

Response to Reviewer 3

This manuscript presents data on the influence of elephant carcasses on nutrient availability in South African savanna soils. It would be a surprise if a decaying elephant did not increase nutrient concentrations in the proximity of the carcass, but there are some interesting differences among nutrients in terms of the distance over which the effects extend. There are parallels with other nutrient hotspots in tropical ecosystems, including glades in African savannas (e.g. Augustine 2003) and leafcutter ant nests in tropical forests (e.g. Hudson et al. 2009) - it would be worth introducing these into the discussion for comparison. I have several questions about methodology and results that should be addressed before this manuscript could be acceptable for publication.

AUTHORS' RESPONSE: Thank you for all of your feedback. We have made substantial changes in response to your suggestions, including rewriting the methods section to include more details on the soil lab analyses. We have updated the introduction to better explain the importance of cations and cation exchange in savanna soils. We have also updated the discussion to more thoroughly address the ecological significance of our results, including comparison with other nutrient hotspots like the cattle bomas (Augustine 2003) and leafcutter ant nests (Hudson et al. 2009) suggested by the reviewer.

The most significant critique throughout this review was concern that freezing the soil samples prior to ion analysis may have resulted in elevated ammonium and nitrate levels. We agree that this is an important concern, but we are reassured by the findings in the literature showing that nitrogen measurements (especially nitrate) are relatively robust to storage method. Indeed, in Turner and Romero (2009) (a paper the reviewer cites), freezing did not impact nitrate concentrations relative to fresh soils except in cases of high soil acidity, which were not present in our study. Other studies show that nitrate is unaffected by freezing treatment for at least seven weeks post collection, well within the time frame of analysis for our samples (Esala, 1995; Sollen-Norrlin & Rintoul-Hynes, 2024). Soil ammonium can increase when frozen, although the increase is often relatively small (<1 mg/kg per week frozen; Esala 1995, Fig. 1). It is true that freezing can have a large impact on ammonium in peaty soils, but freezing has only minimal effects on ammonium measurements in clay soils such as ours (Esala, 1995; Sollen-Norrlin & Rintoul-Hynes, 2024). Further, we have compared the soil % nitrogen, nitrate, and ammonium values from the 15m distance in our study (essentially representing the background levels of nutrients in the soils in Kruger) to those found in other soil analysis research in Kruger, and our values are consistent with that prior research (Aranibar et al. 2003; Rughöft et al. 2016; see table below). Our foliar N:P values were consistent with the Kruger literature as well. We found much higher soil nitrogen values at 0-5m distances from the carcass site than those found in these papers, but that is what we hypothesized would happen with nutrient inputs from elephant carcasses. Moreover, even if the absolute values of nitrogen in our study are elevated due to freezing, which there is little evidence to support, there is no reason that the effects of freezing would differ with distance from an elephant carcass, so we are confident that the overall trends in this manuscript are robust.

All major updates are appended to the end of this document, including methods section 2.3, supplemental tables, and main and supplemental figures.

Metric	Source	Mean	Range	Method
Soil N	Reed et al.	11.4%	5 – 16%	Stable isotope analysis
	Aranibar et al. 2003		~5 – 23%	Stable isotope analysis
Soil Nitrate	Reed et al.	57.1 mg/kg	11.1 – 95.7 mg/kg	1:2 water extract analysis
	Rughöft et al. 2016	28.9 mg/kg	0.0 – 121.9 mg/kg	2:5 water extract analysis
Soil Ammonium	Reed et al.	1.38 mg/kg	0.01 – 6.5 mg/kg	1:2 water extract analysis
	Rughöft et al. 2016	11.3 mg/kg	0.7 – 33.3 mg/kg	2:5 water extract analysis
Soil Plant-Available P	Reed et al.	2.20 mg/kg	0.01 – 9.62 mg/kg	P Bray I
	Craine et al. 2008	38.52 mg/kg	3.23 – 85.43 mg/kg	P Bray II
Leaf N:P Ratio	Reed et al.	7.0	2.5 – 13.9	
	Craine et al. 2008	5.8	3.2 – 9.2	

*For Reed et al., we used values from the 15m distance, and for Craine et al. 2008, we used values from the control plots, as in both cases these best represent the background levels of soil nutrients.

Aranibar, J. N., Macko, S. A., Anderson, I. C., Potgieter, A. L. F., Sowry, R. & Shugart, H. H. Nutrient cycling responses to fire frequency in the Kruger National Park (South Africa) as indicated by stable isotope analysis. *Isotopes Environ. Health Stud.*, 39, 141-158, 2003.

Rughöft, S., Hermann, M., Lazar, C. S., Cesarz, S., Levick, S. R., Trumbore, S. E. & Küsel, K. Community composition and abundance of bacterial, archaeal and nitrifying populations in savanna soils on contrasting bedrock material in Kruger National Park, South Africa. *Frontiers in Microbiology*, 7, 2016.

Craine et al. Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytologist*, 179, 829-836, 2008.

Esala, M. J. Changes in the extractable ammonium- and nitrate-nitrogen contents of soil samples during freezing and thawing. *Communications in Soil Science and Plant Analysis*, 26, 61-68, 1995.

Sollen-Norrin, M. & Rintoul-Hynes, N. L. J. Soil sample storage conditions affect measurements of pH, potassium, and nitrogen. *Soil Science Society of America Journal*, 88, 930-941, 2024.

Turner, B. L. & Romero, T. E. Short-term changes in extractable inorganic nutrients during storage of tropical rainforest soils. *Soil Science Society of America Journal*, 73, 1972-1979, 2009.

Line 38 – these are not graves. A grave is an excavation for burial.

AUTHORS' RESPONSE: We have changed the word gravesite to carcass site.

Line 77 – what about the amounts of cations in an elephant?

AUTHORS' RESPONSE: This is an interesting question. We estimated the N, P, and C quantities in an elephant based on the body size to macronutrient scaling rules described in Sterner & Elser (2002). Unfortunately, we are not aware of a well-established scaling rule for cations that would allow us to estimate cation concentrations in elephant tissue.

Sterner, R. W. & Elser, J. J. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press. 2002.

Line 89 – cations are not micronutrients. Is there direct evidence for widespread (or any) cation limitation of growth in savanna ecosystems?

AUTHORS' RESPONSE: Cation exchange is essential for soil fertility, and there is evidence of cation limitation (particularly K^+ and Ca^{2+}) on African savannas (Lathwell & Grove, 1986; Agbenin & Yakubu, 2006). We now refer to this idea in the manuscript. Further, we have edited the manuscript to refer to these elements as cations rather than micronutrients for clarity.

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

Lathwell, D. J. & Grove, T. L. Soil-Plant Relationships in the Tropics. *Annual Review of Ecology and Systematics*, 17, 1-16, <https://www.jstor.org/stable/2096986>, 1986.

Line 99 – please include classifications for the granitic and basaltic soils in one of the internationally recognized systems. In Soil Taxonomy these are presumably Inceptisols / Alfisols and Vertisols, respectively?

AUTHORS' RESPONSE: Thanks for the suggestion. The granitic soils are inceptisols, while the basaltic soils may be vertisols or andisols (Khomu et al. 2017). We agree that these classifications are important for understanding the impacts of carcass-derived nutrients on different soil types and have updated the methods section as follows: “The two dominant soil types in KNP are granitic soils (inceptisols) and basaltic soils (vertisols or andisols) (Khomu et al. 2017). The clay-rich basaltic soils have relatively large surface area, enabling them to retain larger quantities of water than granitic soils, which drain water more quickly and therefore are lower in water-soluble nutrients (Buitenwerf, Kulmatiski, & Higgins, 2014).”

Khomo, L., Trumbore, S., Bern, C. R., & Chadwick, O. A. Timescales of carbon turnover in soils with mixed crystalline mineralogies. *SOIL*, 3, 17-30, <https://doi.org/10.5194/soil-3-17-2017>, 2017.

Buitenwerf, R., Kulmatiski, A. & Higgins, S. I. Soil water retention curves for the major soil types of the Kruger National Park. *Koedoe*, 56, a1228, <http://dx.doi.org/10.4102/koedoe.v56i1.1228>, 2014.

Line 138 – freezing soil has implications for subsequent measurements of extractable nutrients (e.g. Turner and Romero 2009). This should be mentioned here. Given the apparently very high values for some measurements (see below) I suspect that pretreatment had a major impact on results.

AUTHORS' RESPONSE: As detailed above, we acknowledge that freezing may have an impact on soil nitrogen measurements, though the literature is mixed on this topic. Generally, it seems that freezing more often impacts concentrations of ammonium but not nitrate (Esala, 1995; Turner & Romero, 2009; Sollen-Norrlin & Rintoul-Hynes, 2024). Indeed, in the Turner and Romero (2009) paper that the reviewer cites, freezing did not impact nitrate concentrations relative to fresh soils except in cases of high soil acidity, which were not present in our study. They write, “Frozen storage of the Pipeline Road and Fort Sherman soils preserved NO₃ at similar concentrations to fresh samples (Table 2), but caused a marked decline for the acidic Albroom soil, indicating a possible effect of soil pH on NO₃ stability. (Note: NO₃ determined after 3 mo of storage in the Albroom soil)” (pg. 1974). The impacts of freezing on ammonium are also relatively minimal (<1 mg/kg per week of freezing according to Esala, 1995). Thus, based on what is known from the literature any impacts of freezing on the concentrations of nutrients in our samples were likely quite minimal. Further, we have compared the soil % nitrogen, nitrate, and ammonium values from the 10 and 15m distances in our study (those most similar to the background soils in Kruger) to those found in other soil analysis research in Kruger, and our values are consistent with that prior research (Aranibar et al. 2003; Rughöft et al. 2016).

Metric	Source	Mean	Range	Method
Soil %N	Reed et al.	11.4%	5 – 16%	Stable isotope analysis
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*For Reed et al., we used values from the 15m distance, and for Craine et al. 2008, we used values from the control plots, as in both cases these best represent the background levels of soil nutrients.

If freezing the samples did alter the measured soil ammonium concentrations, there is no reason to believe that the effect size would differ with distance from the carcass. Thus, even if absolute values are elevated by freezing, for which there is little evidence in the literature, the overall trends of decreasing ammonium and nitrate with carcass distance should still stand. We have added these citations and explanation to the discussion.

Esala, M. J. Changes in the extractable ammonium- and nitrate-nitrogen contents of soil samples during freezing and thawing. *Communications in Soil Science and Plant Analysis*, 26, 61-68, <https://doi.org/10.1080/00103629509369280>, 1995.

