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REPORT

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Decline of an apex vertebrate scavenger increases carrion use by invertebrates

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Abstract

Apex consumers are declining worldwide. While the effects of apex predator declines on ecosystems are widely documented, the cascading effects of apex scavenger declines are poorly understood. We evaluated whether disease-induced declines of an apex scavenger, the Tasmanian devil (*Sarcophilus harrisii*), increased carrion use by invertebrate scavengers. We manipulated devil access to 36 carcasses across a gradient of devil density from east to west Tasmania and measured carcass use by invertebrates. We found the amount of carcass removed within 5 days was 3.58 times lower at sites with the lowest devil densities. Adult carrion beetle (*Ptomaphila lacrymosa*) and blow fly (Calliphoridae) larvae abundances were two times higher at open-access carcasses at low-density sites than at intermediate- and high-density sites. Adult beetles persisted for 10 days at the low-density site but declined after 5 days when devils had access to carcasses in intermediate- and high-density sites. Blow fly larvae abundance was not affected by devils in the low-density site but decreased with devil access in intermediate- and high-density sites. Our results suggest that apex scavenger declines may increase invertebrate scavenger abundance and their contribution to carrion decomposition, with potential cascading effects on nutrient cycling and ecosystems.

KEYWORDS

blow fly, carcass, carrion beetles, carrion food webs, indirect effects, scavenging, Tasmanian devil, trophic cascade

INTRODUCTION

Apex consumers, which occupy the highest trophic level in an ecosystem, are declining at unprecedented rates worldwide (Estes et al., 2011; Ripple et al., 2014). Declines of apex predators alter the abundance and behavior of mesopredators and herbivores, eliciting strong indirect effects on primary producers (Estes et al., 2011, Ripple et al., 2014). Many apex scavengers, which are species able to locate and consume carcasses more efficiently than other scavengers, are also at risk of extinction; however, it is less clear if scavenger declines transform ecosystems in similar ways to declines of apex predators (Buechley & Şekercioğlu, 2016; Newsome et al., 2021; Wilson & Wolkovich, 2011). This highlights our limited understanding of how interactions between apex scavengers and other carrion consumers, including vertebrate scavengers as well as invertebrate and microbial decomposers, affect carcass decomposition (Bartel et al., 2024).

Carcasses are hotspots for interkingdom interactions because carrion is used by microbial, invertebrate, and vertebrate consumers, and scavenger declines could affect entire communities. Apex scavengers can limit carcass consumption by subordinate scavengers (Atwood & Gese, 2008; Fielding et al., 2022; O'Bryan et al., 2019) while competing with invertebrates for carrion (Sugiura & Hayashi, 2018). For instance, adult blow flies often discover and deposit eggs on carcasses within minutes (Benbow et al., 2016; Dawson et al., 2022; Pechal et al., 2014), but their offspring can be killed if apex scavengers consume the carcass before eggs hatch or during larval feeding; vertebrate scavengers could similarly impact carrion beetles that often discover carrion within days (Farwig et al., 2014). Declines in apex scavengers can reduce competition for carrion, benefitting subordinate scavengers and invertebrates (Bartel et al., 2024). However, few studies directly assess potential cascading effects of apex scavenger declines on invertebrate scavengers and whether such interactions affect carcass decomposition rates or other ecosystem properties.

Here, we assessed whether declines of an apex scavenger, Tasmanian devil (*Sarcophilus harrisii*), increased carcass persistence and use by invertebrates. Tasmanian devils have suffered severe population declines from a transmissible cancer, devil facial tumor disease, which was detected in Northeast Tasmania 26 years ago and has spread (Cunningham et al., 2021). Devils are apex scavengers that rapidly consume carcasses of species like pademelon (*Thylogale billardierii*), and devil declines strongly affect vertebrate abundance and behavior (Cunningham et al., 2018; Fielding et al., 2022; Hollings et al., 2014, 2015). Across Tasmania, devil facial tumor disease has caused a gradient of devil declines, providing a model system to test effects of apex scavengers on carrion food webs. With fewer devils, the greater the likelihood carcasses will be consumed by mesoscavengers such as forest ravens (*Corvus tasmanicus*), spotted-tailed quolls (*Dasyurus maculatus*), eastern quolls (*Dasyurus viverrinus*), and currawongs (*Strepera fuliginosa*) (Cunningham et al., 2018). Here, we test whether such effects extend to invertebrate scavengers.

