**Journal:**

**Title**: Apex scavenger declines have cascading effects on carrion food webs and soil properties

**Authors:**

Savannah L. Bartel1, Laurel Lynch2,Torrey Stephenson2, Kawinwit Kittipalawattanapol3, Menna E. Jones3, Michael S. Strickland2, Andrew Storfer4, Tara Hudiburg5, David W. Crowder1

**Addresses:**

1 Washington State University, Department of Entomology, 166 FSHN Building, Pullman, WA, USA, 99164

2 University of Idaho, Department of Soil and Water Systems, 875 Perimeter Drive, Moscow, ID, USA, 83844

3 University of Tasmania, School of Natural Sciences, Life Sciences Building, Hobart, Tasmania, 7001

4 Washington State University, School of Biological Sciences, 410 Dairy Road, Pullman, WA, USA, 99164

5 University of Idaho, Department of Forest, Rangeland and Fire Sciences, 875 Perimeter Drive, Moscow, ID, USA, 83844

**Abstract**

Populations of many dominant scavenger species are in global decline. The loss of these species affects competition for carrion, which affects the population dynamics of other mesoscavengers, invertebrate scavengers, and microbial decomposers. However, it is poorly understood whether the loss of dominant scavengers alsos impact nutrient cycling by slowing carrion consumption and increasing flow of carrion-derived resources through lower order vertebrate and invertebrate scavenger communities. Here we assessed this by testing if declines of a dominant scavenger, the Tasmanian devil (*Sarcophilus harrisii*), affected carcass persistence, scavenging activity by other vertebrate and invertebrate scavengers, and belowground inputs of carrion-derived nutrients near carcasses. Specifically, we manipulated adult devil access to 68 carcasses during the summer and winter in Tasmania across a gradient of devil population densities, and used structural equation models to measure direct and indirect effects of devils on carrion food webs and soil properties. We show that adult devil scavenging significantly reduced carcass persistence in both seasons, and juvenile devil scavenging also reduced carcass persistence in summer. In the summer, devil scavenging also indirectly reduced invertebrate scavenging activity and soil ammonium inputs. Our results suggest Tasmanian devils shape carrion persistence, scavenging communities, and belowground delivery of carrion-derived nutrients in Tasmanian forests. Rapid declines of devils could thus have broad, cascading effects on invertebrate scavengers and ecosystem processes.

**Introduction**

Populations of many apex predator and scavengers are declining worldwide, with major effects on communities (Estes *et al.* 2011; Ripple *et al.* 2014; Fielding *et al.* 2022). While most attention has focused on apex predators, many dominant scavengers are at risk of extinction, and evidence shows scavengers can strongly shape vertebrate communities (Olson *et al.* 2012; Buechley and Sekercioglu 2016; Bartel *et al.* 2023). In some cases, dominant scavengers facilitate carcass use by subordinate species by providing cues of carcass locations (Beasley *et al.* 2015; Naves-Alegre *et al.* 2022). Alternatively, dominant scavengers can limit carcass use by other species by more rapidly discovering and consuming carcasses (Olson *et al.* 2012; Fielding *et al.* 2022). However, evidence of how changes in dominant scavenger abundance affect carrion food webs and flow of carrion-derived nutrients to soils, is limited (Buchley and Sekercioglu 2016; Bartel *et al.* 2023).

Carrion decomposition is fundamental to nutrient cycling (Benbow *et al.* 2019; Newsome *et al.* 2021). As organisms compete for carrion, changes in scavenger populations may also affect flow of carrion-derived nutrients to soil (Newsome *et al.* 2021; Bartel *et al.* 2023). When carrion is consumed by vertebrates, a large portion of carrion-derived nutrients are delivered back to soil through dispersed waste excretion (Wilson and Wolkovich 2011; Bartel *et al.* 2023). However, declines in vertebrate scavengers can increase carcass use by microbes and invertebrates, where carrion-derived nutrients are delivered below the carcass and create biogeochemical hotspots (Macdonald *et al.* 2014; Keenan *et al.* 2018; Quaggiotto *et al.* 2019). Microbial decomposition also releases soluble organic matter into soil during bloat and seepage stages(Macdonald *et al.* 2014; Keenan *et al.* 2018), and may relieve nutrient constraints on soil microbial metabolism (Bartel *et al.* 2023). Although overlooked, scavenger declines may affect the delivery of carrion-derived nutrients to soil in ways that influence ecosystem productivity (Bartel *et al.* 2023).

