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Life after Death – Does Carcass Biodiversity scale with carcass body size?

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By

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Abstract

Mammals play a large role in the ecosystems where some, especially large-bodied mammals, act as ecosystem engineers. Mammal carcasses, particularly those of large body mass act as a temporary island of dense nutrients that support other organisms, including other mammal species, for an extended period. Research in this field currently focuses on the link between mammal carcass size and nutrient availably or on non-mammalian size and biodiversity, but little is available on the correlation between mammal carcass size and its influence on ecosystem biodiversity. Here we ask, does the available biomass (i.e., body size) of the carcass affect its role in ecosystem function? Using a camera-trap monitoring system in a forested, sparsely populated site in the Arkansas River Valley, we measured the biodiversity associated with three mammal carcasses of small and medium size. A medium mammal carcass (5.5 kilograms) attracted 9 mammal species, with some up to 27 kilograms, over a period of two weeks. A second medium-sized mammal carcass (2.2 kilograms) attracted 7 species over a period of two weeks. A third small-sized mammal (1.2 kilograms) attracted 5 species over a period of two weeks. All mammals exploited the carcass in some manner, either by scavenging the carcass or feeding off the insects that also consume the carcass. When compared to the controlled observations at the same region, when no carcasses were present, there is an increase in the diversity and abundance of species observed. This demonstrates that living mammals exploit mammal carcasses for resources and suggests that the larger a carcass is, the more it may serve as an important resource to the nutrient cycling of an ecosystem. These results can be used to understand the impacts of biodiversity loss, specifically the loss of large-bodied mammals.

Introduction and Background

Mammal biodiversity is rapidly declining, as a result of human activity (Johnson et al., 2007). These changes are not isolated from the wider ecosystem; a change in one-part results in changes elsewhere. The cascading effects of large mammal biodiversity loss are largely negative to the health of the global ecosystem (Estes et al., 2011; Johnson et al., 2007), yet the full extent of the role that mammals play in the ecosystem is unclear (Lacher et al., 2019). This study will examine an understudied function of mammals: the role their carcasses play in the ecosystem after death.

Large mammals serve critical roles in maintaining the balance and health of an ecosystem (Lundgren et al., 2021). They are significant in the maintenance of complex trophic networks (food chains), as large mammals fill a wide range of roles, from predator to prey across the globe (Bilney et al., 2010; Lacher et al., 2019). Large mammals from all levels of the food chain have been observed to shape ecosystems through vegetation modification and landscapes of fear (Lacher et al., 2019). As ecosystem engineers, the decline and impending extinction of many large mammal species across the globe has ecological implications for the surviving species, including humans (Barton et al., 2016).

Ecological studies of the necrobiome (life associated with decomposing matter) indicate that carcasses and other decomposing matter are necessary to maintain the health of a biological system (Benbow et al., 2018). Decomposing matter, including mammal carcasses, contain essential nutrients like nitrogen and phosphorous, that are recycled back into the ecosystem by other organisms (Jenkinson et al., 1990). The decomposition process may even provide long-term sources of energy to an ecosystem, as is the case in “whale-drops” (whale carcasses that become large sinks of nutrients) on the seafloor or the consumption of terrestrial animal carcasses by scavengers (Feldman et al., 1998; Smith et al., 2015; Subalusky et al., 2017). Decomposition is indisputably important in ecosystem function, yet as biological diversity declines, particularly among large mammals, other questions arise. Does the available biomass (i.e., body size) of the carcass change its role? How is the carcass exploited by other members of the ecosystem? This research seeks to understand the role of mammal body size during carcass decomposition and its role in maintaining living mammal diversity.