We hypothesized that sites with lower devil density will have increased carcass persistence and use by invertebrates. We tested this by manipulating devil access to 36 carcasses across the natural gradient of devil density. We measured carcass consumption rates and the abundance of adult carrion beetles (*Ptomaphila lacrymosa*), beetle larvae, and blowfly (Calliphoridae) larvae at carcasses over 30 days. We predicted carcass consumption rates would be slower at sites with lower devil densities or where devils were excluded, and invertebrate scavengers would be more abundant at sites with low devil densities or in devil exclusion treatments. Our goal was to assess how declines of an apex scavenger can mediate carcass persistence and availability to other scavengers. More broadly, we provide evidence that shows how variation in carcass availability due to apex scavenger declines can cause indirect effects on entire communities.

METHODS

Our experiment spanned three sites across a devil density gradient (Appendix S1: Figure S1). The sites have been monitored for devils since 1985 using standardized surveys that show they have been diseased for 26, 15, or 3 years and that devil densities have declined by ≈80, 60, or 5% from their original carrying capacity, respectively (Cunningham et al., 2021). We refer to the sites as "low," "intermediate," and "high" devil densities. At each site, we set up six blocks separated by >1 km for spatial independence (Cunningham et al., 2018). Each block had two plots, one with a carcass allowing adult devil access (open treatment) and one with a carcass in an exclosure to exclude adult devils (excluded treatment). Open plots had an adult pademelon carcass (1.5–8 kg) staked to the ground with a 45-cm star picket through the chest. Exclosure plots had one adult pademelon carcass staked and enclosed by a weld-mesh box with 10 × 10 cm openings to allow access to invertebrate and mammalian scavengers except adult devils; subadult devils (<18 months) were small enough to enter. Exclosures were 1.1 × 1.7 × 1.0 m, including weld-mesh bottoms to prevent entry by digging (Appendix S1: Figure S2). Plots in a block were spaced 200 m apart to minimize environmental differences, but far enough to limit impacts of devil activity at open plots on nearby exclusion plots. Carcasses were deployed in February 2023, the warmest time of the year in Tasmania when invertebrate activity is highest (Bonham et al., 2002; Woinarski & Cullen, 1984). Our 36 carcasses maximized sample size despite the logistical constraints of needing to deploy carcasses and sample all sites across the island within 3 days.

To assess carcass removal, at 5, 10, and 30 days after deployment, we visually estimated the percentage of internal organs, muscle, bones, tail, and hide removed, and calculated a weighted sum based on the relative biomass of each body part (30% organs, 35% muscle, 25% bones, 5% tail/hide). For example, if 10% of organs and 10% of tail/hide were consumed, it would be 3.5% consumption: (0.3 × 0.10) + (0.05 × 0.10). To monitor vertebrates, we used motion-sensing cameras (Swift Enduro, Outdoor Cameras Australia, QLD, Australia) positioned 0.5–1 m away from each carcass. We reviewed all photos to observe foraging patterns and assess our treatments. Visitations were considered unique if over 30 min separated the next detection (Cunningham et al., 2018). We found that devil activity at open-access carcasses was consistent with expectations, and the mean numbers of unique adult devil visitations at the low-, intermediate-, and high-devil density sites were 2.0, 3.6, and 6.5, respectively. Adult devils never entered an exclosure, although subadult devils, spotted-tailed quolls, eastern quolls, forest ravens, and currawongs were observed across all sites and treatments (Appendix S1: Table S1). Importantly, we found no significant differences in the total number of visitations by other vertebrate scavengers across the devil density and devil access treatments (Appendix S1: Table S2).