The island of Tasmania offers a unique system to assess effects of a top scavenger decline. The Tasmanian devil (*Sarcophilus harrisii*) is the top predator and scavenger (Cunningham *et al.* 2018; Fielding *et al.* 2022); but populations have declined since a highly transmissible cancer (devil facial tumor disease) emerged in 1996 (Hawkins *et al.* 2006). As devil facial tumor disease spread, devil declines of over 80% have been observed (Lazenby et al. 2018; Cunninham et al. 2021). Devil declines have cascading effects on carrion decomposition, and carcasses persist 3-fold longer at sites with major declines than at locations with uninfected, “healthy” populations (Cunningham *et al.* 2018). By rapidly consuming carcasses, devils limit carcass use by microbes and invertebrates, possibly reducing metabolic byproducts at carcasses (Parmenter *et al.* 2009; Voss *et al.* 2009). However, research is still lacking that broadly assesses whether devil declines can affect soil nutrient delivery through direct and indirect trait-mediated pathways.

We hypothesized that scavenging by Tasmanian devils reduces carrion persistence, leading to indirect negative effects of devils on invertebrate scavenging and the influx of carrion-derived nutrients belowground. We tested this by manipulating adult devil access to 68 carcasses across the gradient of devil abundance caused by the east-to-west spread of devil facial tumor disease. At each site, we measured devil and mesoscavenger activity, carcass persistence, invertebrate scavenger abundance, soil nutrient concentrations, and soil microbial communities (summarized using r:K ratios). We predicted greater devil scavenging activity would reduce mammalian and avian mesoscavenger activity and carcass persistence. We also predicted invertebrate scavenging activity, soil nutrient concentration, and soil microbial R:K ratios would increase with longer carcass persistence. Our study reveals how declines of a dominant scavenger may indirectly govern community structure and the delivery of carrion-derived nutrients through ecosystems.

**Methods**

*Experimental design*

Our experiment used three sites along a gradient of devil density caused by spread of devil facial tumor disease (Appendix S1: Fig. S1). Devil facial tumor disease outbreaks, and subsequent devil declines, began 26 years ago at Blue Tier, 15 years ago at West Takone, and 3 years ago at Salmon River (Cunningham *et al.* 2021). We conducted our experiment at each site in winter (July-August) and summer (February-March). At each site in each season, we established six replicate blocks separated by > 1 km. Within each block, we assessed effects of adult devils by establishing two plots, separated by 200 m: one plot contained a carcass with full devil access, and one contained a carcass inside an exclosure that excluded adult devils. Full-access plots had one adult pademelon carcass staked to the ground with a 45 cm star picket. Exclosures had one carcass staked to the ground and enclosed by a weld-mesh box with 10 × 10 cm openings that allowed access to all mammalian and invertebrate scavengers except adult devils; subadult devils less than 15 months old were small enough to enter. Exclosures were 1.1 × 1.7 × 1.0 m in size. Weld-mesh bottoms were added to the exclosures in summer to prevent entry by digging.

*Carcass persistence and vertebrate scavenging activity*

During the winter (July 2023), we deployed 34 carcasses for 26 d; unforeseen weather events led to removal of two plots (1 exclosure, 1 full access) at Salmon River. During summer (Feb 2023), we deployed 34 carcasses for 30 d; we removed one block from West Takone due to a failure of an exclosure. Carcasses were visited every 5 to 10 d to assess the presence or absence of internal organs, muscle, bones, tail, and hide at each carcass. Carcass persistence was quantified by the number of days a carcass persisted until the internal organs and muscle were fully consumed.