Sollen-Norrlin, M. & Rintoul-Hynes, N. L. J. Soil sample storage conditions affect measurements of pH, potassium, and nitrogen. *Soil Science Society of America Journal*, 88, 930-941, <https://doi.org/10.1002/saj2.20653>, 2024.

Turner, B. L. & Romero, T. E. Short-term changes in extractable inorganic nutrients during storage of tropical rainforest soils. *Soil Science Society of America Journal*, 73, 1972-1979, doi:10.2136/sssaj2008.0407, 2009.

Aranibar, J. N., Macko, S. A., Anderson, I. C., Potgieter, A. L. F., Sowry, R. & Shugart, H. H. Nutrient cycling responses to fire frequency in the Kruger National Park (South Africa) as indicated by stable isotope analysis. *Isotopes Environ. Health Stud.*, 39, 141-158, 2003.

Rughöft, S., Hermann, M., Lazar, C. S., Cesarz, S., Levick, S. R., Trumbore, S. E. & Küsel, K. Community composition and abundance of bacterial, archaeal and nitrifying populations in savanna soils on contrasting bedrock material in Kruger National Park, South Africa. *Frontiers in Microbiology*, 7, 2016.

Craine et al. Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytologist*, 179, 829-836, 2008.

Line 145/146 – please explain the difference between phosphate and plant-available P. As written, it appears they were both measured in the water extracts. Most plant-available P tests are not conducted in water (e.g. Olsen, Mehlich, Bray, etc).

AUTHORS' RESPONSE: We have updated the methods section as follows to include more details on soil nutrient analyses, including distinguishing between the methods used for phosphate and plant-available P.

“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 macro-element concentrations of ammonium $[\text{NH}_4]^+$, nitrate $[\text{NO}_3]^-$, phosphate $[\text{PO}_4]^{3-}$, and plant-available P. Samples were air-dried and sieved through < 2mm mesh prior to chemical analysis. Plant available P, the

proportion of water-soluble P in soil that is available for uptake by plants, was extracted from 4 g of soil and 30 ml extraction fluid (1:7.5 ratio) using an acid–fluoride solution (P Bray-1), measured colorimetrically using a SysTea EasyChem200 analyser, and expressed as mg/kg. The limit was 0.5 mg/kg, and plant available P measurements <0.5 mg/kg were replaced with half the detection limit (0.25 mg/kg). Water-soluble nitrate and phosphate anions were extracted from volume on volume 100 ml soil and 200 ml deionized water, analyzed by ion chromatography on a Metrohm 930 Compact Flex System, and expressed as mg/L. Ammonium (also 1:2 water extract) was analyzed colorimetrically using a SysTea EasyChem200 analyzer and expressed as mg/L. Detection limits for soil ions were 0.01 mg/L, and soil ion concentrations measured as <0.01 mg/L were replaced with half the detection limit (0.005 mg/L). To convert the nitrate, ammonium, and phosphate units from mg/L to mg/kg, we multiplied by 2, based on the 1:2 soil to water extraction ratio.”

Line 158 – was there any inorganic C in the samples? Savanna Vertisols developed in basalt can have considerable carbonate concentrations, albeit often in subsoil. Soil pH values would help indicate this possibility – how did carcasses affect soil pH?

AUTHORS’ RESPONSE: We did not directly measure inorganic C, but we did measure soil pH and found no significant difference in soil pH with soil type or distance from the carcass center. We have added this result to the manuscript (Table S1, Figure S4B).

Line 161 – was moisture standardized prior to the incubations?

AUTHORS’ RESPONSE: We did not standardize moisture prior to incubations, since the impact of carcasses on soil moisture was one of our questions (Figure S5 in original manuscript, Figure S4 below). However, we did account for soil moisture after the incubations following the methods process described in lines 163-167: “After soil respiration measurements, we determined sample dry weight by drying each sample at 60°C for 24-48 hours until stable mass was achieved. We subtracted dry weight from starting weight to obtain soil water content. Finally, we used the dry weights and the Ideal Gas Law to standardize all respiration measurements to CO₂ µg h⁻¹g dry soil⁻¹.” These methods are described in further detail in Lemoine et al. 2024, which is cited earlier in that paragraph.

Lemoine, N. P., Budny, M. L., Rose, E., Lucas, J., & Marshall, C. W. Seasonal soil moisture thresholds inhibit bacterial activity and decomposition during drought in a tallgrass prairie. *Oikos*, 2024, e10210, <https://doi.org/10.1111/oik.10201>, 2024.

Line 182 – an alternative is to set values to ½ detection limit.

AUTHORS’ RESPONSE: We have re-run the analyses using 0.005 mg/L as the replacement value for any zeros in the soil ion concentration data, as that is half of the detection limit (0.01 mg/L). The tables with these updated results are appended at the end of this document, but this

update did not result in any changes to statistical significance or model performance in the results. We have updated the methods as follows:

“Plant available P, the proportion of water-soluble P in soil that is available for uptake by plants, was extracted from 4 g of soil and 30 ml extraction fluid (1:7.5 ratio) using an acid–fluoride solution (P Bray-1), measured colorimetrically using a Sysmex EasyChem200 analyser, and expressed as mg/kg. The detection limit was 0.5 mg/kg, and plant available P measurements <0.5 mg/kg were replaced with half the detection limit (0.25 mg/kg)..... Detection limits for soil ions were 0.01 mg/L, and soil ion concentrations measured as <0.01 mg/L were replaced with half the detection limit (0.005 mg/L).”

Line 188 – I understand that there were insufficient carcasses to allow inclusion of carcass age in models. However, major differences would be expected between carcasses aged 1 month vs 2.5 years. Is there any way to provide an indication of the magnitude of the age effect? How would distance effects look if young carcasses were excluded, for example?

AUTHORS’ RESPONSE: Thanks for bringing this up. We made a figure showing soil ions (ammonium, nitrate, and phosphate) and respiration potential plotted against carcass age. In these four cases, it is clear that these soil metrics are higher at fresher carcasses. In fact, the trends are so compelling that we have added this figure to the main text (Figure 5). This figure suggests the pattern of elevated soil nutrients that we found may be even stronger when considering younger carcasses given how quickly the nutrients decline with age.

Line 228 – It is perhaps not surprising that P concentrations showed little variation with distance, given that P was measured in water extracts (i.e. the extraction is recovering a relatively small pool of soluble P).

AUTHORS’ RESPONSE: This is an interesting point. The results included in this manuscript are soil phosphate (1:2 water extract) and plant-available P (P Bray-I), but we also measured mineral phosphorus (P₃₁) in mg/kg using the same method we did for soil Na, Mg, Fe, Ca, and K—microwave-assisted digestion in a solution of 9 mL 65% nitric acid (HNO₃) and 3 mL 32% hydrochloric acid (HCl) (full methodological details appended to the end of this document). We have added this result to the manuscript (Figure 2G; Table S1), thereby increasing the proportion of total soil P covered by our analyses. All three individual measurements of soil P (phosphate, plant-available P, and mineral P) indicate an interaction between distance and soil type in which P decreases with distance from the carcass center, but only in granitic soils.

Line 230 – how is plant-available P defined here?

AUTHORS’ RESPONSE: Plant-available P refers to P measured via the P Bray I method. We have updated the methods as follows: “Plant available P was extracted from 4 g of soil and

30 ml extraction fluid (1:7.5 ratio) using an acid–fluoride solution (P Bray-1), measured colorimetrically using a Systea EasyChem200 analyser, and expressed as mg/kg. The detection limit was 0.5 mg/kg, and plant available P measurements <0.5 mg/kg were replaced with half the detection limit (0.25 mg/kg).”

Line 286 – Soil extractable nutrients should be expressed on the basis of dry soil, not volume.

AUTHORS’ RESPONSE: We have updated the manuscript so that here and throughout, soil ion concentrations are given in mg/kg soil rather than mg/L. The updated tables and figures are appended to the end of this document.

Line 286 - these very high extractable nitrogen concentrations are presumably in part a consequence of soils being frozen prior to analysis. Another factor is time between sampling and freezing - or storage prior to freezing. Please provide a statement about sample treatment prior to analysis (time from sampling to freezing, storage conditions during this time, etc, as relevant).

AUTHORS’ RESPONSE: We have updated the methods section to include more details on soil storage as follows: “Soil samples were stored in a cooler during fieldwork. On the day they were collected, we used 5 g of each soil sample for soil respiration measurements (described below). The rest of each sample was stored plastic bags in a -20°C freezer until nutrient analyses; they were stored in coolers with ice blocks during the transition from the freezer at the field site to the freezers at the labs.” As we discuss above, there were likely negligible, if any, impacts of freezing on nitrate concentrations given the data available in the literature. Similarly, the impacts on ammonium were likely also minor. Further, we have also compared our measured nitrogen concentrations to those from other studies performed in Kruger (% N, Aranibar et al. 2003; ammonium and nitrate, Rughöft et al. 2016; see table below). We used the 15m distance in our dataset for comparison, since that is most representative of the baseline nitrogen concentrations. Our values were similar to those found by other researchers in Kruger, which increases our confidence that the measurements we took are accurate. The nitrogen concentrations that we found at the 0-5m distances are indeed much higher than those found elsewhere, but we attribute this to the presence of the elephant carcass.

Metric	Source	Mean	Range	Method
Soil %N	Reed et al.	11.4%	5 – 16%	Stable isotope analysis
	Aranibar et al. 2003		~5 – 23%	Stable isotope analysis
Soil Nitrate	Reed et al.	57.1 mg/kg	11.1 – 95.7 mg/kg	1:2 water extract analysis
	Rughöft et al. 2016	28.9 mg/kg	0.0 – 121.9 mg/kg	2:5 water extract analysis
Soil Ammonium	Reed et al.	1.38 mg/kg	0.01 – 6.5 mg/kg	1:2 water extract analysis
	Rughöft et al. 2016	11.3 mg/kg	0.7 – 33.3 mg/kg	2:5 water extract analysis
Soil Plant-Available P	Reed et al.	2.20 mg/kg	0.01 – 9.62 mg/kg	P Bray I
	Craine et al. 2008	38.52 mg/kg	3.23 – 85.43 mg/kg	P Bray II
Leaf N:P Ratio	Reed et al.	7.0	2.5 – 13.9	

	Craine et al. 2008	5.8	3.2 – 9.2	
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*For Reed et al., we used values from the 15m distance, and for Craine et al. 2008, we used values from the control plots, as in both cases these best represent the background levels of soil nutrients.