Numerous studies address the role of decomposition in the health of an ecosystem (Enríquez et al., 1993; Scholes et al., 1997; Swift et al., 1979). For example, mammal carcasses affect insect succession and diversity (Pavaraj et al., 2018; Turner et al., 2017; van Klink et al., 2020) and changes in decomposing plant biomass availability influences species diversity. Yet, how the size of an animal carcass influences the necrobiome is unknown. While the decomposition of all organisms is important, the nutrients derived from decomposition, time available, and the type of species supported differs substantially between animal carcasses and plant biomass (Benbow et al., 2018). Mammal carcasses, particularly those of large body mass, have a disproportionate effect on an ecosystem in that they act as a temporary island of dense nutrients that support organisms throughout the ecosystem, including other mammal species, for an extended period (Benbow et al., 2018; Carter et al., 2007).

The research project proposed here will test the prediction that mammal carcass size is positively correlated with the number of mammal species and mammal abundance associated with that carcass. The findings of this study will contribute to an understanding of the full range of mammalian ecosystem functions: from life through decomposition. This information is increasingly urgent to gather as numerous large mammals face extirpation (local extinction) and, even more devastatingly, total extinction. I predict that the body size of a carcass influences how much diversity a carcass can support; that is, alpha diversity will be positively correlated with body size.

Methods and Materials

Carcass Collection: With permission from the City of Fayetteville Police Department and Arkansas Game and Fish Commission, roadkill was used as the source for the carcasses. The timeframe for collection was 0–2 days after death, to ensure the carcass was at early stages of decomposition.

Figure 1: (From top to bottom, in order) Images of the carcasses used in carcass trials: a racoon, rabbit, and opossum. Carcasses were estimated to have been found within 0-2 days of death to ensure minimal decomposition had taken place.

Two categories of mammal body mass were selected for the carcasses: small (0.4–4.9kg) and medium (5.0–34.9kg). These masses correspond to the common masses of micromammals (e.g., squirrels and rodents) and mesomammals (e.g., raccoons and dogs). While mammal sizes vary considerably more, mammals of extreme sizes (>100kg) have been extirpated from Arkansas and thus were not considered for this study. We obtained average body mass estimates from the Mass of Mammals Database (MOM v10.2), which includes estimates for most late Quaternary mammals (Smith et al., 2003). Three mammal carcasses of different weights were collected and placed in Northwest Arkansas (Fig. 1): Rabbit (1.2kg), Opossum (2.2kg), Racoon (5.5kg)

Site Selection and Carcass Placement: The study site is located on approximately 150 acres of private property located in Dover, AR (Fig. 2). Permission was obtained from the Funk family who own and occupy roughly 10 acres within this private property. This site was chosen for its remote location bordering the

Ozark National Forest. The property is primarily forested with human development (e.g., roads and shopping centers) to the south and southwest. Since the project is set in an area with human development, some anthropogenic (human) effects were expected on the study. Thus, domestic animals, such as human pets or feral livestock, were included in the data collection.

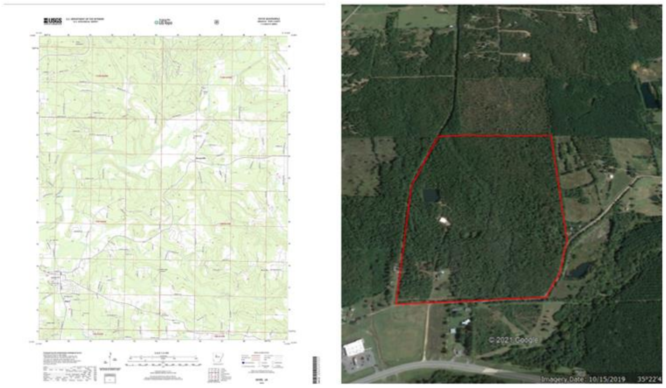

Figure 2: (From left to right) A topographic map of the study area and google earth imagery of the study site. On the google earth image, the boundaries of the study site are denoted in red (courtesy of Dr. Amelia Villasenor and Dr. Lucas Delezene).