Remote wildlife cameras (Swift Enduro, Outdoor Cameras Australia, QLD) were placed at each carcass to confirm measurements of carcass persistence and to assess vertebrate scavenger activity. Each camera was fastened to a tree at 0.5 to 1.0 m, facing the ventral side of the carcass. Cameras were active for 24 h a day and set at high sensitivity to capture five photos per trigger. We identified vertebrate species captured on images using the Mega-Efficient-Wildlife-Classifier software (Brook *et al.* 2023). We tagged species using DigiKam software (digiKam team, 2020) and used the camtrapR package in R (v. 4.3.2) to export the date, time, and species tag for each photo (Niedballa *et al.* 2016). Tasmanian devils were also scored by age (adult or subadult) based on their body size and head width. For all vertebrate photos, we scored foraging behavior as a binary variable: 1 if they were consuming the carcass and 0 if not. We captured repeated scavenging (i.e., scavenging at > 1 carcass) by adult devils, subadult devils, spotted-tailed quolls (*Dasyurus maculatus*), eastern quolls (*Dasyurus viverrinus*), forest ravens (*Corvus tasmanicus*), and black currawongs (*Strepera fuliginosa*). We grouped scavengers for analysis by functional group: (i) adult devil, (ii) subadult devil, (iii) mammalian mesoscavenger (*D. maculatus*, *D. viverrinus*), and (v) avian scavenger (*C. tasmanicus*, *S. fuliginosa*). We also summed the total number of foraging photos for each group to estimate the intensity of foraging activity.

*Invertebrate scavenging activity*

We placed two pitfall traps (120 mL jars with preservative buried flush with soil) at each carcass. Traps were set 20 cm from the top (mouth) and bottom (cloaca) openings of each carcass, and were collected and refilled 5, 10, and 30 d after deployment. Traps were processed to count carrion beetle adults and blow fly larvae. In winter, adult carrion beetles were never detected and blow fly abundance was low, and we categorized invertebrate scavenger response as present or absent based on whether blow fly larvae were captured in traps or visually observed in carcasses. Invertebrate scavengers were present at all carcasses in summer, and we quantified invertebrate abundance from traps. For each trap-collection period, a few traps were destroyed by vertebrate scavengers, so we calculated the average number of invertebrate scavengers at each carcass, excluding destroyed traps. Invertebrate scavenger abundance at each carcass was estimated as the total number of adult carrion beetle and blow fly larvae across all trap-collection periods.

*Soil properties and microbial communities*

To measure soil nutrients and microbial communities below carcasses, we collected soil samples from the top 7 cm of soil after removing the organic horizon using a 4-cm soil corer sterilized with ethanol. Soil samples were homogenized by hand and then divided into subsamples. We placed a subsample for microbial analyses on ice in a freezer at -20 ℃ within 48 h of collection. Remaining subsamples were oven-dried at 60 ℃ to determine percent moisture, then sieved to 2 mm and stored at ambient temperature. During both the winter and summer period, we collected soil samples on the day of carcass placement and again at the conclusion of the experiment.

We quantified inorganic nutrients, ammonium (NH4-N), and phosphate (PO4-P) from the subsamples. We used 50 ml of a 0.05 M K2SO4 solution to extract 10 g of thawed soil by mixing at 200 rpm for 1 h on an orbital shaker and filtering with Whatman #1 filter paper. Extracts were frozen and thawed within 24 h of analysis. We measured inorganic nutrients using colorimetric analysis on a Spectramax M2 spectrophotometer, NH4-N using the phenol-hypochlorite method (Weatherburn 1967), and PO4-P using the malachite green procedure (Lajtha *et al.* 1999).