Aranibar, J. N., Macko, S. A., Anderson, I. C., Potgieter, A. L. F., Sowry, R. & Shugart, H. H. Nutrient cycling responses to fire frequency in the Kruger National Park (South Africa) as indicated by stable isotope analysis. *Isotopes Environ. Health Stud.*, 39, 141-158, 2003.

Rughöft, S., Hermann, M., Lazar, C. S., Cesarz, S., Levick, S. R., Trumbore, S. E. & Küsel, K. Community composition and abundance of bacterial, archaeal and nitrifying populations in savanna soils on contrasting bedrock material in Kruger National Park, South Africa. *Frontiers in Microbiology*, 7, 2016.

Craine et al. Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytologist*, 179, 829-836, 2008.

Line 308 – the high available P and tissue N:P ratios (see below) indicate that there is no P limitation here. This might limit the likely influence of carcasses on foliar P, as found here (i.e. foliar P is not a strong indicator of the extent to which carcasses change P availability in general).

AUTHORS' RESPONSE: Thanks for bringing this up. We appreciate your comments here and below suggesting that P limitation might not be strong at our sites, and we have updated this paragraph in the discussion as follows:

“Elevated soil phosphate (Figure 2E) and plant-available P (Figure 2F) at the center of carcass sites were also consistent with expectations from the literature (Bump et al. 2009a; Parmenter & MacMahon, 2009). However, elevated P levels in soil did not translate to elevated P in grass leaves (Figure 4C), which could suggest a lag between trends in soil and plants that is longer for P than for N. This lag could occur because phosphate easily forms chemical bonds with other soil ions (e.g., iron and aluminum in acidic soils and calcium in basic soils). Nitrate does not form these bonds and therefore has greater water solubility and soil mobility (Wiersum, 1962; Arai & Sparks, 2007). However, it is also possible that P limitation in Kruger is not as strong as it is in some other African savanna systems (Pellegrini, 2016). The foliar N:P ratios measured in this experiment were consistently low, indicating that N limitation is more likely (Güsewell, 2004).”

We also compared our plant-available P and foliar N:P ratios with other studies in Kruger and found that our plant-available P results were actually lower, while our foliar N:P ratios were in about the same range.

Metric	Source	Mean	Range	Method
Soil Plant-Available P	Reed et al.	2.20 mg/kg	0.01 – 9.62 mg/kg	P Bray I
	Craine et al. 2008	38.52 mg/kg	3.23 – 85.43 mg/kg	P Bray II

Leaf N:P Ratio	Reed et al.	7.0	2.5 – 13.9	
	Craine et al. 2008	5.8	3.2 – 9.2	

Craine et al. Nutrient concentration ratios and co-limitation in South African grasslands. New Phytologist, 179, 829-836, 2008.

Line 322 – water-extractable P represents a tiny proportion of the total soil P, so reliance on this procedure probably limits the possibility of detecting change in soil P.

AUTHORS' RESPONSE: We have updated the results to include mineralized P in soils in addition to phosphate and plant-available P, as described above in response to line 228.

Line 323- 330 – this text largely repeats results.

AUTHORS' RESPONSE: Thank you for this feedback. The goal of this section is to demonstrate the impacts of soil ammonium on grass productivity and succession. We have edited to these lines to remove some of the repetition of results and instead focus on the main point that *U. mosambicensis*, one of the only grass species found at the center of carcass sites, may have 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 very fresh carcass sites.

Line 340 - missing here is a discussion of the ecological consequences of the findings. What are the implications for plant and microbial ecology in savanna ecosystems?

AUTHORS' RESPONSE: Thanks for this feedback. We will update the discussion section to include a paragraph on the importance of these nutrient hotspots on plant and microbial diversity and functioning. We will include comparisons with well-known nutrient hotspots in Kruger (e.g., termite mounds; Davies, Baldeck, & Asner, 2016) as well as in other tropical/sub-tropical systems, such as those recommended by the reviewer.

Davies, A. B., Levick, S. R., Robertson, M. P., van Rensburg, B. J., Asner, G. P. & Parr, C. L. Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales, 2016.

Figure 2B, C – these values should be presented in mg/kg soil.

AUTHORS' RESPONSE: We have updated the manuscript so that here and throughout, soil ion concentrations are given in mg/kg soil rather than mg/L. To do this conversion, we multiplied the

volume in mg/L by 2 based on the 1:2 soil to water extraction ratio, as the reviewer helpfully described below. The updated tables and figures are appended to the end of this document.

Figure 2B – these are extremely high nitrate concentrations, even out to 15 m. For example, 100 mg/L is equivalent to 200 mg/kg based on a 1:2 soil to water extraction ratio. Extractions done quickly after sampling and in 2 M KCl are in the range of 1-5 mg/kg. This seems to be a clear indication of storage effects.

AUTHORS' RESPONSE: We have found our N measurements to be consistent with other studies in Kruger. As we discuss in several places above, there is unlikely to be any significant storage effects on these measurements.

Metric	Source	Mean	Range	Method
Soil %N	Reed et al.	11.4%	5 – 16%	Stable isotope analysis
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Aranibar, J. N., Macko, S. A., Anderson, I. C., Potgieter, A. L. F., Sowry, R. & Shugart, H. H. Nutrient cycling responses to fire frequency in the Kruger National Park (South Africa) as indicated by stable isotope analysis. *Isotopes Environ. Health Stud.*, 39, 141-158, 2003.

Rughöft, S., Hermann, M., Lazar, C. S., Cesarz, S., Levick, S. R., Trumbore, S. E. & Küsel, K. Community composition and abundance of bacterial, archaeal and nitrifying populations in savanna soils on contrasting bedrock material in Kruger National Park, South Africa. *Frontiers in Microbiology*, 7, 2016.

Figure 2B, C – are these values as NO₃/NH₄ or on an N basis?

AUTHORS' RESPONSE: These values are on an N-basis (as are the values from Rughöft et al. 2016 in the tables above, and we have updated the figure legend to clarify.

Figure 2D – please express stable isotope ratios as $\delta^{15}\text{N}$. This may be how the results are presented, but this is not clear from the units.

AUTHORS' RESPONSE: We have changed the notation here and throughout the manuscript to $\delta^{15}\text{N}$.

Figure 2F – these are very high available P concentrations for a natural ecosystem, although there is no mention of the method used.

AUTHORS' RESPONSE: We have updated the methods section to include the method used to measure plant-available P as follows: “Plant available P, the proportion of water-soluble P in soil that is available for uptake by plants, was extracted from 4 g of soil and 30 ml extraction fluid (1:7.5 ratio) using an acid–fluoride solution (P Bray-1), measured colorimetrically using a Sysmex EasyChem200 analyser, and expressed as mg/kg. The detection limit was 0.5 mg/kg, and plant available P measurements <0.5 mg/kg were replaced with half the detection limit (0.25 mg/kg).”

In comparison with the literature, we found that our soil plant-available P values were actually lower than those from other studies performed in Kruger on the same granitic and basaltic soil types.

Metric	Source	Mean	Range	Method
Soil Plant-Available P	Reed et al.	2.20 mg/kg	0.01 – 9.62 mg/kg	P Bray I
	Craine et al. 2008	38.52 mg/kg	3.23 – 85.43 mg/kg	P Bray II

*For Reed et al., we used values from the 15m distance, and for Craine et al. 2008, we used values from the control plots, as in both cases these best represent the background levels of soil nutrients.

Craine et al. Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytologist*, 179, 829-836, 2008.

Figure 4 – it looks like foliar N:P ratios are around 4 (2% N, 0.5%P) – these very low values that suggest strong N limitation. This is incompatible with the very high nitrate values presented in Figure 2. This further indicates storage problems with N measurements.

AUTHORS' RESPONSE: The reviewer brings up an interesting point about the stoichiometry of the grass we sampled around the elephant carcasses. We now analyze foliar N:P ratios and found that they were overall higher in granitic soils compared to basaltic soils and decreased with

distance from the carcass center in both soil types. The median foliar N:P ratio was 9.38 at the 0m distance and 4.83 at the 15m distance, which may indicate that N limitation may be relatively stronger further from the carcass site, and P limitation may be relatively stronger closer to the center. These new results have been added to the manuscript (Figure 4D, Table S2) and are appended to the end of this document. Interestingly, some previous work in Kruger with this same species of grass, as well as other grasses, showed that N:P ratios in grasses responded similarly to the addition of N fertilizer (Crane et al. 2008). Under control nutrient conditions the grasses in their study had a N:P of 5.8 on average. But similar to our study, under N fertilization grasses had a N:P of 9.9 on average. These data argue against the reviewer's point that having high N availability in the soil necessarily increases the N:P to high levels that one would expect to indicate P limitation. This example, and the data we present above, suggest that the storage methods for the soils that we used are not impacting our dataset.

Craine et al. Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytologist*, 179, 829-836, 2008.

Augustine, D. J. (2003). Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology*, 40(1), 137-149.

Hudson et al. (2009). Temporal patterns of nutrient availability around nests of leaf-cutting ants (*Attaolombica*) in secondary moist tropical forest. *Soil Biology and Biochemistry*, 41(6), 1088-1093.

Turner, B. L., & Romero, T. E. (2009). Short-term changes in extractable inorganic nutrients during storage of tropical rain forest soils. *Soil Science Society of America Journal*, 73, 1972-1979.

AUTHORS' RESPONSE: Thank you for providing these references. We have found the Turner and Romero (2009) manuscript particularly instructive in interpreting the soil nitrogen data. We have updated the discussion to include comparisons with other types of savanna nutrient hotspots such as those found in the Augustine (2003) and Hudson et al. (2009) papers.

Revised Methods

2.1 Study system and sample collection

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

During the wet season in March 2023, we identified ten elephant carcass sites (1-26 months post-death), five on relatively nutrient-rich basaltic soil and five on nutrient-poor granitic soil. KNP section rangers provided precise GPS locations of where elephant carcasses had been found. Most elephants died of old age, illness, injury, or, in the case of one young bull, territorial fighting. 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. Based on pilot data, we treat the 10-15m distances as controls, since the high degree of landscape heterogeneity in the system (e.g., differences in hill slope, vegetation, water drainage, proximity to termite mounds) made random transects difficult for interpretation. 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. Soil samples were stored in a cooler during fieldwork. On the day they were collected, we used 5 g of each soil sample for soil respiration measurements (described below). The rest of each sample was stored in plastic bags in a -20°C freezer until nutrient analyses; they were stored in coolers with ice blocks during the transition from the freezer at the field site to the freezers at the labs. Leaf samples were stored in paper bags at room temperature until dried for analyses (see below).

