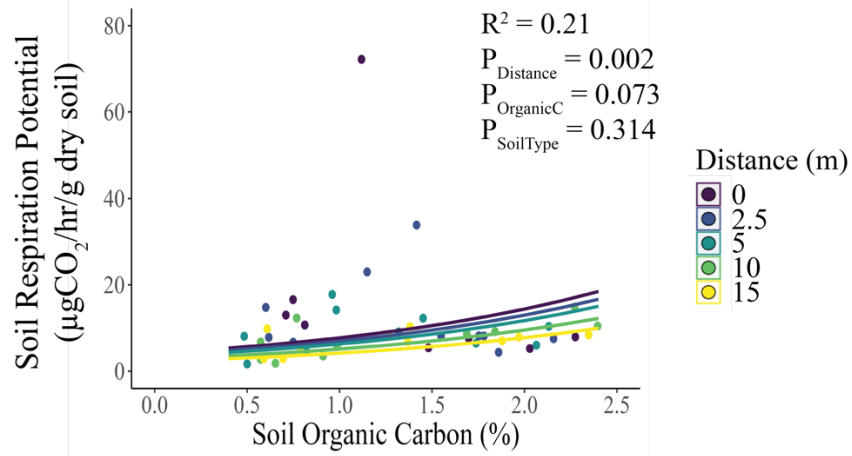
762 **Figure 1.** Hypothesized impacts of elephant megacarcasses on soil and plant nutrients. First  
 763 (H1), we hypothesized that elephant carcasses would release pulses of nutrients into the soil,  
 764 resulting in higher concentrations of soil ions such as nitrogen (ammonium,  $[\text{NH}_4]^+$ ), phosphorus  
 765 (phosphate,  $[\text{PO}_4]^{3-}$ ), and soil organic C. Second (H2), we hypothesized that C inputs from the  
 766 carcass would result in increased soil microbial respiration potential. Third (H3), we  
 767 hypothesized that plants would take up nutrients from the carcass soil, resulting in plants with  
 768 distinct nutrient profiles and increased concentrations of key limiting nutrients such as N and P.

769 Image credit: Kirsten Boeh.



770

771 **Figure 2.** Soil N and P responses to elephant carcasses. (A) Soil N (%) was greater in basaltic  
 772 soils, and in granitic soils it decreased with distance from the carcass site. (B) Soil nitrate  
 773 nitrogen decreased with distance but did not differ with soil type. (C) Soil ammonium nitrogen  
 774 and (D)  $\delta^{15}\text{N}$  were both greater in granitic soils and decreased with distance from the carcass. (E)  
 775 Soil phosphate, (F) plant-available P, and (G) mineralized P decreased with distance in granitic  
 776 soils but not basaltic soils. Points represent individual measurements taken at 0, 2.5, 5, 10, and  
 777 15m and are offset to be visible when they would otherwise overlap. Lines show predictions  
 778 calculated from the top model (see Table S1). Shading indicates the 95% confidence interval.