To sample invertebrates, we placed two pitfall traps (120-mL jars with propylene glycol and buried flush with soil) at each carcass. Traps were set 20 cm from the top (mouth) and bottom (cloaca) openings of the carcass, openings used by invertebrates to access carcasses (Spencer et al., 2020). Traps were collected and refilled 5, 10, and 30 days after deployment, leading to measurements of invertebrate abundance for 0–5, 5–10, and 10–30 days. Traps were processed in the lab within a week of collection to identify and count invertebrates. The counts of the total number of individuals captured during a time period served as an estimate of abundance for each invertebrate group (i.e., adult carrion beetles, larval carrion beetles, and larval blowflies).

Data analysis

We first used a generalized linear mixed-effects model to test how devil density and access affected carcass removal. We used linear mixed-effects models to test how devil density and access affected (i) adult and (ii) larval carrion beetle abundance, as well as (iii) larval blowfly abundance. Carcass removal was the proportion of the carcass removed after 5 days and was treated as a binary response. Models of invertebrate abundance used log-transformed trap counts from a specific time period as the response; models with Poisson or negative binomial distributions of the count data failed to converge, and thus the log transformation was used (Ives, 2015). All models included fixed effects of devil density (high, intermediate, or low), devil access (open or excluded), and their interaction, and the random effects of block nested within site. However, as the types and availability of data differed across responses, model structures were different for each (Appendix S1: Table S3). Specifically, we analyzed data from only a single period for models of carcass removal (0–5 days), larval beetle abundance (10–30 days), and larval blowfly abundance (5–10 days). For carcass removal, the first five days reflect the early stages of decomposition and overall scavenger activity, but limit potential for a carcass to be fully consumed. For the abundance variables, data from a single time period were used due to low data availability. We only assessed the effects of devil access and density on an invertebrate group's abundance during the time period(s) in which they were active and captured. Since carrion beetle larvae and blowfly larvae were only captured during one time period (10–30 days and 5–10 days, respectively), we only analyzed abundance data of those groups from those respective time periods. The model of adult carrion beetle abundance included the two time periods in which they were active and captured (0–5 days and 5–10 days), using sampling period as a fixed effect. As some traps were destroyed, we included trap count as a random effect for all models assessing invertebrate abundance. Full model specifications (i.e., fixed and random effects and time periods) are provided in Appendix S1: Table S3.

We next used linear mixed-effect models to test whether carcass removal affected beetle and blowfly abundance; we also used linear mixed-effect models to assess whether adult carrion beetle abundance at Day 5 affected larval carrion beetle abundance at Day 30 (Appendix S1: Table S4). We used the lme4 package (Bates et al., 2015) in R v. 4.4.0 to construct models, with the "performance" (Lüdecke et al., 2021) and "lmerTest" (Kuznetsova et al., 2017) packages to check model quality. Although we focused the results section on describing significant effects, outputs of all statistical analyses are shown in Appendix S1: Tables S5 and S6.

RESULTS

After 5 days, the amount of carcass removed was significantly and negatively related to devil density, with the amount removed 3.58 times lower at the low devil density site than at the intermediate- and high-density sites ($\beta = 1.78$, SE $= 0.43$, $\chi^2 = 21.3$, df $= 2$, $p < 0.001$) (Figure 1). Similarly, across the density gradient, significantly more carcass was removed in open treatments (31.8%) than in exclusion treatments (13.2%) (Figure 1) ($\beta = 1.33$, SE $= 0.19$, $\chi^2 = 50.4$, df $= 1$, $p < 0.001$). There was a significant interaction between devil density and devil access on carcass removal ($\beta = -0.16$, SE $= 0.23$, $\chi^2 = 6.12$, df $= 2$, $p = 0.047$). Specifically, the proportion of the carcass removed in open treatments was significantly lower at