2.3 Hypothesis testing

We tested our first hypothesis that elephant megacarcass decomposition would release nutrients into the soil by performing soil nutrient analyses. We sent 250 g of each soil sample to Eco-Analytica laboratory at the North-West University in Potchefstroom, South Africa for measurements of soil macro-element concentrations of ammonium $[\text{NH}_4]^+$, nitrate $[\text{NO}_3]^-$, phosphate $[\text{PO}_4]^{3-}$, and plant-available P. Samples were air-dried and sieved through < 2mm mesh prior to chemical analysis. Plant available P was extracted from 4 g of soil and 30 ml extraction fluid (1:7.5 ratio) using an acid-fluoride solution (P Bray-1), measured

colorimetrically using a Sysmex EasyChem200 analyser, and expressed as mg/kg. The detection limit was 0.5 mg/kg, and plant available P measurements <0.5 mg/kg were replaced with half the detection limit (0.25 mg/kg). Water-soluble nitrate and phosphate anions were extracted from volume on volume 100 ml soil and 200 ml deionized water, analyzed by ion chromatography on a Metrohm 930 Compact Flex System, and expressed as mg/L. Ammonium (also 1:2 water extract) was analyzed colorimetrically using a Sysmex EasyChem200 analyzer and expressed as mg/L. Detection limits for soil ions were 0.01 mg/L, and soil ion concentrations measured as <0.01 mg/L were replaced with half the detection limit (0.005 mg/L). To convert the nitrate, ammonium, and phosphate units from mg/L to mg/kg, we multiplied by 2, based on the 1:2 soil to water extraction ratio.

To determine whether soil anions were distinct and elevated at the center of carcass sites relative to soil further from the center, concentrations of sodium (Na), magnesium (Mg), iron (Fe), calcium (Ca), potassium (K), and phosphorus (P) cations were measured using microwave-assisted digestion. Air-dried and sieved (>2 mm) soil samples, weighed to 0.2 g, were microwaved in 9 ml 65% nitric acid (HNO₃) and 3 ml 32% hydrochloric acid (HCl) according to EPA 3051b in a Milestone, Ethos microwave digester with UP, Maxi 44 rotor. A period of 20 minutes allowed the system to reach 1800 MW at a temperature of 200 °C which was maintained for 15 minutes. After cooling, the samples were brought up to a final volume of 50 ml and analyzed on an Agilent 7500 CE ICP-MS fitted with CRC (Collision Reaction Cell) technology for interference removal. The instrument is optimized using a solution containing Li, Y, Ce, and Tl (1 ppb) for standard low-oxide/low interference levels ($\leq 1.5\%$) while maintaining high sensitivity across the mass range. The instrument was calibrated using ULTRASPEC® certified custom mixed multi-element stock standard solutions containing all the elements of interest (De

Bruyn Spectroscopic Solutions, South Africa). Calibrations spanned the range of 0 – 30 ppm for the mineral elements Ca, Mg, Na, and K and 0 – 0.3 ppm for the rest of the trace elements.

Elemental concentrations were expressed as mg/kg.

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

To test our second hypothesis that nutrient inputs to the soil would stimulate microbial activity, we measured soil organic C, water content, and microbial respiration potential. We sent 10 g of each sample to the BIOGRIP laboratory for measurements of soil organic C using a Vario TOC Cube (Elementar, Germany). Samples (dried and milled as above) were weighed off (10 – 60 mg), acidified using 10% HCl to remove the total inorganic C (carbonates), and dried overnight at 60°C. All samples were analyzed through combustion at 950°C. The released CO_2

was measured by a non-dispersive infrared (NDIR) sensor. A high organic C (7.45 ± 0.14 %C) soil standard from Elemental Microanalysis Ltd (UK) was included during the analysis. The quantification limit for %C is 0.14%. The precision for the %C was 0.09% and was determined using the low organic C (LOC) standard (1.86 ± 0.14 %C), which was run multiple times throughout the analysis.

To quantify soil respiration and water content, we used an incubation method (Lemoine et al. 2024) in which 5 g (± 0.2 g) of each sample was placed into a 100 ml clear glass bottle, sealed, and flushed with CO₂-free air. Following flushing, we incubated the bottles for one hour at 25°C. We then recorded CO₂ concentrations using an LI-850 CO₂/H₂O infrared gas analyzer. After soil respiration measurements, we determined sample dry weight by drying each sample at 60°C for 24-48 hours until stable mass was achieved. We subtracted dry weight from starting weight to obtain soil water content. Finally, we used the dry weights and the Ideal Gas Law to standardize all respiration measurements to CO₂ $\mu\text{g h}^{-1}\text{g dry soil}^{-1}$.

To test our third hypothesis that carcass-derived nutrients would move from soil into plants, we measured foliar nutrient concentrations in *U. mosambicensis*. Two grams of each dried leaf sample was sent to the BIOGRIP laboratory for preparation and measurements of %N and $\delta^{15}\text{N}$ via stable isotope analysis as described above. A Sorghum flour standard (1.47 ± 0.25 %N) from Elemental Microanalysis Ltd (UK) was used for calibration, along with two international reference standards (USGS40 and USGS41). The quantification limit for $\delta^{15}\text{N}$ on the IRMS is 1 nA, and the quantification limit for %N is 1.3%. The precision for the %N was 0.02% and for $\delta^{15}\text{N}$ is $\pm 0.08\%$. Limits were determined using the sorghum flour standard, which was run multiple times throughout the analysis. Additionally, we sent 5 g per sample to Cedara Analytical Services Laboratory to quantify micronutrients in grass tissue (P, Na, Mg, K, Ca, and Fe) using

Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES 5800, Agilent, USA). Samples were dried (110°C overnight) and milled to a fine powder. Subsamples (0.5 g) were ashed at 450°C for 4 hours, and the ash was re-wet using 2 mL conc. HCl (32%). Samples were evaporated to dryness then re-suspended in 25 mL 1M HCl before filtering. Lastly, the filtrate was diluted with de-ionized water in a ratio of 5:20 filtrate to water. To calibrate the ICP-OES, solutions containing known amounts of each element were measured (10-20 ppm for Na and C, 200-1500 ppm for Fe, 0.5-3.75% for K, and 0.125-0.5% for P), prepared from 1000 ppm primary single standards. At three of the ten sites, we did not find sufficient plant material at the central point for analysis, resulting in a sample size of $N = 7$ for the center (distance = 0-0.5m) measurement for leaf nutrient analyses.

To test whether each response variable for the three hypotheses was significantly associated with soil type and/or distance from the carcass center, we performed a model selection procedure. For each response variable, we ran five generalized linear mixed models using the gamma family (link = log) in the package *lme4* (Bates et al. 2015): (i) soil type + distance + soil type \times distance interaction, (ii) soil type + distance, (iii) soil type, (iv) distance, and (v) a null model indicating no significant difference in slope or intercept after accounting for carcass site. All models included carcass site as a random effect to account for individual variation. Each model included 50 observations (10 sites \times 5 distances per site). For samples in which the nutrient level was listed as 0 or undetectable, we accounted for the uncertainty by using half the detection level. 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 $\Delta\text{AICc} \leq 2$ 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).

Revised Main Figures

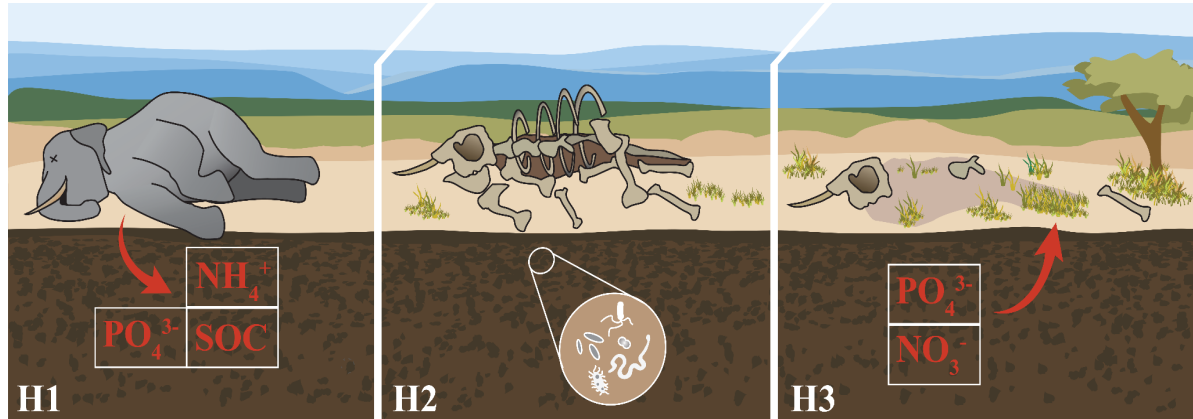


Figure 1. Hypothesized impacts of elephant megacarcasses on soil and plant nutrients. First (H1), we hypothesized that elephant carcasses would release pulses of nutrients into the soil, resulting in higher concentrations of soil nutrients such as nitrogen (ammonium, $[\text{NH}_4]^+$), phosphorus (phosphate,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

Image credit: Kirsten Boeh.