Each carcass was separated by at least 5km to prevent one site from influencing another. Sites were chosen based on their relative proximity to animal game trails. While weather (e.g., temperature and precipitation) may influence the types of animals that visit the carcasses, the timeline for carcass placement and data collection took place over multiple seasons to mitigate its influence. The carcasses were held in place using rope and rebar spikes (Fig. 3) that have been hammered into the soil. These precautions ensured that the carcasses were not dragged away immediately. Once in place, carcasses were then monitored for approximately 3-4 weeks. The data collected focused on mammal occurrences, particularly those that exploited the carcasses.

Figure 3: Photo of rabbit carcass secured at the experiment site to prevent movement.

Field Data Collection-Camera Traps and Carcass Position: Three control studies were conducted over a period of three years in either March or April (2020-22).

Figure 4: Pilot study camera image of setup and mammal (possum) interaction with the carcass more than a week after the carcass was set (images taken in conjunction with Troy Warfield and Dr. Amelia Villasenor).

Control sites were on the opposite the human-occupied portion of the property and cameras were placed on game trails. Game trails were defined as narrow paths where vegetation was clearly eroded, and animal prints were often present. No carcasses were present during the control trials and motion-captured photos of animals using the game trails were collected to serve as a baseline of mammal composition and diversity on the property.

Figure 5: (From left to right) Images taken showing the position of the camera traps at each site, with two cameras in two locations capturing mammal occurrences. The yellow circle indicates where a camera is placed.

Two types of game cameras were used during data collection: Bushnell and Reconyx, both cameras had motion triggers that captured two photos and a video. During carcass trials, a minimum of two cameras were present per carcass, with each camera capturing different angles of the carcass. The cameras were positioned roughly 10–20 feet from the carcass to allow for observation of the carcass and surrounding area (Fig. 5). Any motion at the site also triggered multiple photos and a video. Additionally, the Reconyx camera captured a time lapse of the site (one photo was taken every five minutes over each 24-hour period).

Statistical Analysis: Mammal occurrences were compiled from control trial and carcass trial camera trap images, which were collected over two-to-three-week periods. Species richness is defined as the number of different animal species observed at a site within a specified time-period (e.g., 15-20 days). When calculating abundance, a species was counted as a new occurrence if it was not observed for at least 30 minutes (Reece et al., 2021; Stein et al., 2008). If multiple individuals of a single species were observed, the maximum number of species observed within a 30-minute period is counted as the abundance of that group (Hansen et al., 2020). Mammals were identified using lists of the types of mammals present in Northwest Arkansas (via historical and current data – Arkansas Game and Fish Commission and available mammal lists).

An alpha diversity metric, the Shannon-Weiner index, was used to quantify diversity. The formula for the Shannon-Weiner index is, $H = -\Sigma[(p_i) * \log(p_i)$, where pi is the proportion of each species measured. This metric thus accounted for both the species richness and relative abundance (Chao et al., 2014). Alpha diversity was calculated for each carcass and for two control periods where no carcasses were present. Species accumulation curves were also used to estimate sampling differences within and between the control and carcass trials. Diversity index calculations and species accumulation curves were performed using the package ‘vegan’ and plots were created using ‘ggplot’ (Oksanen et al., 2016). All other calculations were performed in base R (Team, 2013).

Biosafety: University of Arkansas biosafety policies were followed when in contact with the carcass (e.g., the use of personal protective equipment, disposable bags, etc.). Following the completion of observation, the carcasses were disposed of following University of Arkansas biohazard policies.

Results

Sample	Shannon index (alpha diversity)	Richness	Observation (days)	Total observations (n)	Body size (kg)
Racoon	1.420891	9	17	656	5.5kg
Opossum	1.261525	6	14	276	2.2
Rabbit	1.174358	5	14	79	1.2
April control 2020	1.083565	7	20	649	NA
March control 2022	0.7393213	3	15	31	NA
April control 2021	0.36	3	15	66	NA

Table 1: Summary results table indicating the sample measured (i.e., carcass or control group), the corresponding alpha diversity calculated from Shannon-Weiner Diversity Index, and taxa present (richness). The table also includes the number of days each sample was observed, the total number of observations (total animal occurrences), and body size where applicable.