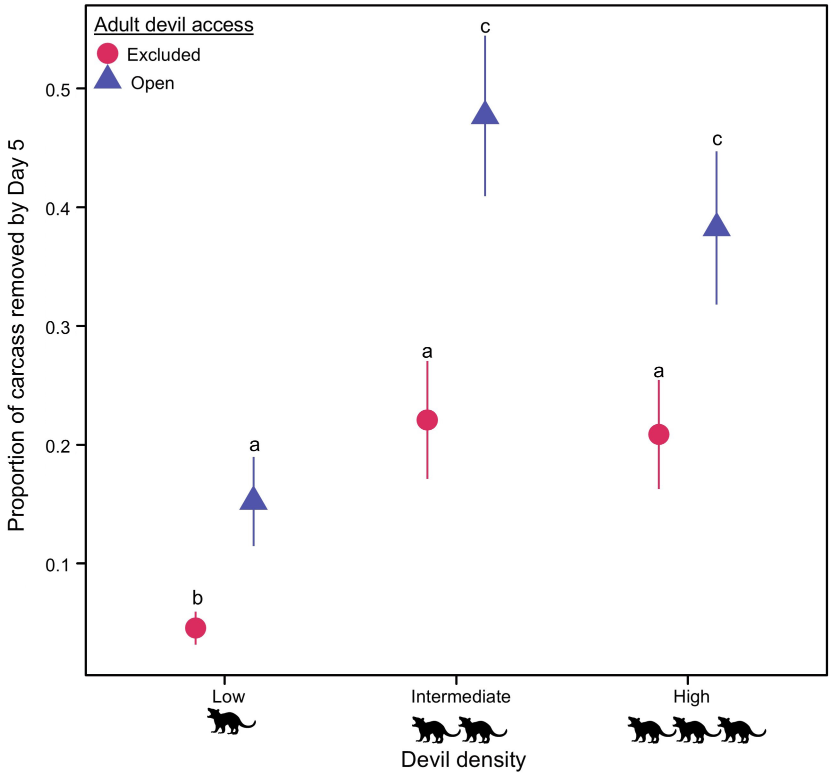

FIGURE 1 Effects of adult devil access and devil density on the proportion of pademelon carcass removed after 5 days. Symbols show the estimated marginal means for excluded (red) or open (blue) carcasses at three sites with varying devil densities, and error bars show the SE for each treatment ($n = 6$ for each). Letters denote significant differences between groups ($\alpha = 0.05$). Illustrative materials were created by Savannah Bartel.

the low-density site than at either the intermediate- or high-density site (15.2% vs. 38.2% vs. 47.7%).

Adult beetle abundance was affected by the interaction between devil density and sampling period ($\beta = -0.79$, SE $= 0.78$, $F_{2,29} = 22.0$, $p < 0.001$) and the interaction of devil density, devil access, and sampling period ($\beta = -2.63$, SE $= 1.05$, $F_{2,28} = 3.31$, $p = 0.051$). Adult carrion beetle abundance increased from Days 5 to 10 in the low-density site, was constant in the intermediate-density site, and declined in the high-density site (Figure 2A). Abundance of adult carrion beetles was also lower in open carcasses than in excluded carcasses at the intermediate-density site, but did not vary between treatments at other sites (Figure 2A). There was a significant negative relationship between carcass removal on Day 5 and abundance of adult carrion beetles between Days 5 and 10 ($\beta = -0.03$, SE $= 0.01$, $F_{1,22} = 32.6$, $p < 0.001$, $R^2_{\text{Conditional}} = 0.62$, $R^2_{\text{Marginal}} = 0.49$, Figure 2B).

Carrion beetle larvae were affected by the interaction of devil density and devil access ($\beta = -2.34$, SE $= 0.79$, $F_{14} = 4.70$, $p = 0.027$, Appendix S1: Table S5). Devil exclusion led to lower larval abundances in the low-density site, but no change in abundance at intermediate- and high-density sites (Figure 3A). The abundance of carrion beetle larvae was positively associated with adult carrion beetle abundance ($\beta = 0.60$, SE $= 0.12$, $F_{1,27} = 21.61$, $p < 0.001$, $R^2_{\text{Conditional}} = 0.56$, $R^2_{\text{Marginal}} = 0.38$, Appendix S1: Table S6) but not by the proportion of carcass removed ($\beta = 0.01$, SE $= 0.01$, $F_{1,31} = 0.63$, $p = 0.43$). Blow fly larvae abundance was affected by devil access ($\beta = -0.50$, SE $= 0.93$, $F_{2,68} = 15.88$, $p = 0.001$, Appendix S1: Table S5). Blow fly larvae abundance did not vary with devil access in the low-density site, but in the intermediate- and high-density sites, larval abundance was lower at open-access carcasses than devil-excluded carcasses between Days 5 and 10 (Figure 3B).