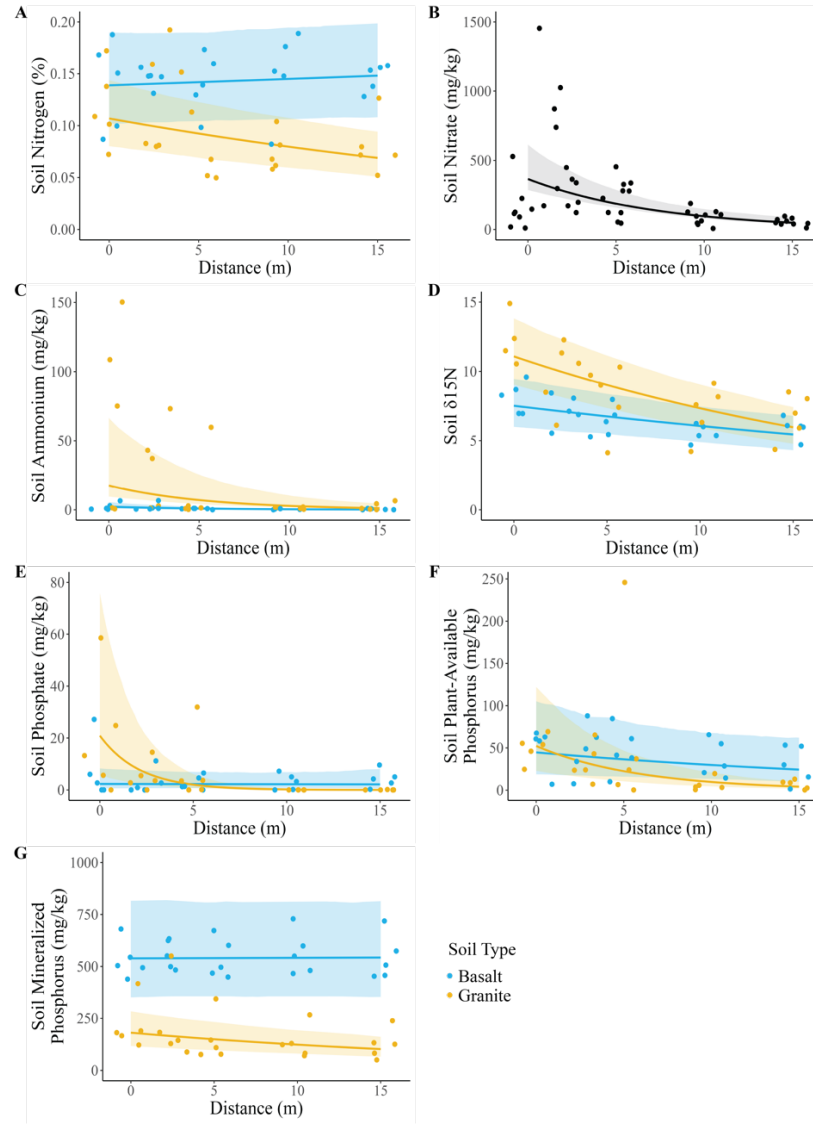


Figure 2. Soil N and P responses to elephant carcasses. (A) Soil N (%) was greater in basaltic soils, and in granitic soils it decreased with distance from the carcass site. (B) Soil **nitrate nitrogen** decreased with distance but did not differ with soil type. (C) **Soil ammonium nitrogen** and (D)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

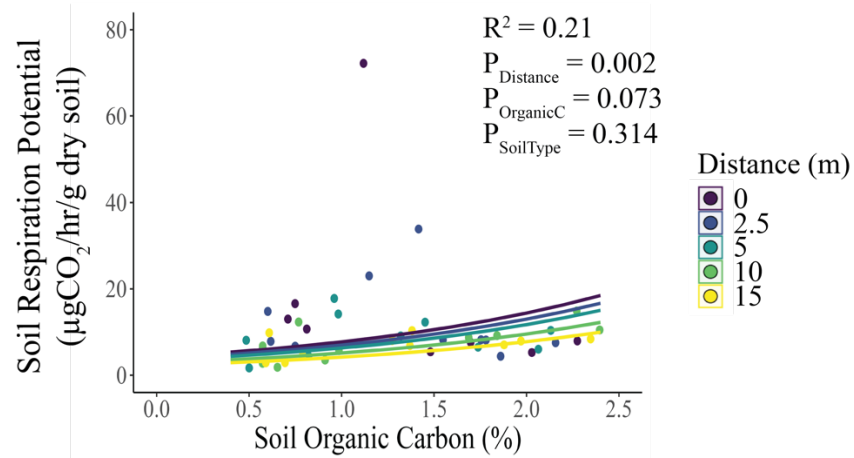


Figure 3. Soil respiration potential was marginally positively correlated with soil organic C (%) and decreased significantly with distance from the carcass. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap. Lines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

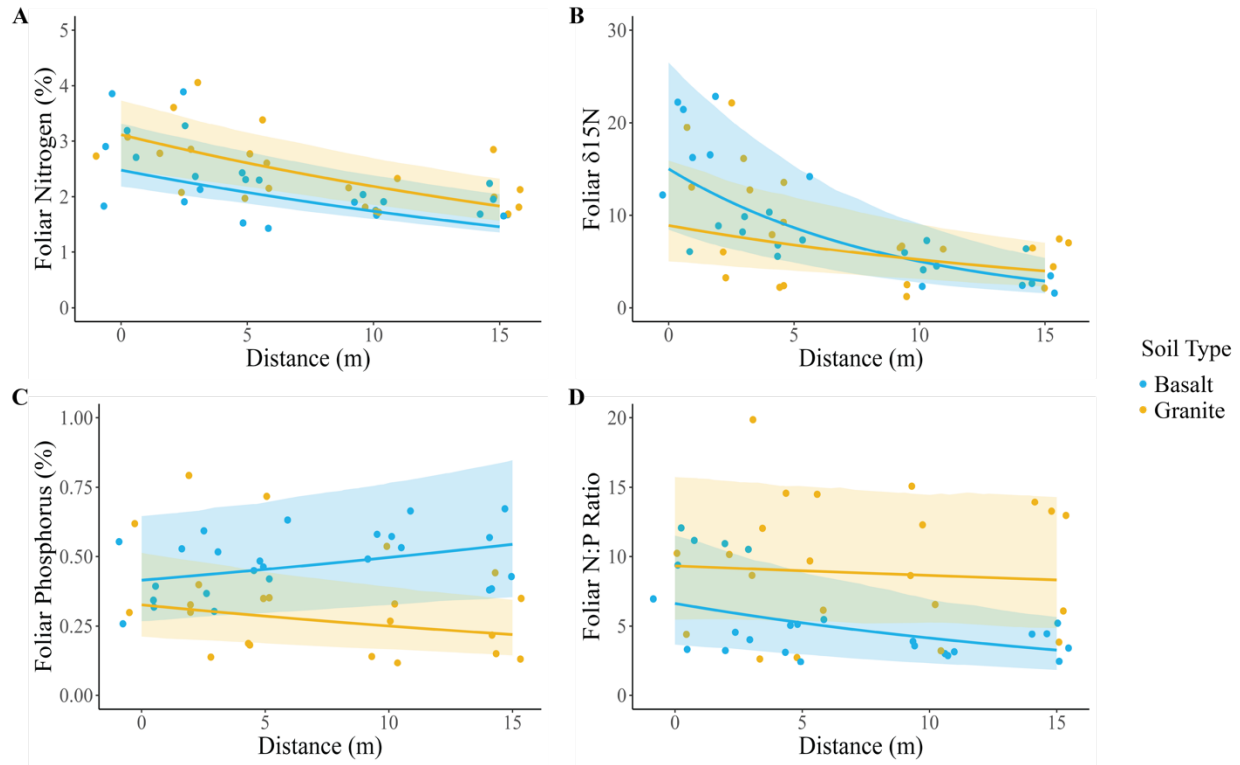
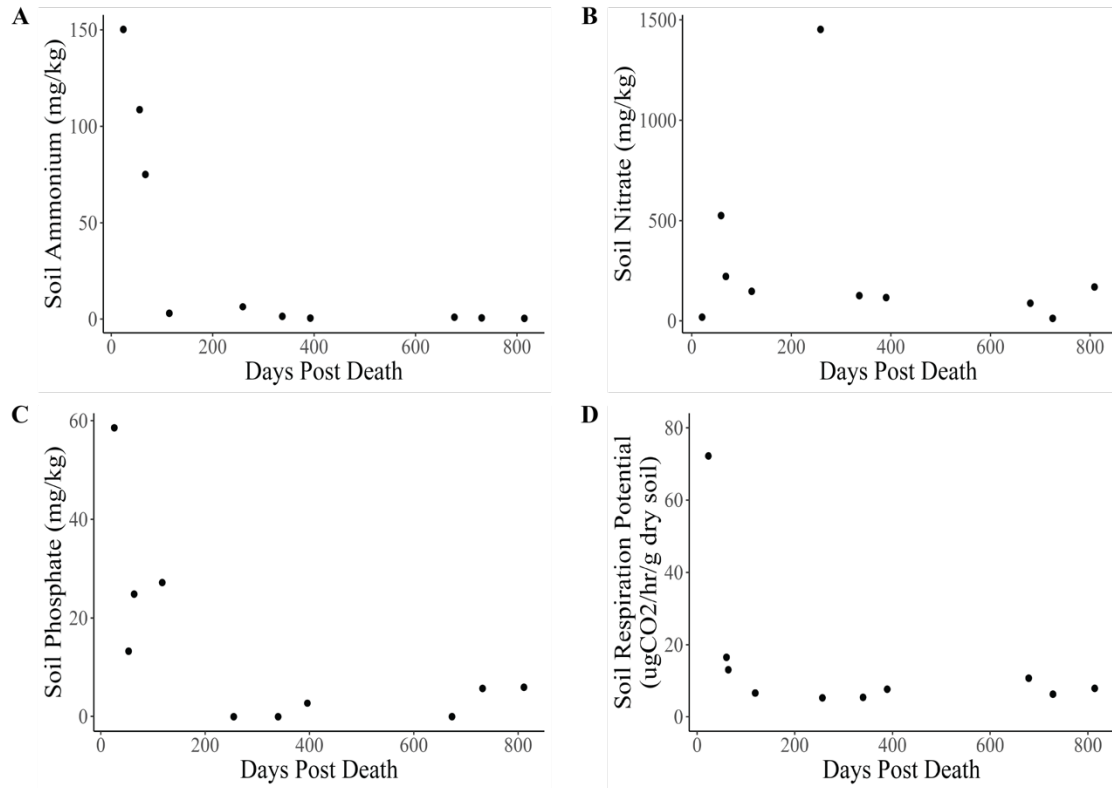


Figure 4. Foliar N and P responses to elephant carcasses. (A) Foliar %N and (B) $\delta^{15}\text{N}$ both decreased with distance from the carcass center. (C) Foliar P was greater in basaltic soils and decreased with distance in granitic soils. (D) Foliar N:P ratio was greater in granitic soils and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



Relationship between carcass age and key metrics (soil ion concentrations and respiration potential). (A) Soil ammonium, (B) soil nitrate, (C) soil phosphate, and (D) soil respiration potential are all higher at fresher carcass sites. Points represent values at the center of the carcass site (distance = 0-0.5m).