We extracted DNA from soil subsamples with PowerSoil Pro Kits (Qiagen, Valencia, CA, USA). The resulting extracts were diluted 10 times prior to PCR amplification of bacterial 16S genes using primer pair 515F/518R (Strickland *et al.* 2017). PCR products were cleaned, pooled, and sequenced with an Illumina MiSeq with 250-bp paired-end reads at Duke’s Sequencing and Genomic Technologies shared resource. We processed the raw data using DADA2 and assigned taxonomy using the SILVA database (Quast *et al.* 2013) prior to constructing a phyloseq object (R package ‘phyloseq’; McMurdie *et al.* 2013). The object was refined by removing samples with fewer than 10,000 reads andnon-target or unknown sequences, then rarefying to the lowest sample. Finally, we calculated a bacterial r:K ratio, representing balance between faster-versus slower-growing phyla in the soil microbiome, as the sum of “Proteobacteria” and “Bacteroidota” divided by the sum of “Verrucomicrobiota” and “Acidomicrobiota” (Andrews *et al.* 1986).

*Data analysis*

We used piecewise structural equation modelling (Lefcheck 2015) to test *a priori* predictions, with Tasmanian devil foraging activity as a predictor, and mammalian mesoscavenger foraging activity, avian scavenger foraging activity, invertebrate scavenger activity (presence in winter, abundance in summer), carcass persistence, soil ammonium, soil phosphate, and r:K ratio of soil microbial communities as responses (Fig. 1). We ran separate structural equation models for the winter and summer seasons due to differences in exclosure design and invertebrate distributions. Subadult devil foraging activity was included as a response in the summer but not in the winter model because subadults are not active in winter. To construct structural equation models, we first fit individual regressions that comprised the models (Appendix S1: Tables S1-S4). We used linear mixed effects models to assess effects of adult devil scavenging on vertebrate scavenger groups and generalized linear mixed effects model with a Poisson distribution to model effects on carcass persistence. We used a generalized linear mixed effects model with a binomial distribution for invertebrate scavenger presence in the winter, and a linear mixed effects model for invertebrate scavenger abundance in the summer. We used linear mixed effects models to assess soil ammonium, soil phosphate, and the microbial r:K ratio. Models were fit using the ‘lme4’ and the ‘piecewiseSEM’ R packages (Lefcheck 2015; Bates et al. 2015). We calculated the overall fit of the structural equation model using Shipley's test of d-separation, which tests the assumption that all variables are conditionally independent. The hypothesized relationships were considered consistent with the data when Fisher's C had *P* > 0.05, indicating there were no missing relationships and the structural equation model represented the data well.

**Results**

Carcasses persisted for an average of 10.1 d (min = 2, max = 25) in the summer and 13.8 d (min = 0, max = 26) in the winter. In the winter, carcasses with one or more Tasmanian devil visits that were documented on camera traps persisted an average of 10.8 d, while carcasses that were never visited by devils persisted an average of 18.6 d. In the summer, carcasses visited by adult devils persisted an average of 5.4 d, carcasses visited by juvenile devils persisted an average of 9.6 d, and carcasses never visited by devils persisted an average of 14.8 d. In the winter, we detected blow fly larvae at 11 out of 33 carcasses. In the summer, invertebrate scavengers (adult carrion beetles and/or blow fly larvae) were detected at 32 out of 34 carcasses.

In the winter, Tasmanian devil foraging activity had a significant negative effect on carcass persistence (β = -56.6, *P* = 0.003, Fig. 2A). In summer, carcass persistence was also negatively correlated to adult (β = -0.60, *P* < 0.001, Fig. 2B) and subadult devil foraging activity (β = -0.39, *P* < 0.029, Fig. 2C). However, we did not detect major indirect effects of devil foraging activity in winter, as carcass persistence was not significantly related to invertebrate scavenger presence, soil ammonium or phosphate concentrations, or bacterial r:K ratios (Fig. 3A). In contrast, effects of adult and subadult devil foraging activity in reducing carcass persistence indirectly affected invertebrate scavenger activity and soil ammonium, and the magnitude of all direct and indirect effects was smaller for subadult than adult devils (Fig. 2B). Specifically, invertebrate scavenger activity (β = 0.50, *P* = 0.008, Fig. 4A) and soil ammonium concentrations (β = 0.387, *P* = 0.012, Fig. 4B), were positively correlated with carcass persistence, such that invertebrate scavengers and soil ammonium decreased with greater density of devils or at full-access carcasses.