DISCUSSION

Our study shows that declines of an apex scavenger reduced carcass consumption and increased carcass use by invertebrate scavengers, modifying the form and function of carrion food webs. We provide empirical evidence that disease-induced devil declines substantially reduce carrion consumption, supporting our hypothesis that

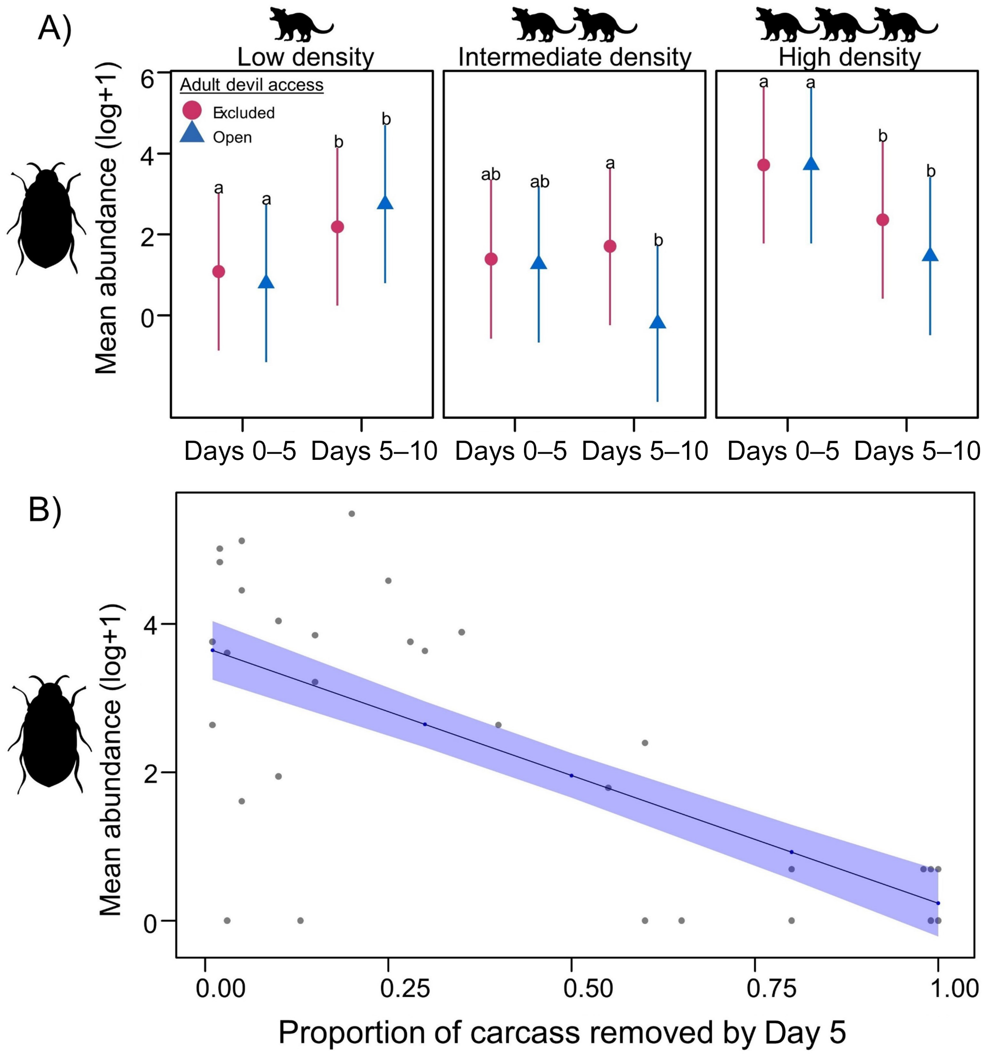

FIGURE 2 (A) Effects of adult devil access and devil density on adult carrion beetle abundance (log transformed) from Days 0 to 5 and 5 to 10. Symbols show estimated marginal means for excluded (red) or open (blue) carcasses at three sites with varying devil densities, and error bars show the SE for each treatment ($n = 6$). Letters denote significant differences between groups ($\alpha = 0.05$). (B) The association between the proportion of carcass removed at 5 days and abundance of adult carrion beetles from 5 to 10 days. Line and shading represent model fit and SE, respectively. Illustrative materials were created by Savannah Bartel.