Control Trials: The three control trials, which occurred over three years (2020-22) when no mammal carcasses were present, were lower in diversity compared to trials where carcass were present (Table 1). Only one control trial, April 2020, captured a similar number of species (7) to animal carcass trials (Fig 6A). During the control trials, the mammal community was largely dominated by herbivores, such as deer and rabbits (Fig 6 A-C).

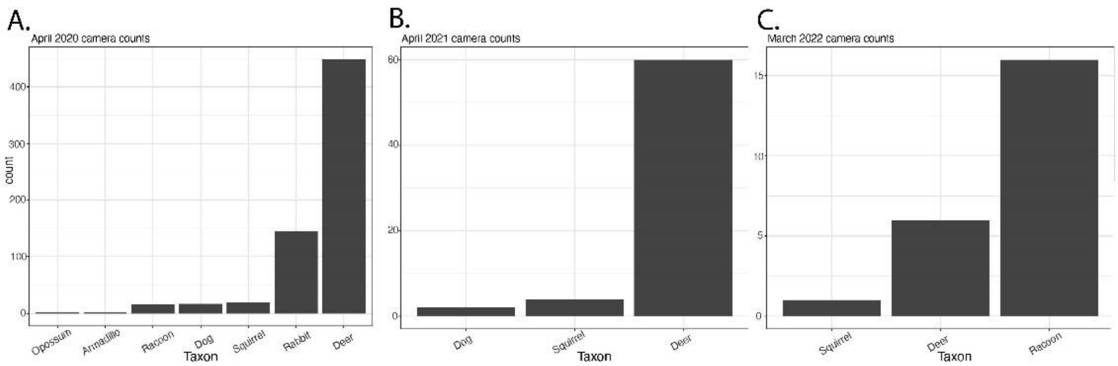

Figure 6: Counts of taxa observed at each location plotted against the counts of taxa richness for the control sites. The highest taxa counts were that of deer and raccoon.

Species accumulation curves demonstrated that control trials were slower to accumulate species richness over time compared to mammal carcass sites (Fig. 7). Further, the trials from 2021 and 2022, likely under sampled community diversity and are not appropriate baselines for the total species richness for the area. However, the trials from 2021-22 demonstrate that, without carcasses, it can take greater than 15 days to accumulate a representative sample of mammalian species.

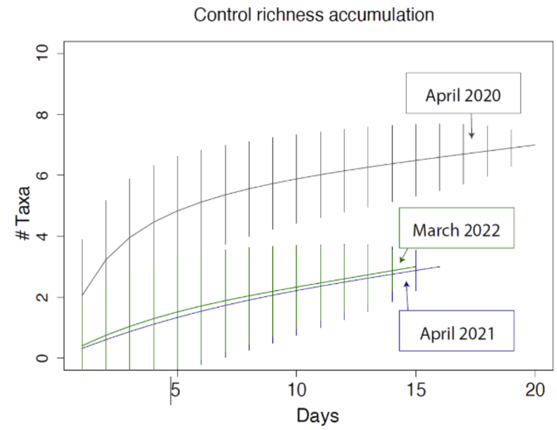

Figure 7: A graph plotting the days of observation versus number of taxa observed to estimate the species accumulation curve at each camera site.