**Discussion**

By manipulating adult Tasmanian devil access to carcasses at sites spanning a gradient of devil density, we revealed that Tasmanian devil scavenging dramatically affects carrion persistence, carrion availability for other scavengers and decomposers, and soil properties. During summer, sites with low devil density (or plots with devil exclusion) had greater abundance of invertebrate scavengers and higher soil ammonium concentrations, illustrating the exceptional role that top scavengers can play in nutrient cycling. However, while declines in devil scavenging activity also increased carcass persistence in winter, relatively low invertebrate and microbial activity dampened any indirect effects of devils on soil in the wineter season. Taken together, our results indicate that rapid devil declines due to devil facial tumor disease may have cascading effects on carrion food webs that vary across seasons. During periods when invertebrates and microbes are able to access carcasses, devil declines can dramatically alter soil properties such as ammonium concentrations, revealing that trophic cascades in carrion food webs may be temporally pulsed.

Soil properties and seasonality of tropic cascades – explain importance of ammonium inputs, explain seasonal differences and plug forthcoming Torrey papers to explain why r:K and pH changes weren’t detected here (e.g., we didn’t detect a significant effect on pH or r:K for this reason but further research may do this).

Our study adds to evidence that apex scavengers like the Tasmanian devil can determine availability of carrion resources and the relative participation of other consumer guilds in carrion decomposition (Olson *et al.* 2012; Allen *et al.* 2015; Cunningham *et al.* 2018). Yet, scavenging by mammalian or avian mesoscavengers did not have the same effect on carcass persistence or invertebrate scavengers, supporting prior studies in our system and others that mesoscavengers do not functionally replace dominant scavengers (Cunningham *et al*. 2018; Tobajas *et al.* 2021). Additional studies that manipulated carcass access to all mammalian or vertebrate scavengers also did not detect changes in carcass persistence due to compensation by avian or invertebrate scavengers (Sugiura *et al.* 2013; Sugiura and Hayashi 2018; Turner *et al.* 2020), which may be because dominant scavengers were absent from these systems. Our results provide insights into the distinctive role of dominant scavengers by revealing how they indirectly affect invertebrate scavengers and carrion-derived nutrient flows in ways that greatly exceed effects of mammalian and avian mesoscavengers. Some dominant scavengers may even have broader impacts on ecosystem processes that extend beyond carcass locations through the effects of their scat on soil chemical properties and microbial communities at latrine sites (Stephenson *et al.* 2024).

While devil scavenging affected carcass persistence, carrion food webs, and soil in ways that exceeded effects of other scavengers, our study also facilitated comparisons of adult and juvenile devils. We found the magnitude of a scavenger’s effects on decomposition can be age dependent, as all direct and indirect effects we detected were greater for adult than for subadult devils, even though juvenile devils were more efficient scavengers than other vertebrates. Given that devil facial tumor disease largely affects adult devils over 2 years old, the disease’s spread had led to changes in devil demography and life history (Jones *et al.* 2008; Lachish *et al.* 2009). Infected populations can be comprised almost entirely of individuals less than 3 years old, with substantial increases in precocial breeding by 1-year-old females (Jones *et al.* 2008; Lachish *et al.* 2009). For these reasons, understanding how devil declines affect not only population size but also age structure could aid in predicting effects on communities and ecosystems.