devil declines may have indirect positive effects on invertebrate scavengers by reducing carcass removal and thereby increasing carrion availability. These results have broad implications for our understanding of carrion food webs. First, apex scavengers limit the availability of carrion for animals at lower trophic levels through competition and may limit access by invertebrate scavengers. Second, declines of apex scavengers may have cascading positive effects on carcass use by invertebrates. Third, alterations of carrion availability and carrion food webs driven by declines of apex scavengers could have major implications for nutrient cycling, soil properties, and other ecosystem dynamics (Bartel et al., 2024; Stephenson et al., 2024).

Adult carrion beetles accessed carcasses within 5 days, but their abundance declined after 5 days in sites with the highest devil densities. This shows that rapid carcass consumption by devils reduced carrion beetle carcass use. The abundance of beetle larvae was affected by adult abundance regardless of carcass persistence, suggesting that in cases where devils rapidly consume carcasses, larvae emerge with limited carcass resources. In the intermediate devil density site, adult beetles persisted between Days 5 and 10 when adult devils were excluded, suggesting that beetles persisted longer when devils were at low densities. In contrast, beetles declined between Days 5 and 10 in the high-density site with or without devils, suggesting that scavenging by subadult devils and mesoscavengers may limit invertebrates. Whereas apex scavenger declines can promote carrion use by mesoscavengers, our results provide

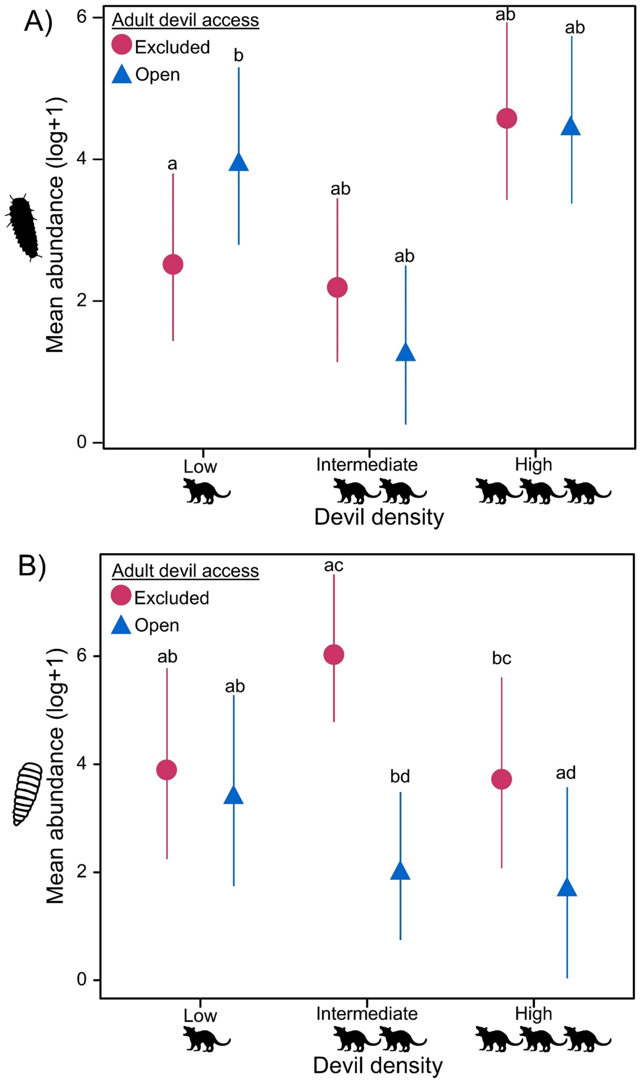

FIGURE 3 Effects of adult devil access and devil density on (A) carrion beetle larval abundance from Days 10 to 30 and (B) blowfly larval abundance from Days 5 to 10. Symbols show the estimated marginal means for excluded (red) or open (blue) carcasses at three sites with varying devil densities, and error bars show the SE for each treatment ($n = 6$). Letters denote significant differences between groups ($\alpha = 0.05$). Illustrative materials were created by Savannah Bartel.