Figure 5. Relationship between carcass age and key soil metrics (soil ion concentrations and respiration potential). (A) Soil ammonium, (B) nitrate, (C) phosphate, and (D) respiration potential are all higher at fresher carcass sites. Points represent individual measurements taken at the center of the carcass site (distance = 0-0.5m).

Revised Supplemental Tables

Table S1. Generalized linear mixed model results for soil variables. The same five models were run for each response variable, including a null model, and each included site as a random effect to account for repeat measurements. AICc is Akaike's Information Criterion, and ΔAICc is the difference between a given model and the best fit model for that response variable. Cum.Wt stand for cumulative weight; it gives the sum of Akaike's weights and indicates the likelihood that the models up to that point are the best in the set. Models with a ΔAICc value of 2 are considered roughly equivalent in fit and are italicized. Marginal R^2 is the proportion of variance explained by both fixed and random effects in a model, and conditional R^2 is the proportion of variance explained by fixed effects. Coefficients (\pm standard error) are shown for each predictor and model and are in log units. Rows are organized in blocks by response variable. Within blocks, models are listed in order of increasing ΔAICc .

Model	Model Fit					Coefficients \pm SE		
	AICc	ΔAICc	Cum.Wt	Mar. R^2	Con. R^2	Soil	Distance	Soil \times Distance
Nitrogen (%)								
<i>Soil \times Distance</i>	-227.32	0.00	0.99	0.54	0.74	-0.26 \pm 0.22	0.00 \pm 0.01	-0.03 \pm 0.01
Soil + Distance	-216.13	11.20	1.00	0.46	0.67	-0.48 \pm 0.21	-0.01 \pm 0.00	
Distance	-214.95	12.37	1.00	0.04	0.52		-0.01 \pm 0.00	
Soil	-212.36	14.97	1.00	0.40	0.62	-0.47 \pm 0.21		
Null	-211.23	16.09	1.00					
$\delta^{15}\text{N}$								
<i>Soil \times Distance</i>	180.87	0.00	0.77	0.55	0.70	0.39 \pm 0.16	-0.02 \pm 0.01	-0.02 \pm 0.01
Soil + Distance	184.66	3.79	0.88	0.50	0.66	0.26 \pm 0.15	-0.03 \pm 0.00	
Distance	184.67	3.79	1.00	0.34	0.60		-0.03 \pm 0.00	
Soil	219.35	38.47	1.00	0.20	0.34	0.28 \pm 0.14		
Null	219.96	39.09	1.00					
Nitrate (mg/kg)								
Distance	624.84	0.00	0.70	0.48	0.52		-0.14 \pm 0.02	

Soil + Distance	627.06	2.23	0.93	0.48	0.52	-0.14 ± 0.27	-0.14 ± 0.02	
Soil × Distance	629.51	4.67	1.00	0.48	0.52	-0.24 ± 0.39	-0.14 ± 0.03	0.02 ± 0.04
Null	649.77	24.93	1.00					
Soil	651.82	26.99	1.00	0.01	0.04	-0.18 ± 0.31		
Ammonium (mg/kg)								
Soil + Distance	219.52	0.00	0.65	0.58	0.77	2.49 ± 0.66	-0.18 ± 0.03	
Soil × Distance	220.94	1.43	0.97	0.60	0.77	2.91 ± 0.73	-0.15 ± 0.04	-0.07 ± 0.06
Distance	225.87	6.35	1.00	0.21	0.77		-0.18 ± 0.02	
Soil	244.57	25.05	1.00	0.34	0.70	2.51 ± 0.76		
Null	249.38	29.86	1.00					
Phosphate (mg/kg)								
Soil × Distance	167.99	0.00	0.98	0.52	0.79	2.20 ± 0.96	0.00 ± 0.05	-0.46 ± 0.08
Soil + Distance	178.68	10.69	1.00	0.18	0.18	-0.38 ± 0.70	-0.14 ± 0.06	
Null	180.65	12.66	1.00					
Soil	Model did not converge							
Distance	Model did not converge							
Plant Available Phosphorus (mg/kg)								
Soil × Distance	447.18	0.00	0.94	0.34	0.63	0.16 ± 0.62	-0.04 ± 0.03	-0.13 ± 0.04
Distance	453.68	6.50	0.98	0.20	0.55		-0.10 ± 0.02	
Soil + Distance	454.80	7.62	1.00	0.26	0.55	-0.66 ± 0.55	-0.11 ± 0.02	
Null	467.35	20.17	1.00					
Soil	469.19	22.01	1.00	0.03	0.30	-0.35 ± 0.47		
Mineral Phosphorus (mg/kg)								
Soil × Distance	537.77	0.00	1.00	0.86	0.95	-1.09 ± 0.32	0.00 ± 0.00	-0.04 ± 0.01
Soil + Distance	560.48	22.71	1.00	0.82	0.92	-1.35 ± 0.31	-0.02 ± 0.00	
Distance	566.38	28.61	1.00	0.04	0.76		-0.02 ± 0.00	
Soil	573.55	35.78	1.00	0.78	0.89	-1.33 ± 0.31		
Null	579.62	41.85	1.00					
Sodium (mg/kg)								
Soil × Distance	438.56	0.00	0.73	0.29	0.59	0.22 ± 0.35	-0.03 ± 0.01	-0.04 ± 0.02
Distance	441.09	2.53	0.94	0.22	0.54		-0.05 ± 0.00	
Soil + Distance	443.53	4.97	1.00	0.22	0.54	-0.06 ± 0.35	-0.05 ± 0.01	
Null	464.02	25.45	1.00					

Soil	466.38	27.82	1.00	0.00	0.34	0.00 ± 0.00		
Potassium (mg/kg)								
<i>Soil × Distance</i>	676.07	0.00	0.94	0.29	0.81	-0.23 ± 0.42	0.01 ± 0.00	-0.02 ± 0.01
Null	682.93	6.86	0.97					
Soil	684.55	8.48	0.99	0.25	0.78	-0.37 ± 0.41		
Distance	685.17	9.10	1.00	0.00	0.72		0.00 ± 0.00	
Soil + Distance	686.89	10.82	1.00	0.26	0.78	-0.37 ± 0.41	0.00 ± 0.00	
Calcium (mg/kg)								
<i>Soil</i>	749.09	0.00	0.60	0.82	0.94	-1.45 ± 0.41		
<i>Soil + Distance</i>	751.01	1.92	0.83	0.82	0.94	-1.45 ± 0.01	0.00 ± 0.00	
Soil × Distance	753.00	3.91	0.91	0.82	0.94	-1.42 ± 0.41	0.00 ± 0.01	-0.01 ± 0.01
Null	753.55	4.46	0.97					
Distance	755.37	6.27	1.00	0.00	0.81		0.00 ± 0.00	
Iron (mg/kg)								
<i>Soil</i>	914.44	0.00	0.67	0.88	0.96	-1.22 ± 0.28		
Soil + Distance	916.83	2.39	0.87	0.88	0.96	-1.22 ± 0.28	0.00 ± 0.00	
Soil × Distance	918.54	4.10	0.95	0.88	0.96	-1.19 ± 0.28	0.00 ± 0.00	0.00 ± 0.01
Null	920.27	5.83	0.99					
Distance	922.55	8.11	1.00	0.00	0.82		0.00 ± 0.00	
Magnesium (mg/kg)								
<i>Soil</i>	700.88	0.00	0.63	0.87	0.96	-1.53 ± 0.37		
Soil + Distance	703.33	2.45	0.81	0.87	0.96	-1.53 ± 0.37	0.00 ± 0.00	
Soil × Distance	703.97	3.09	0.95	0.88	0.96	-1.48 ± 0.37	0.00 ± 0.00	-0.01 ± 0.01
Null	706.40	5.52	0.99					
Distance	708.75	7.87	1.00	0.00	0.84		0.00 ± 0.00	
Water (mmol/mol)								
<i>Null</i>	111.87	0.00	0.32					
<i>Distance</i>	112.09	0.22	0.61	0.03	0.38		0.02 ± 0.01	
<i>Soil</i>	112.92	1.05	0.80	0.12	0.40	0.45 ± 0.38		
<i>Soil + Distance</i>	113.27	1.40	0.96	0.14	0.42	0.45 ± 0.38	0.02 ± 0.01	
Soil × Distance	115.86	3.99	1.00	0.14	0.42	0.44 ± 0.42	0.02 ± 0.02	0.00 ± 0.03
pH								
<i>Soil × Distance</i>	55.04	0.00	0.37	0.07	0.44	0.05 ± 0.07	0.00 ± 0.00	-0.01 ± 0.00
<i>Null</i>	55.26	0.22	0.71					

<i>Distance</i>	<i>56.94</i>	<i>1.90</i>	<i>0.86</i>	<i>0.01</i>	<i>0.38</i>		<i>0.00 ± 0.00</i>	
Soil	57.63	2.59	0.96	0.00	0.37	0.00 ± 0.07		
Soil + Distance	59.41	4.37	1.00	0.01	0.38	0.00 ± 0.00	0.00 ± 0.00	

Table S2. Generalized linear mixed model results for leaf variables. The same five models were run for each response variable, including a null model, and each included site as a random effect to account for repeat measurements. AICc is Akaike’s Information Criterion, and Δ AICc is the difference between a given model and the best fit model for that response variable. Cum.Wt stand for cumulative weight; it gives the sum of Akaike’s weights and indicates the likelihood that the models up to that point are the best in the set. Models with a Δ AICc value of 2 are considered roughly equivalent in fit and are italicized. Marginal R^2 is the proportion of variance explained by both fixed and random effects in a model, and conditional R^2 is the proportion of variance explained by fixed effects. Coefficients (\pm standard error) are shown for each predictor and model and are in log units. Rows are organized in blocks by response variable. Within blocks, models are listed in order of increasing Δ AICc.