Our study provides further evidence that infectious diseases can exert top-down control of wildlife populations and mediate trophic cascades that affect nutrient flows (Holdo *et al.* 2009; Hollings *et al.* 2014; Buck *et al.* 2017; Monk *et al.* 2022). For example, in a protected area of Argentinia, puma kills provided carrion resources to scavenging Andean condors, but a mange (*Sarcoptes scabiei*) outbreak in vicuña prey populations caused drastic declines in condors due to long-term declines in vicuña carcasses(Monk *et al.* 2022). In the African Serengeti, rinderpest (*Rinderpest morbillivirus*) infection in populations of dominant grazers (*Connochaetes taurinus*) affected ecosystem carbon pools through changes in grazing and wildfire incidence (Holdo *et al.* 2009). The spread of devil facial tumor disease in Tasmania has similarly caused declines in devil populations and greater carcass persistence (Cunningham *et al.* 2018; 2021), which we show can alter community properties and flow of carrion-derived nutrients to soil. The cascading effects of devil declines on ecosystems may be further compounded by the projected decline in Tasmanian forest carbon pools due to loss of devil scat inputs (Stephenson *et al.* 2024). Our results provide a link between wildlife disease, scavengers, and ecosystem nutrient dynamics by suggesting that a disease-induced decline of Tasmanian devils increases invertebrate scavenging activity and belowground input of ammonium at carcass locations. More broadly, these findings provide an case study supporting the assertion that global declines in dominant scavengers could fundamentally alter scavenging communities, decomposition processes, and nutrient dynamics in ecosystems (Buchley and Sekercioglu 2016; Newsome *et al.* 2021; Bartel *et al.* 2023).

**References**

Allen ML, Elbroch LM, Wilmers CC, and Wittmer HU. 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. *Am Nat* **185**: 822–833.

Bartel SL, Stephenson T, Crowder DW, *et al.* 2023. Global change influences scavenging and carrion decomposition. *Trends Ecol Evol* **39**: 152-164.

Bates D, Mächler M, Bolker B, and Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Software* **67**: 1–48.

Beasley JC, Olson ZH, and DeVault TL. 2015. Ecological role of vertebrate scavengers. In: Benbow ME, Tomberlin JK, and Tarone AM (Eds). *Carrion Ecology, Evolution, and Their Applications*. Boca Raton, FL: CRC Press.

Benbow ME, Barton PS, Ulyshen MD, *et al.* 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecol Monogr* **89**: e01331.

Buechley ER and Şekercioğlu ÇH. 2016. The avian scavenger crisis: looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biol Conserv* **198**: 220–228.

Buck JC and Ripple WJ. 2017. Infectious agents trigger trophic cascades. *Trends Ecol Evol* **32**: 681–694.

Cunningham CX, Johnson CN, Barmuta LA, *et al.* 2018. Top carnivore decline has cascading effects on scavengers and carrion persistence. *Proc R Soc B Biol Sci* 2**85**: 20181582.

Cunningham CX, Comte S, McCallum H, *et al.* 2021. Quantifying 25 years of disease-caused declines in Tasmanian devil populations: host density drives spatial pathogen spread. *Ecol Lett* **24**: 958–969.

Fielding MW, Cunningham CX, Buettel JC, *et al.* 2022. Dominant carnivore loss benefits native avian and invasive mammalian scavengers. *Proc R Soc B Biol Sci* **289**: 20220521.

Hawkins CE, Baars C, Hesterman H, *et al.* 2006. Emerging disease and population decline of an island endemic, the Tasmanian devil *Sarcophilus harrisii*. *Biol Conserv* **131**: 307–324.

Holdo RM, Sinclair ARE, Dobson AP, *et al.* 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biol* **7**: e1000210.

Hollings T, Jones M, Mooney N, and McCallum H. 2014. Trophic cascades following the disease-induced decline of an apex predator, the Tasmanian devil. *Conserv Biol* **28**: 63–75.

Jones ME, Cockburn A, Hamede R, *et al.* 2008. Life-history change in disease-ravaged Tasmanian devil populations. *Proc Natl Acad Sci* **105**: 10023–10027.

Lachish S, McCallum H, and Jones M. 2009. Demography, disease and the devil: life-history changes in a disease-affected population of Tasmanian devils (*Sarcophilus harrisii*). *J Anim Ecol* **78**: 427–436.

Lajtha K, Driscoll CT, Jarrell WM, and Elliott ET. 1999. Soil phosphorus: characterization and total element analysis. In: Coleman DC, Bledsoe CS, and Sollins P (Eds). *Standard Soil Methods for Long-Term Ecological Research*. Oxford, UK: Oxford University Press.