Carcass Trials: All three carcass trials exhibited higher alpha diversity than any of the control trials. Unlike the control trials, the mammal community associated with the carcass trials was largely dominated by carnivores, such as racoons, and animals that were rarer in control trials, such as opossums and foxes, were more common at some of the carcass trials (Fig. 8B). some carcasses were shown, however, to not have

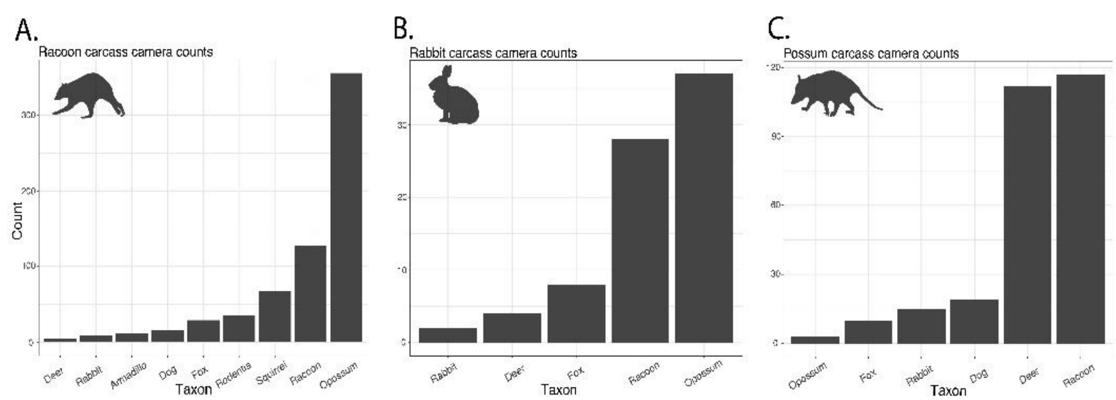

Figure 8: (from Left to Right) Counts of taxa observed at each location plotted against the counts of each taxa (richness). The left graph (A) is the largest carcass (racoon) and shows nine taxa, where opossum and racoon have the highest counts. The middle graph (B) is the smallest carcass (rabbit) and shows 5 taxa, with opossum and racoon having the highest counts. The right graph (C) is the second largest carcass (opossum) and shows six taxa, where racoon and deer have the highest counts.

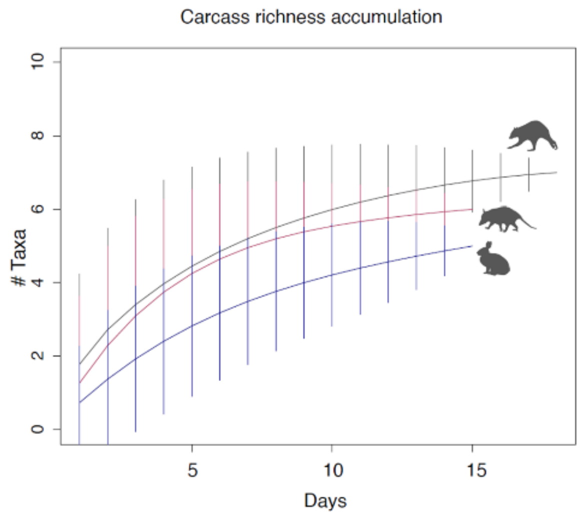

Figure 9: A graph plotting the days of observation versus number of taxa observed to estimate the species accumulation curve for each carcass type (indicated by animal silhouette). The smaller carcasses tend towards lower/less steep accumulation curves, indicating less mammal diversity associated with smaller carcasses.

representation from some species within their community composition, such as with the absence of opossums at the opossum carcass. Further, species accumulation curves (Fig. 9) of the carcasses trials show that species richness is accumulates more quickly over shorter periods compared to the control trials. Thus, carcasses draw a broader range of species to carcasses at a faster rate than when no carcasses are present. Finally, larger carcasses are associated with higher diversity, suggesting carcasses draw more species and have more even occurrences of those species through time.

Discussion and Conclusion

The results of this study support the prediction that the body mass of a mammalian carcass is positively correlated with the mammalian diversity associated with that carcass. There are caveats to this prediction, however. It appears that some species, particularly carnivores, avoid cannibalism when utilizing carrion (Moleón et al., 2017), which may account for the notable lack of opossums within the scavenger assemblage at the opossum carcass site. In future trials, we expect that larger species' carcasses, such as deer, would draw a broader diversity of mammals over longer periods. These results reinforce the idea that carcasses are hotspots for diversity across ecosystems (Smith et al., 2015; Taylor et al., 2020) and that animal body size is correlated with its function in the ecosystem, and thus should be considered for future studies.