Model	Model Fit					Coefficients \pm SE		
	AICc	Δ AICc	Cum.Wt	Mar. R^2	Con. R^2	Soil	Distance	Soil \times Distance
Nitrogen (%)								
<i>Distance</i>	<i>56.12</i>	<i>0.00</i>	<i>0.64</i>	<i>0.40</i>	<i>0.60</i>		<i>-0.03 \pm 0.00</i>	
<i>Soil + Distance</i>	<i>57.79</i>	<i>1.67</i>	<i>0.92</i>	<i>0.43</i>	<i>0.61</i>	<i>0.13 \pm 0.14</i>	<i>-0.03 \pm 0.00</i>	
<i>Soil \times Distance</i>	<i>60.33</i>	<i>4.20</i>	<i>1.00</i>	<i>0.43</i>	<i>0.61</i>	<i>0.15 \pm 0.15</i>	<i>-0.03 \pm 0.01</i>	<i>0.00 \pm 0.01</i>
<i>Null</i>	<i>89.78</i>	<i>33.66</i>	<i>1.00</i>					
<i>Soil</i>	<i>91.66</i>	<i>35.53</i>	<i>1.00</i>	<i>0.03</i>	<i>0.21</i>	<i>0.10 \pm 0.13</i>		
$\delta^{15}\text{N}$								
<i>Soil \times Distance</i>	<i>229.95</i>	<i>0.00</i>	<i>0.95</i>	<i>0.51</i>	<i>0.77</i>	<i>-0.52 \pm 0.43</i>	<i>-0.11 \pm 0.01</i>	<i>0.06 \pm 0.02</i>
<i>Distance</i>	<i>236.55</i>	<i>6.60</i>	<i>0.99</i>	<i>0.44</i>	<i>0.70</i>		<i>-0.08 \pm 0.01</i>	
<i>Soil + Distance</i>	<i>238.97</i>	<i>9.02</i>	<i>1.00</i>	<i>0.45</i>	<i>0.70</i>	<i>-0.12 \pm 0.40</i>	<i>-0.08 \pm 0.01</i>	
<i>Null</i>	<i>282.45</i>	<i>52.50</i>	<i>1.00</i>					
<i>Soil</i>	<i>284.30</i>	<i>54.34</i>	<i>1.00</i>	<i>0.04</i>	<i>0.36</i>	<i>-0.30 \pm 0.41</i>		
Phosphorus (%)								
<i>Soil \times Distance</i>	<i>-87.04</i>	<i>0.00</i>	<i>0.99</i>	<i>0.47</i>	<i>0.75</i>	<i>-0.24 \pm 0.31</i>	<i>0.02 \pm 0.01</i>	<i>-0.04 \pm 0.01</i>
<i>Soil</i>	<i>-76.10</i>	<i>10.94</i>	<i>1.00</i>	<i>0.38</i>	<i>0.68</i>	<i>-0.55 \pm 0.31</i>		
<i>Null</i>	<i>-75.98</i>	<i>11.06</i>	<i>1.00</i>					

Soil + Distance	-73.69	13.34	1.00	0.38	0.68	-0.55 ± 0.31	0.00 ± 0.01	
Distance	-73.68	13.36	1.00	0.00	0.56		0.00 ± 0.01	
N:P Ratio								
Soil × Distance	209.64	0.00	0.86	0.41	0.71	0.34 ± 0.38	-0.05 ± 0.01	0.04 ± 0.01
Distance	214.60	4.96	0.94	0.09	0.59		-0.03 ± 0.01	
Soil + Distance	214.85	5.21	1.00	0.36	0.67	0.62 ± 0.01	-0.03 ± 0.00	
Null	225.74	16.10	1.00					
Soil	226.21	16.57	1.00	0.23	0.57	0.55 ± 0.37		
Sodium (mg/kg)								
Soil + Distance	839.97	0.00	0.60	0.62	0.78	-0.99 ± 0.32	-0.03 ± 0.01	
Soil × Distance	841.56	1.59	0.88	0.62	0.79	-0.88 ± 0.34	-0.03 ± 0.01	-0.02 ± 0.01
Distance	843.18	3.21	1.00	0.09	0.64		-0.03 ± 0.01	
Soil	852.98	13.02	1.00	0.53	0.71	-1.00 ± 0.32		
Null	856.49	16.52	1.00					
Magnesium (mg/kg)								
Soil × Distance	722.20	0.00	0.99	0.45	0.80	-0.20 ± 0.28	0.00 ± 0.00	-0.02 ± 0.01
Distance	731.74	9.54	0.99	0.07	0.66		-0.01 ± 0.00	
Soil + Distance	732.78	10.58	1.00	0.39	0.76	-0.36 ± 0.28	-0.01 ± 0.00	
Null	743.56	21.36	1.00					
Soil	744.46	22.26	1.00	0.31	0.69	-0.37 ± 0.28		
Potassium (mg/kg)								
Distance	936.99	0.00	0.73	0.20	0.57		-0.03 ± 0.00	
Soil + Distance	939.50	2.51	0.94	0.20	0.57	0.02 ± 0.25	-0.03 ± 0.00	
Soil × Distance	941.96	4.97	1.00	0.20	0.57	0.05 ± 0.26	-0.02 ± 0.01	0.00 ± 0.01
Null	956.55	19.57	1.00					
Soil	958.95	21.96	1.00	0.00	0.38	0.00 ± 0.24		
Calcium (mg/kg)								
Null	799.64	0.00	0.42					
Distance	800.68	1.04	0.67	0.01	0.50		0.00 ± 0.00	
Soil	801.22	1.58	0.86	0.14	0.53	-0.20 ± 0.21		
Soil + Distance	802.36	2.72	0.96	0.14	0.54	-0.20 ± 0.21	0.00 ± 0.00	
Soil × Distance	804.45	4.81	1.00	0.15	0.54	-0.16 ± 0.22	0.01 ± 0.01	-0.01 ± 0.01
Iron (mg/kg)								
Distance	591.87	0.00	0.69	0.21	0.57		-0.08 ± 0.01	

Soil + Distance	594.14	2.27	0.92	0.23	0.58	-0.26 ± 0.50	-0.08 ± 0.01	
Soil × Distance	596.15	4.27	1.00	0.23	0.59	-0.09 ± 0.39	-0.07 ± 0.00	-0.02 ± 0.02
Null	616.95	25.08	1.00					
Soil	619.06	27.19	1.00	0.02	0.48	-0.31 ± 0.00		

Table S3. Generalized linear mixed model results testing for correlations between leaf and soil micronutrients. The same model was run for each of five micronutrients (Na, K, Ca, Mg, and Fe) with leaf micronutrient concentration as the response variable, soil micronutrient + distance as the main effects, and site as a random effect. Marginal R^2 is the proportion of variance explained by both fixed and random effects in a model, and conditional R^2 is the proportion of variance explained by fixed effects. Coefficients (\pm standard error) are shown for each predictor and model.

Leaf Micronutrient	Mar. R^2	Con. R^2	Soil Micronutrient Coefficient \pm SE	Distance Coefficient \pm SE
Sodium	0.08	0.82	11.56 \pm 11.67	-146.47 \pm 43.04
Potassium	0.29	0.73	0.00 \pm 0.00	-0.06 \pm 0.01
Calcium	0.12	0.58	0.00 \pm 0.00	0.00 \pm 0.00
Magnesium	0.17	0.79	0.00 \pm 0.00	0.00 \pm 0.00
Iron	0.11	0.32	0.00 \pm 0.01	-52.85 \pm 20.57

Revised Supplemental Figures

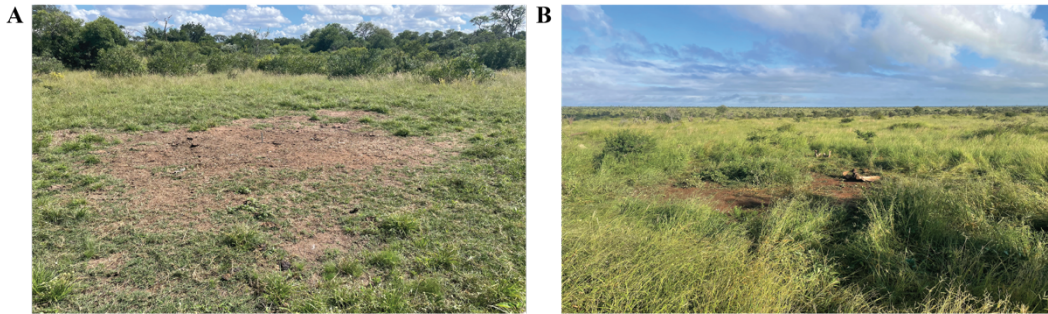


Figure S1. Representative photos of two elephant carcass sites of different ages and soil types.

(A) The first site is 67 days post-death and is on granitic soil. (B) The second site is 811 days post-death and is on basaltic soil. In both images, there is a visible impact zone with reduced vegetation coverage. At the first site, elephant bones have all been dispersed, though some are still present at the second site. Photos taken by Deron Burkepile at time of sample collection in March 2023.

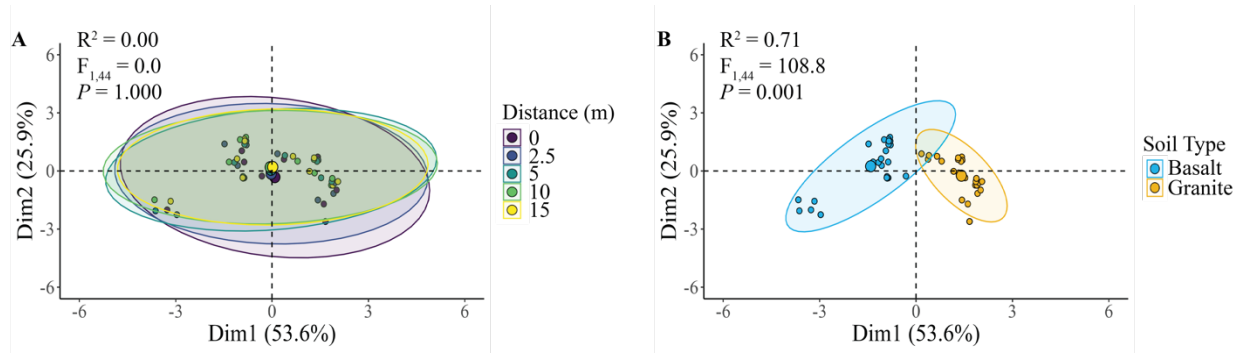


Figure S2. (A) Soil micronutrient composition did not differ significantly with distance from the carcass but (B) was distinct in different soil types.