Lazenby BT, Tobler MW, Brown WE, *et al.* 2018. Density trends and demographic signals uncover the long-term impact of transmissible cancer in Tasmanian devils. *J Appl Ecol* **55**: 1368–1379.

Lefcheck JS. 2015. PiecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol Evol* **7**: 573-579.

Macdonald BCT, Farrell M, Tuomi S, *et al.* 2014. Carrion decomposition causes large and lasting effects on soil amino acid and peptide flux. *Soil Biol Biochem* **69**: 132–140.

McMurdie PJ, and Holmes S. 2013. phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS ONE* **8**: e61217.

Monk JD, Smith JA, Donadio E, *et al.* 2022. Cascading effects of a disease outbreak in a remote protected area. *Ecol Lett* **25**: 1152–1163.

Muñoz-Lozano C, Martin-Vega D, Martinez-Carrasco C, *et al.* 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. *PLoS ONE* **14**: e0221890.

Naves-Alegre L, Morales-Reyes Z, Sánchez-Zapata JA, and Sabastian-Gonzalez E*.* 2022. Scavenger assemblages are structured by complex competition and facilitation processes among vultures. *J Zool* **318**: 260–271.

Newsome TM, Barton B, Buck JA, *et al.* 2021. Monitoring the dead as an ecosystem indicator. *Ecol Evol* **11**: 5844–5856.

Niedballa J, Sollmann R, Courtiol A, and Wilting A. 2016. CamtrapR: an R package for efficient camera trap data management. *Methods Ecol Evol* **7**: 1457-1462.

Olson ZH, Beasley JC, DeVault TL, and Rhodes OE. 2012. Scavenger community response to the removal of a dominant scavenger. *Oikos* **121**: 77–84.

Parmenter RR and MacMahon JA. 2009. Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. *Ecol Monogr* **79**: 637–661.

Quaggiotto M-M, Evans MJ, Higgins A, *et al.* 2019. Dynamic soil nutrient and moisture changes under decomposing vertebrate carcasses. *Biogeochem* **146**: 71–82.

Quast C, Pruesse E, Yilmaz P, *et al.* 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res* **41**: D590–D596.

Ripple WJ, Estes JA, Beschta RL, *et al.* 2014. Status and ecological effects of the world’s largest carnivores. *Science* **343**: 1241484.

Sawyer SJ, Eubanks MD, Beasley JC, *et al.* 2022. Vertebrate and invertebrate competition for carrion in human-impacted environments depends on abiotic factors. *Ecosphere* **13**: e4151.

Strickland MS, Callaham Jr MA, Gardiner ES, *et al.* 2017. Response of soil microbial community composition and function to a bottomland forest restoration intensity gradient. *Appl Soil Ecol* **119**: 317–326.

Sugiura S and Hayashi M. 2018. Functional compensation by insular scavengers: the relative contributions of vertebrates and invertebrates vary among islands. *Ecography* **41**: 1173–1183.

Sugiura S, Tanaka R, Taki H, and Kanzaki N. 2013. Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. *Biol Conserv* **159**: 206–213.

Stephenson T, Hudiburg T, Mathias JM, *et al.* 2024. Do Tasmanian devil declines impact ecosystem function? *Global Change Biol* **30**: e17413.