Decomposing carcasses are a sink of essential nutrients that are recycled back into the environment (Benbow et al., 2018; Scholes et al., 1997; Swift et al., 1979) Elements like nitrogen and phosphorous remain evident at high levels in soil composition for up to five years following a carcass placement (Barton et al., 2016; Benninger et al., 2008; van Klink et al., 2020). Further, the larger a species' biomass, the greater density of biochemical nutrients it reserves during life and releases after death (Elser et al., 2000; Elser & Hamilton, 2007; Vanni et al., 2013). The relationship between biomass and biochemical density emphasizes the importance of large animals within an ecosystem because dense pockets of valuable nutrients can support an increase in the carrying capacity of environments. This phenomenon is exemplified during whale-falls that occur in largely nutrient deficient locations (at the bottom of the ocean) but are still evident in comparatively nutrient-rich areas like forests and grasslands (Bump et al., 2009; Smith et al., 2015; Subalusky et al., 2017).

Studies conducted in other continents show that the relationship between carcass size and the associated mammal diversity can be complicated by biotic interactions, such as competition. Similar studies examining the mammal diversity associated with carcasses were conducted on the Majete Wildlife Reserve (Malawi) and Hluhluwe-iMfolozi Park (South Africa). These reserves are not only different from this study in species composition but are different in that they retain megaherbivores and megacarnivores (>44kg)- a characteristic that many ecosystems outside of Africa and Asia lack. Within Malawi and South Africa, megafauna included elephants, hippopotamuses, rhinoceroses, lions, and hyenas. These megafauna are vastly larger than any animals found in Arkansas at present, where the largest wildlife are elk and black bears (Moleón et al., 2015; Reece et al., 2021). Contrary to the study presented here, the studies in southern Africa found that as carcass size increased, the diversity of species at the carcass decreased (Moleón et al., 2015; Reece et al., 2021). Large carnivores competitively excluded smaller carnivores at the sites where larger carcasses were available. Larger carnivores monopolize carcasses and continue to feed on it over time, thus preventing an increase in the medium and small scavengers. At sites with small carcasses, mammals were composed of only small and medium carnivores. It was also noted that small carnivores were likely to avoid these larger carcasses due to the possibility of predation by the larger carnivore (Moleón et al., 2015).

Since few large carnivore species are present outside of Africa and Asia, this has largely removed the ecological pressures placed on small and medium sized carnivores and has resulted in the increase in mesocarnivore populations via “mesocarnivore release” (Allen et al., 2015; Berger et al., 2008). Ecological communities are structured by various trophic levels that transfer energy sequentially from one to another. As was documented in southern Africa, larger animals tend to dominate the top of these trophic pyramids, requiring larger amounts of resources that pull from the ecosystem around them. When large carnivores are extirpated from ecosystems, as they are in the southern United States, the top non-human predator is usually a mesomammal. In the absence of predation or competition for resources by larger mammals, the population of these animals can increase. Medium-sized mammals have thus filled the empty niches left by the extirpation of large mammals in many parts of the United States. Mesomammals, such as coyotes, raccoons, or opossums can increase their population sizes as they no longer face predation and competition by larger carnivores like wolves, which alters the manner in which carnivores of this size interact with their environments. The lack of large animals in Arkansas, which decreases the likelihood of competitive exclusion mesocarnivores face, may have resulted in the positive correlation between carcass size and diversity found in this study, suggesting that functional roles shift as species are driven to extinction or extirpation.