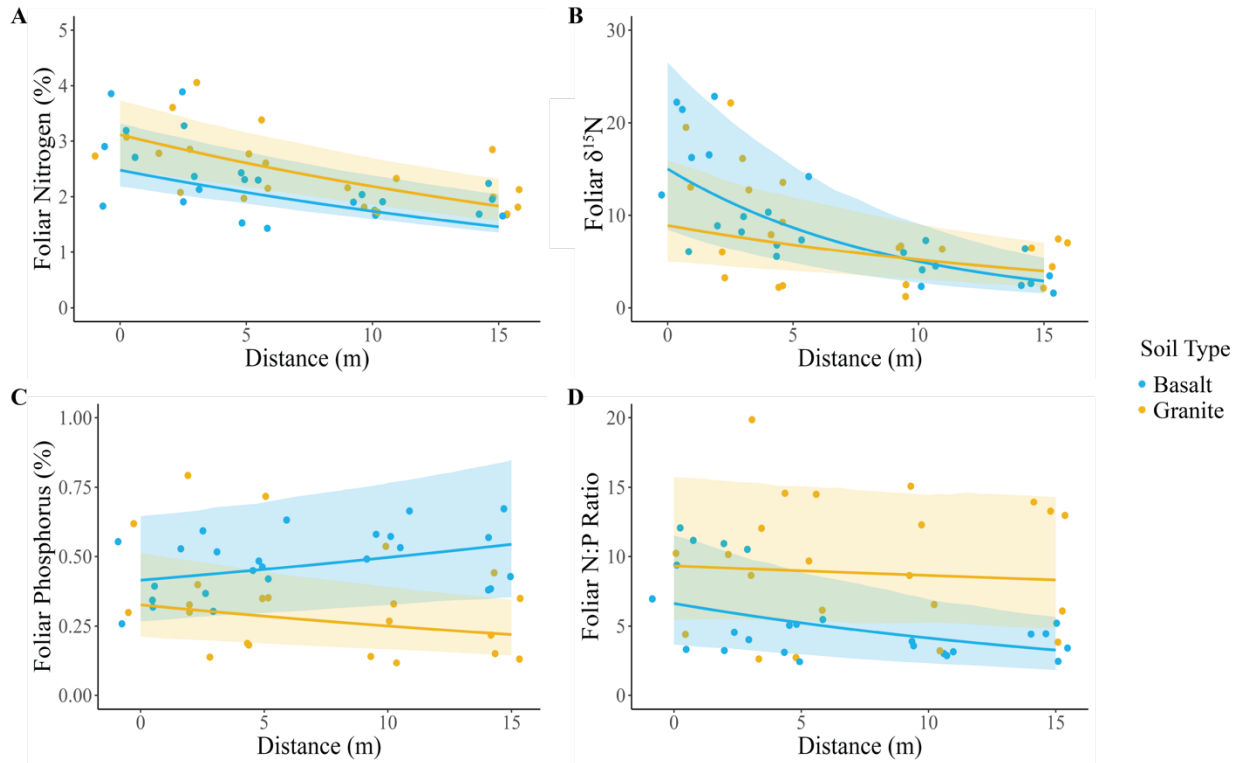
779

780 **Figure 3.** Soil respiration potential was marginally positively correlated with soil organic C (%)

781 and decreased significantly with distance from the carcass. Points represent individual

782 measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would

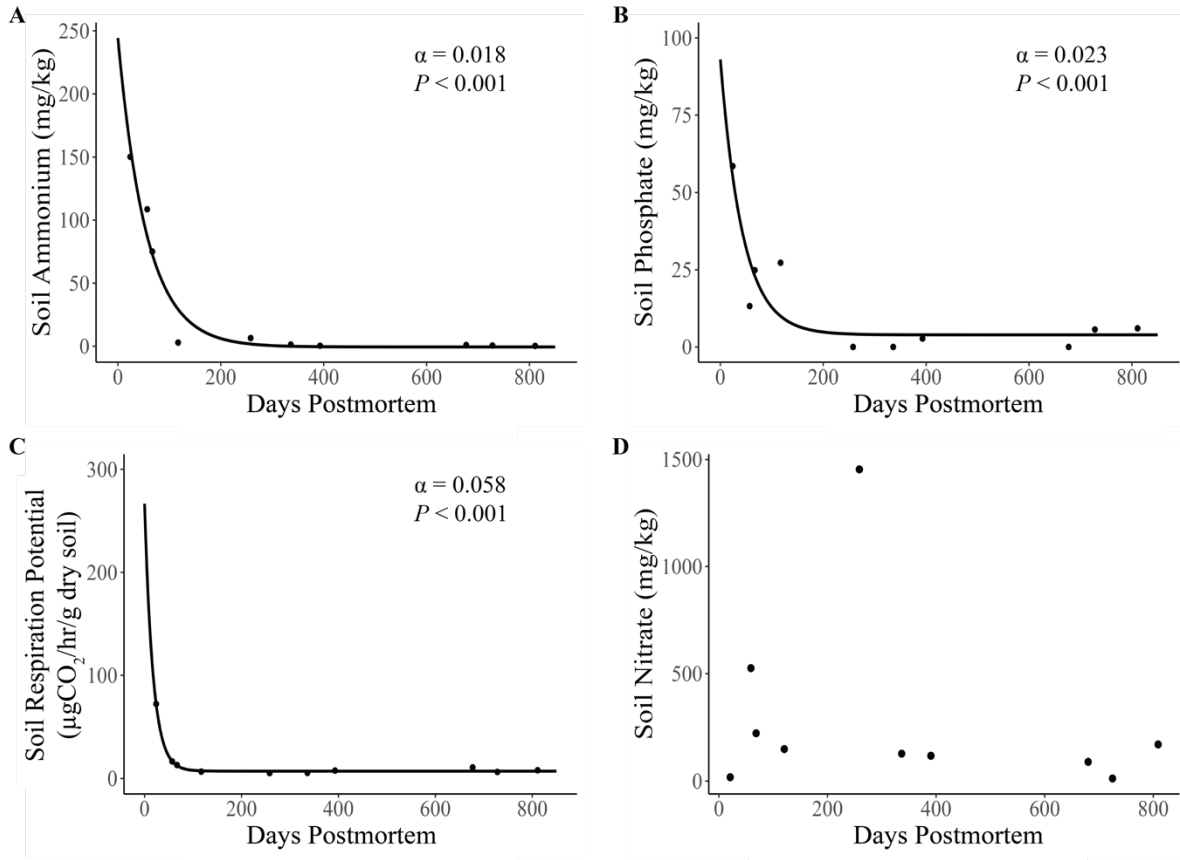
783 otherwise overlap. Lines represent model predictions.



784

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





793

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