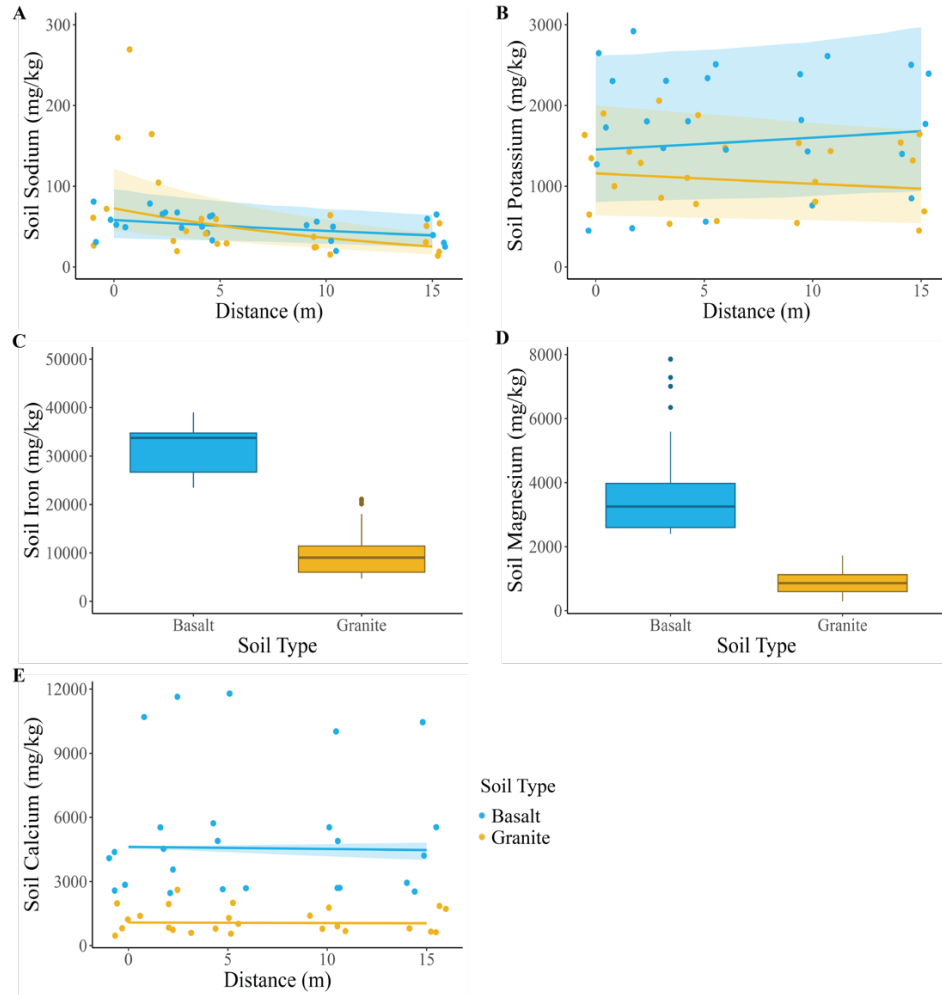


Figure S3. Effects of elephant carcasses on soil micronutrients. (A) Soil sodium decreased significantly with distance from the carcass. (B) Potassium decreased with distance but only in granitic soils. (C) Iron, (D) magnesium, and (E) calcium were greater in basaltic soils. Distance appeared in the top model for calcium, but the effect size was minimal. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap. Lines show predictions calculated from the top model. Shading indicates the 95% confidence interval.

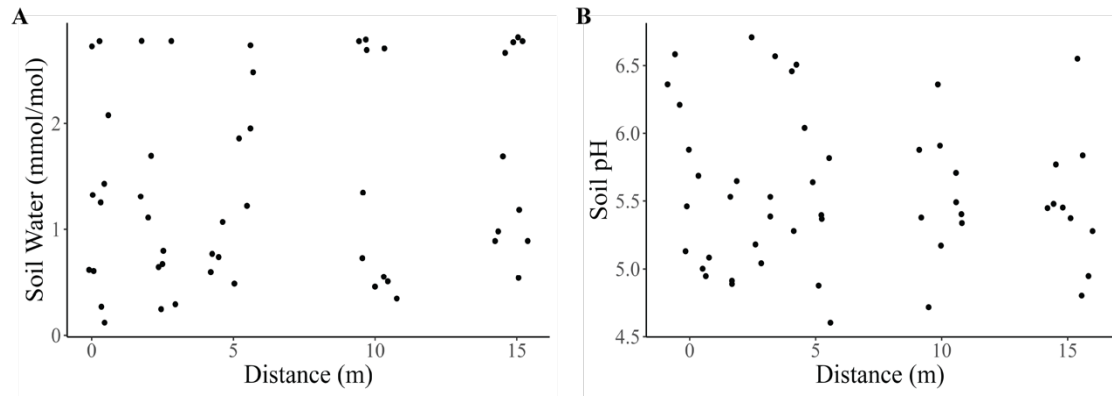


Figure S4. Neither (A) soil water nor (B) soil pH differed with distance or soil type. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap.

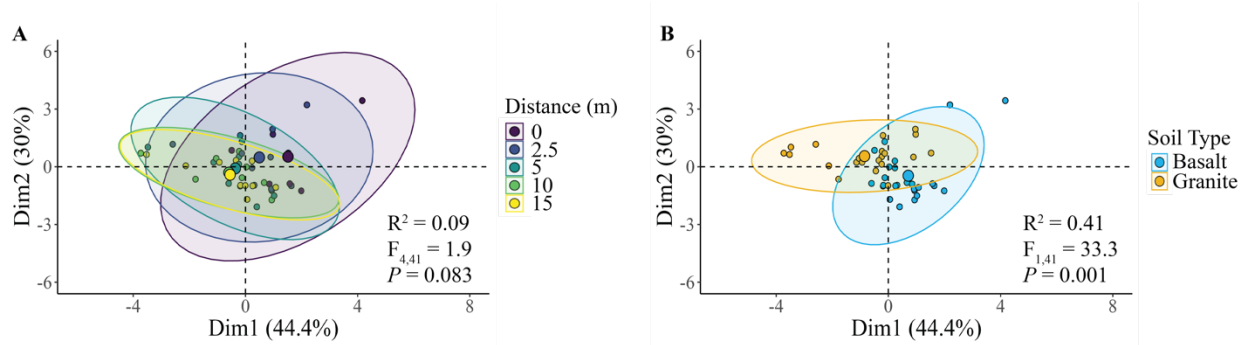


Figure S5. (A) Foliar micronutrient composition did not differ significantly with distance from the carcass but (B) was distinct in different soil types.

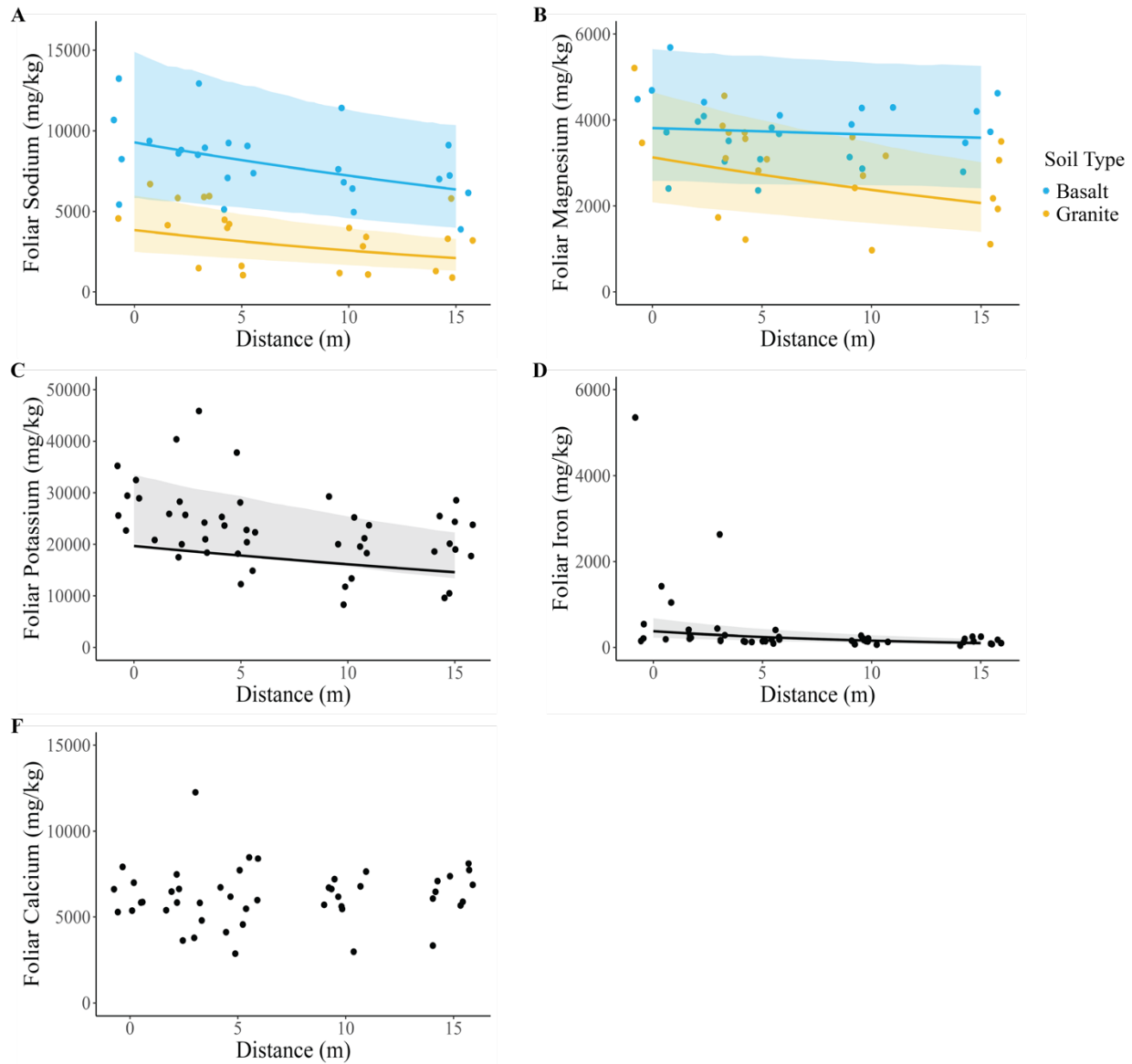


Figure S6. Effects of elephant carcasses on grass foliar micronutrients. (A) Foliar Na and (B) Mg were greatest in basaltic soil and decreased significantly with distance. (C) Foliar K and (D) Fe decreased with distance but did not differ with soil type. (E) Foliar Ca did not differ with distance or soil type. Points represent individual measurements taken at 0, 2.5, 5, 10, and 15m and are offset to be visible when they would otherwise overlap. Lines show predictions calculated from the top model. Shading indicates the 95% confidence interval.