North American ecosystems are fundamentally different than they were over ten thousand years ago in that there is a lack of megafauna throughout much of the United States. Because of this, functional roles once filled by smaller populations of larger mammals have been filled by mesomammals that have dramatically different ways in which they interact with their surroundings. This alters the diversity of many environments and can drastically alter the structure, function, and maintenance of many different ecosystems. These alterations to the environment are often due to anthropogenic factors, one of which is the total removal of carcasses from most urban ecosystems. By removing such nutrient dense sources in ecosystems, humans continue to alter ecosystems in dynamic ways that may leave lasting impacts.

References

Allen, M. L., Elbroch, L. M., Wilmers, C. C., & Wittmer, H. U. (2015). The Comparative Effects of Large Carnivores on the Acquisition of Carrion by Scavengers. *The American Naturalist*, *185*(6), 822-833. https://doi.org/10.1086/681004

Barton, P. S., McIntyre, S., Evans, M. J., Bump, J. K., Cunningham, S. A., & Manning, A. D. (2016). Substantial long-term effects of carcass addition on soil and plants in a grassy eucalypt woodland. *Ecosphere*, *7*(10), e01537. https://doi.org/https://doi.org/10.1002/ecs2.1537

Benbow, M., Barton, P., Ulyshen, M., Beasley, J., DeVault, T., Strickland, M., . . . Pechal, J. (2018). Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, *89*. https://doi.org/10.1002/ecm.1331

Benninger, L. A., Carter, D. O., & Forbes, S. L. (2008). The biochemical alteration of soil beneath a decomposing carcass. *Forensic science international*, *180*(2-3), 70-75.

Berger, K. M., Gese, E. M., & Berger, J. (2008). INDIRECT EFFECTS AND TRADITIONAL TROPHIC CASCADES: A TEST INVOLVING WOLVES, COYOTES, AND PRONGHORN. *Ecology*, *89*(3), 818-828. https://doi.org/10.1890/07-0193.1

Bilney, R. J., Cooke, R., & White, J. G. (2010). Underestimated and severe: small mammal decline from the forests of south-eastern Australia since European settlement, as revealed by a top-order predator. *Biological Conservation*, *143*(1), 52-59.

Bump, J. K., Webster, C. R., Vucetich, J. A., Peterson, R. O., Shields, J. M., & Powers, M. D. (2009). Ungulate Carcasses Perforate Ecological Filters and Create Biogeochemical Hotspots in Forest Herbaceous Layers Allowing Trees a Competitive Advantage. *Ecosystems*, *12*(6), 996-1007. https://doi.org/10.1007/s10021-009-9274-0

Carter, D. O., Yellowlees, D., & Tibbett, M. (2007). Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften*, *94*(1), 12-24.

Chao, A., Gotelli, N. J., Hsieh, T., Sander, E. L., Ma, K., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological monographs*, *84*(1), 45-67.

Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., . . . Schulz, K. L. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, *408*(6812), 578-580.

Elser, J. J., & Hamilton, A. (2007). Stoichiometry and the new biology: the future is now. *PLoS biology*, *5*(7), e181.

Enríquez, S., Duarte, C. M., & Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C: N: P content. *Oecologia*, *94*(4), 457-471.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., . . . Jackson, J. B. (2011). Trophic downgrading of planet Earth. *science*, *333*(6040), 301-306.

Feldman, R. A., Shank, T. M., Black, M. B., Baco, A. R., Smith, C. R., & Vrijenhoek, R. C. (1998). Vestimentiferan on a whale fall. *The Biological Bulletin*, *194*(2), 116-119.

Hansen, C. P., Parsons, A. W., Kays, R., & Millspaugh, J. J. (2020). Does Use of Backyard Resources Explain the Abundance of Urban Wildlife? [Original Research]. *Frontiers in Ecology and Evolution*, *8*(374). https://doi.org/10.3389/fevo.2020.570771

Jenkinson, D. S., Andrew, S. P. S., Lynch, J. M., Goss, M. J., Tinker, P. B., Greenwood, D. J., . . . Walker, A. (1990). The turnover of organic carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *329*(1255), 361-368. https://doi.org/doi:10.1098/rstb.1990.0177

Johnson, C. N., Isaac, J. L., & Fisher, D. O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 341-346.