evidence that mesoscavengers are less efficient at consuming carrion than apex scavengers (Cunningham et al., 2018; Tobajas et al., 2021). Yet, more work is needed to assess interactions among mesoscavengers and invertebrates.

For blowfly larvae, adult devil access did not affect larval abundances in the low devil density site but did reduce their abundances at intermediate- and high-density sites. While we were not able to track larval survival and pupation rates, these results show how apex scavengers that consume carrion within early stages of decomposition may impede the completion of carcass-dependent life cycles that limit invertebrate scavenger populations. Our results reflect past studies that found a negative effect of vertebrate scavengers on carcass use by invertebrates (Muñoz-Lozano et al., 2019; Sawyer et al., 2022; Schlacher et al., 2013) and provide new insight as to how the removal of an apex scavenger may alter competitive interactions among these two scavenging guilds. Moreover, by assessing two invertebrate scavenger species with different traits (e.g., depositing eggs in soil vs. carrion) and duration of maturation, we show how declines of an apex scavenger may have effects that depend on invertebrate scavenger life history.

The identity of carrion consumers shapes the rate and spatial spread of nutrient delivery (Bartel et al., 2024; Lashley et al., 2018; Turner et al., 2017). Our results suggest that adult devils play a unique functional role in Tasmanian ecosystems by consuming carrion more rapidly than other scavengers (Cunningham et al., 2018). These results differ from other systems where invertebrate scavengers outcompete vertebrates in the summer (Ray et al., 2014) or functionally compensate for the loss of vertebrate scavengers (Sugiura & Hayashi, 2018). The lack of a highly efficient apex scavenger like the Tasmanian devil in those systems may explain this difference, as vertebrate scavenging species are not always functionally redundant. For example, scavenging by other vertebrates does not compensate for the loss of devil scavenging (Cunningham et al., 2018). As we detected considerable variation in carcass use by invertebrates across the gradient of devil density, we provide a rare case study showing impacts of apex scavengers on carrion food webs. However, our results should be viewed with caution as differences among sites in devil density may covary with unmeasured variables that could affect carrion food webs.

Although we did not focus on ecosystem dynamics, shifts in carcass consumption over time may alter nutrient cycling. When carrion is decomposed by microbes or invertebrates, nutrients are delivered below the carcass, creating biogeochemical hotspots (Bartel et al., 2024; Keenan et al., 2018). Blowfly larvae also excrete ammonia as a waste product, delivering nitrogen to the soil (Quaggiotto et al., 2019). Dispersal of invertebrates from carcasses can also transport nutrients, but this movement is often limited or concentrated on wind and storm pathways (Lashley et al., 2018; Reynolds et al., 2018). In contrast, vertebrates diffusely deliver nutrients via feces and urine, often several kilometers away from carcasses (Benbow et al., 2019; Devault et al., 2003). Vertebrate-dominated carrion consumption could dampen biogeochemical hotspots, supporting ecosystem function by broadly dispersing nutrients (Bartel et al., 2024; Stephenson et al., 2024). Yet, not all vertebrate scavengers are equal, and "higher quality" feces from species like devils that consume and partially digest bone may affect nutrient cycling more than mesoscavengers (Stephenson et al., 2024). More research manipulating scavenger communities, and measuring nutrients near carcasses, will elucidate how scavengers alter nutrient delivery and soil properties. This study provides evidence that major declines of an apex scavenger could reduce carrion-derived nutrient delivery rates and increase nutrient cycling through invertebrate pathways.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Bartel et al., 2025) are available in the Environmental Data Initiative repository at https://doi.org/10.6073/pasta/656e593cf084f404d037d267d3df717f.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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