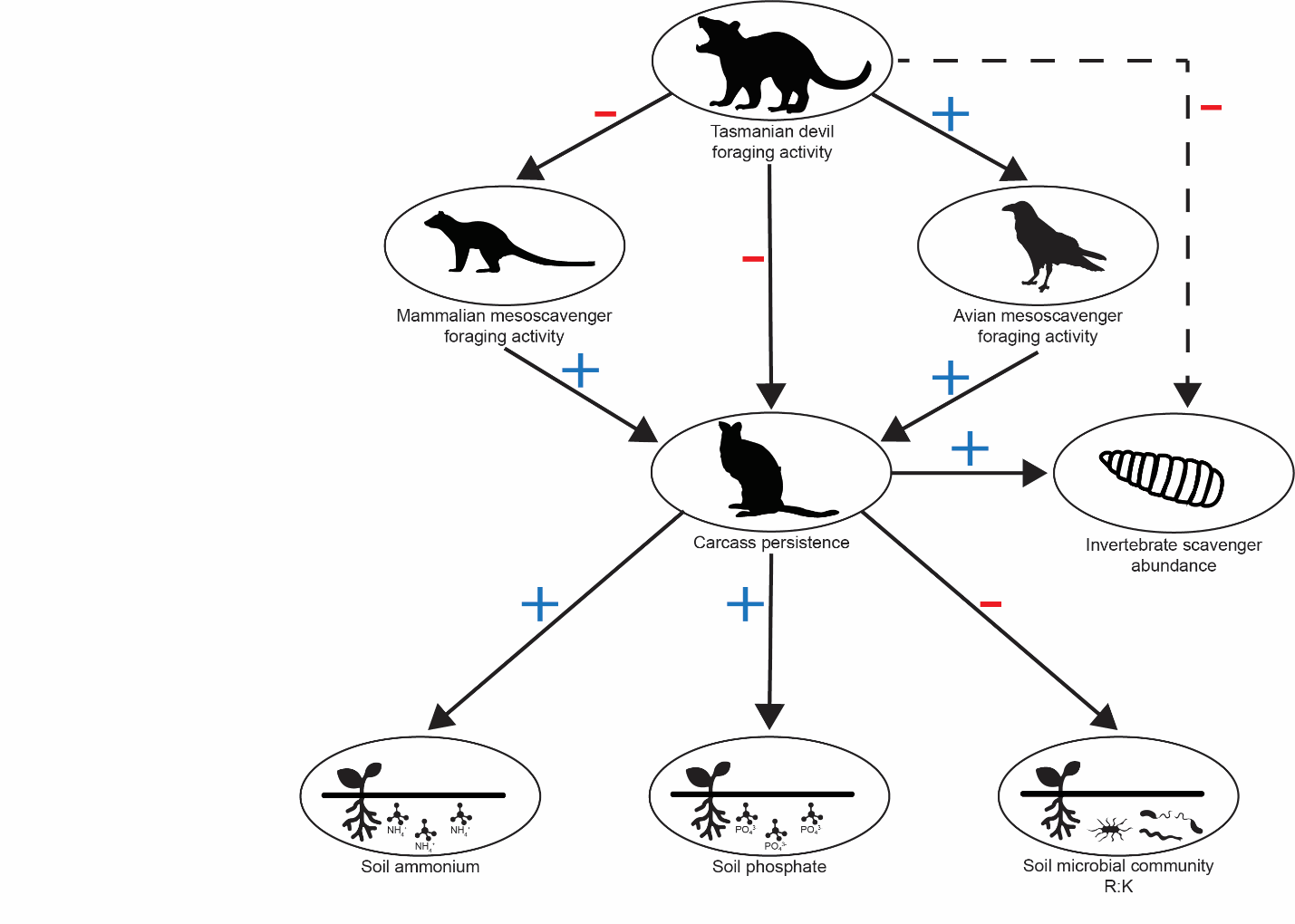
Turner KL, Conner LM, and Beasley JC. 2020. Effect of mammalian mesopredator exclusion on vertebrate scavenging communities. *Sci Rep* **10**: 2644.

Voss SC, Spafford H, and Dadour IR. 2009. Annual and seasonal patterns of insect succession on decomposing remains at two locations in Western Australia. *Forensic Sci Int* **193**: 26–36.

Weatherburn MW. 1967. Phenol-hypochlorite reaction for determination of ammonia. *Annals Chem* **39**: 971–974.

Wilson EE and Wolkovich EM. 2011. Scavenging: how carnivores and carrion structure communities. *Trends Ecol Evol* **26**: 129–135.

**Figure 1**



**Figure 2**

**Diagram

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**Figure 3**

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**Figure 4**

**Graphical user interface, chart

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