Lacher, T. E., Jr., Davidson, A. D., Fleming, T. H., Gómez-Ruiz, E. P., McCracken, G. F., Owen-Smith, N., . . . Vander Wall, S. B. (2019). The functional roles of mammals in ecosystems. *Journal of Mammalogy*, *100*(3), 942-964. https://doi.org/10.1093/jmammal/gyy183

Lundgren, E. J., Ramp, D., Stromberg, J. C., Wu, J., Nieto, N. C., Sluk, M., . . . Wallach, A. D. (2021). Equids engineer desert water availability. *Science*, *372*(6541), 491-495.

Moleón, M., Martínez-Carrasco, C., Muellerklein, O. C., Getz, W. M., Muñoz-Lozano, C., & Sánchez-Zapata, J. A. (2017). Carnivore carcasses are avoided by carnivores. *Journal of Animal Ecology*, *86*(5), 1179-1191. https://doi.org/10.1111/1365-2656.12714

Moleón, M., Sánchez-Zapata, J. A., Sebastián-González, E., & Owen-Smith, N. (2015). Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos*, *124*(10), 1391-1403.

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., . . . Wagner, H. (2016). vegan: Community Ecology Package. R package version 2.2–1. 2015. In.

Pavaraj, M., Eswaran, K., Kumar, A., & Rajan, M. K. (2018). Diversity of forensic insects in a rodent carcass.

Reece, S. J., Radloff, F. G., Leslie, A. J., Amin, R., & Tambling, C. J. (2021). A camera trap appraisal of species richness and community composition of medium and large mammals in a Miombo woodland reserve. *African Journal of Ecology*.

Scholes, M. C., Powlson, D., & Tian, G. (1997). Input control of organic matter dynamics. *Geoderma*, *79*(1), 25-47. https://doi.org/https://doi.org/10.1016/S0016-7061(97)00037-2

Smith, C. R., Glover, A. G., Treude, T., Higgs, N. D., & Amon, D. J. (2015). Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science*, *7*, 571-596.

Smith, F. A., Lyons, S. K., Ernest, S. M., Jones, K. E., Kaufman, D. M., Dayan, T., . . . Haskell, J. P. (2003). Body mass of Late Quaternary mammals: ecological archives E084-094. *Ecology*, *84*(12), 3403-3403.

Stein, A. B., Fuller, T. K., & Marker, L. L. (2008). Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. *17*(14), 3579-3587.

Subalusky, A. L., Dutton, C. L., Rosi, E. J., & Post, D. M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences*, *114*(29), 7647.

Swift, M. J., Heal, O. W., Anderson, J. M., & Anderson, J. (1979). *Decomposition in terrestrial ecosystems* (Vol. 5). Univ of California Press.

Taylor, L. S., Phillips, G., Bernard, E. C., & Debruyn, J. M. (2020). Soil nematode functional diversity, successional patterns, and indicator taxa associated with vertebrate decomposition hotspots. *PLOS ONE*, *15*(11), e0241777. https://doi.org/10.1371/journal.pone.0241777

Team, R. C. (2013). R: A language and environment for statistical computing.

Turner, K. L., Abernethy, E. F., Conner, L. M., Rhodes Jr., O. E., & Beasley, J. C. (2017). Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. *Ecology*, *98*(9), 2413-2424. https://doi.org/https://doi.org/10.1002/ecy.1930

van Klink, R., van Laar-Wiersma, J., Vorst, O., & Smit, C. (2020). Rewilding with large herbivores: Positive direct and delayed effects of carrion on plant and arthropod communities. *PLOS ONE*, *15*(1), e0226946.

Vanni, M. J., Boros, G., & McIntyre, P. B. (2013). When are fish sources vs. sinks of nutrients in lake ecosystems? *Ecology*, *94*(10), 2195-2206.